Most native aquatic vegetation enhances aquatic ecosystems. Some of the benefits that are derived include fish and waterfowl habitat, sediment stabilization, and improved water quality, especially with regard to nutrient removal and water clarity (Smart and Doyle 1995). However, many introduced species can have negative impacts. Aquatic ecosystems are often destroyed as a result of the increased biomass, dense canopy production, and the loss of diversity due to aggressive, weedy growth patterns that overwhelm native vegetation or fill unoccupied niches. One such non-native aquatic plant that causes excessive negative impacts is hydrilla (Hydrilla verticillata (L.f.) Royle).

Hydrilla is native to Southeast Asia and Australia. It was first discovered in the United States in the 1960s (Pieterse 1981). Two distinct biotypes (monoecious and dioecious) exist in the United States (Spencer and Anderson 1986). Dioecious hydrilla was first found in Florida and spread throughout the southeastern United States. Monoecious hydrilla was discovered in 1982 in the Potomac River, just outside Alexandria, Virginia (Steward and others 1984). It has since been found in other parts of Virginia, in addition to North Carolina, Delaware, Maryland, California, and Washington (Spencer and Anderson 1986).

Once hydrilla invades an aquatic ecosystem, the plant spreads rapidly, either by root crown and stolon growth or by drifting fragments or turions. Hydrilla also produces an underground tuber, another reproductive strategy for survival. Monoecious hydrilla (which has both male and female floral structures on the same plant) produces a viable seed, whereas dioecious hydrilla, in the United States, produces only female flowers. Hydrilla can rapidly produce a dense canopy, shading out desirable native vegetation and reducing plant diversity in the system.
cal parameters that affect management strategies.

One mechanism for optimizing the timing of management tactics is to examine the storage of carbohydrate reserves by plants, and to apply control tactics when reserves are at their lowest levels in storage organs. Low carbohydrate reserves can then be correlated to readily observable phenological phenomena (such as the onset of flowering), to provide managers with cues for control.

Previous research has successfully demonstrated this approach for cattail (Linde, Janisch, and Smith 1976). In these studies, a late-June weak point, identified by low carbohydrate reserves in the rhizome, was shown to coincide with the appearance of the staminate (pollen-producing) inflorescence. A similar approach has been used successfully to control terrestrial weeds such as quackgrass (Schirman and Buchholtz 1966).

Scientists at the Waterways Experiment Station (WES) are investigating these phenological cues for the three major nuisance aquatic plants encountered by the Corps of Engineers: hydrilla, waterhyacinth (*Eichhornia crassipes*), and Eurasian watermilfoil (*Myriophyllum spicatum* L.).

Small-scale studies of waterhyacinth phenology and carbohydrate storage patterns, conducted at WES, concluded that potential weak points occurred in early

Carbohydrate allocation in hydrilla

Many aquatic plants have well-defined storage organs for carbohydrate reserves, such as tubers in sago pondweed (*Potamogeton pectinatus*) and American pondweed (*P. nodosus*), turions in curly-leaf pondweed (*P. crispus*), rhizomes in cattail (*Typha* spp.) and yellow pond-lily (*Nuphar advena*), and stembases of waterhyacinth (Linde, Janisch, and Smith 1976; Luu and Getsinger 1988, 1990). These conclusions were verified by pond-scale studies at the Lewisville Aquatic Ecosystem Research Facility (LAERF) in Lewisville, Texas, in which the same timing of potential weak points was observed.

The WES waterhyacinth studies also confirmed the importance of developmental stage of the population. That is, waterhyacinth populations should be controlled before large, mature plants can develop (Madsen, Luu, and Getsinger 1993). This finding substantiates the current practices of maintenance management.

The phenology of Eurasian watermilfoil was also studied at LAERF in a pond-scale study to determine potential weak points. This species lacks any distinct, specialized carbohydrate structures for storage. Instead, carbohydrates are stored in lower shoots and the root crown, which is a mass of underground stems that initiates new shoot growth. Two potential weak points were also observed for the Texas populations of Eurasian watermilfoil, occurring in late June and early October (Madsen 1993).
Typical hydrilla plant indicating the shoots, root crown, stolon, and tubers

Hydrilla has a number of organs that store carbohydrates, such as the root crown and stolons, tubers, and turions (Figure 1). Tubers in particular are specialized for this function. Upper photosynthetic shoots produce excess carbohydrates that are translocated as sugars to these storage organs. Here, sugars are converted to starch for long-term storage. When plant carbohydrate requirements exceed plant production capability, carbohydrates in the root crown and stolon are remobilized and exported to the tissues that need additional carbohydrates. The tubers and turions are storage reserves for times of stress, such as overwintering and drawdown.

During a hypothetical growing season, stored carbohydrates start at high levels. They are consumed by new spring growth as they are exported to upper shoots. At a certain point, plant production exceeds plant requirements, and carbohydrates are then transported to storage organs. Just before this stage, when stored carbohydrates are at their minimum, management techniques will have optimal effect. During the continuing process of carbohydrate production and allocation to storage in autumn, the contents in the storage organs increase to high levels. Carbohydrate storage remains high throughout the winter, when little is used by the dormant plant.

**Experimental approach**

Three areas of study concerning the phenology of dioecious hydrilla are being pursued at the LAERF: seasonal growth and carbohydrate allocation studies, seasonal growth production: upper shoots, and spread dynamics, and tuber and turion production and germination. Monoecious hydrilla has not been studied at the LAERF.

Seasonal growth and allocation of biomass and carbohydrates is being examined through whole-pond studies. Plant samples taken throughout the growing season are separated into lower and upper shoots, root crowns, stolons, tubers, and turions. Tissues are then analyzed for sugar, starch, and total nonstructural carbohydrates (Madsen, Luu, and Getsinger 1993). These studies will provide an indication of a weak point based on carbohydrate storage.

Seasonal control of the spread of hydrilla is being examined in a series of pond experiments. A grid system is used for mapping of all rooted plants and fragments. The grids are examined regularly, and data are used to compute seasonal expansion and decline (Madsen, Eichler, and Boylen 1988).

Students assisted with processing hydrilla samples for the phenological studies at LAERF.
The importance of tubers and turions to hydrilla's overwintering, survival during times of stress, and spread is also being examined.

**Preliminary results**

Total nonstructural carbohydrate (TNC) concentrations in the hydrilla storage organs reached maximum levels of 22 percent in root crowns, 35 percent in stolons, and 70 percent in tubers and turions (Figure 2). Minimum TNC storage of all tissues occurred at the end of July, indicating this may be a primary weak point for hydrilla.

Unlike the Eurasian watermilfoil weak points, which occurred simultaneously with autofragment production and flowering, hydrilla exhibited no concurrent visual indicator. Although hydrilla populations will vary in timing of weak points from year to year (Madsen 1993), these mid-summer low storage levels can be exploited for management purposes to prevent excessive summer growth and to destroy aboveground biomass before the production of new tubers in the fall (Figure 3).

Hydrilla biomass was allocated primarily to the upper and lower stems, a strategy that is consistent with maximizing photosynthetic and production capabilities (Figure 4). Root crown, stolon, tuber, and turion biomass allocation was consistent across the seasons, although an increase in density occurred in the early fall, from October through March of the following year (Figure 3). Increased tuber, turion, and inflorescence production to support hydrilla's reproductive strategies occurred concurrently in the fall, around October (Figure 5). Tuber germination has been shown to occur from mid- to late-summer, too late to be responsible for the rapid regrowth seen after winter senescence in warm temperate populations of dioecious hydrilla.

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**Figure 2.** Total nonstructural carbohydrate (TNC) concentration as percent of dry weight of hydrilla plant parts sampled at LAERF. The hypothesized weak point is indicated.

**Figure 3.** Biomass allocations as percent of total dry mass for hydrilla populations at LAERF. (Legend symbols are RT = root crown, LS = lower stem, US = upper stem, STO = stolon, TUB = tuber, and TUR = turion.)
Conclusions

Studies of phenological weak points caused by the depletion of carbohydrate reserves demonstrate that excellent potential exists for improving the management of *Hydrilla verticillata* through the timing of control measures. Preliminary studies in Lewisville, Texas, suggest one primary weak point in late July, prior to the occurrence of flowering and tuber/turion production. Continued studies of carbohydrate production and phenological events will refine this relationship.

Future studies

Future studies are planned to further define the relative importance of season, water temperature, population age/development with regard to the observed patterns of biomass and carbohydrate allocation in hydrilla populations. These studies may help explain the successes and failures of past hydrilla control efforts. More importantly, it is hoped that continued studies will allow managers to better predict control results in the future.

References


Surface and underwater light intensity was examined for research conducted at LAERF.

Data loggers were deployed to obtain air and water temperatures.


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August 21-23, 1996  South Carolina Aquatic Plant Management Society (SCAPMS), 18th Annual Meeting, Springmaid Beach Recreation and Conference Center, Myrtle Beach, South Carolina, POC: David DeMont, (919) 715-0389

October 8-10, 1996  Florida Aquatic Plant Management Society (FAPMS), 20th Annual Meeting, The Sheraton Harbor Place Hotel, Fort Myers, Florida, POC: Alison Fox, (352) 392-1808

October 16-18, 1996  MidSouth Aquatic Plant Management Society (MSAPMS), 15th Annual Meeting, Gulf Shores State Park, Gulf Shores, Alabama, POC: Stan Cook, (334) 242-3471

This issue reports on a study to identify the potential weak points in the phenological cycle of hydrilla. The weak points are identified based on the relationship between growth characteristics and carbohydrate allocations. These findings will enable field personnel to select the optimal time for control efforts.