

Limnophila and Hygrophila: A Review and Physiological Assessment of Their Weed Potential in Florida¹

WILLIAM SPENCER AND GEORGE BOWES²

ABSTRACT

The potential weed threat to Florida by limnophila (*Limnophila sessiliflora* [Vahl] Blume) and hygrophila (*Hygrophila polysperma* Roxb. T. Anderson) was examined in a comparative study with hydrilla (*Hydrilla verticillata* [L.f.] Royle). Seasonal measurements of standing crop from various Florida locations ranged up to 0.6 kg dry weight/m² for limnophila and hygrophila, of which a substantial proportion was in the surface water. Hygrophila did not show the seasonality in standing crop or photosynthetic temperature sensitivity seen with limnophila. Limnophila and hygrophila grew best at pH 5 to 7, whereas hydrilla had a wide pH tolerance with greatest growth at pH 9. In growth experiments, neither limnophila or hygrophila produced tubers like hydrilla, but hygrophila surpassed the hydrilla regrowth potential from stem fragments. Limnophila had limited vegetative reproduction but produced abundant seeds of which 96% germinated when submersed under aerobic conditions in the light. Like hydrilla, the submersed parts of both plants had low light compensation and saturation points for photosynthesis; exhibited variable CO₂ compensation points, and thus had an environmentally-inducible low photorespiration state. The biochemical mechanism responsible for the low photorespiration state may involve PEP carboxylase, but not to the extent found in hydrilla. Tentatively, we suggest that while neither plant poses the same weed threat as hydrilla, hygrophila has more potential to be a problem weed than limnophila.

Key words: hydrilla, reproductive strategies, photosynthesis, pH effects, competition, standing crop, carboxylases.

INTRODUCTION

Limnophila (also known as ambulia) and hygrophila are rooted, amphibious aquatic angiosperms, having both submersed and emersed plant parts. They are exotic plants to Florida, and appear to have been introduced by aquarium plant dealers (9, 25, 33, 37, 58, 68, 73). In the last five years, both of these species have shown indications of becoming weed problems in certain localities. For example, limnophila is well established in localized areas of Florida such as Dead Lakes (Calhoun County); Lake Seminole in Southern Georgia; Lake Pierce and Lake Weohyakapa (Polk County); the Loxahatchee River (Martin County); and Lake Tsala

Apopka (Citrus County). Limnophila and hygrophila are both found in dense stands in Boggy Creek near Orlando (Osceola County). Hygrophila is present in water management canals in Miramar, as well as in canals of Broward, Hillsborough, Palm Beach, and Lee Counties, and in Lakes Lindsay and Ida of Hernando and Palm Beach Counties, respectively. Hygrophila tends to be more extensive in south Florida (68), with its most northerly location currently being the Suwannee River (Levy County); whereas limnophila has spread to, and apparently thrives in north Florida and south Georgia (37). In the Department of Natural Resources 1982 Florida Aquatic Plant Survey (64), both species were encountered, but neither appeared on the list of the 37 most abundant aquatic plants in the State.

The intent of this study was to assess whether limnophila and hygrophila pose a threat of becoming major aquatic weed problems in Florida. The assessment was derived from comparative measurements of basic physiological processes, such as photosynthesis, photorespiration, and dark respiration; analyses of growth and reproductive potential under different environmental regimes; and an evaluation of the published literature. The comparative portion of this study was predicated upon the premise that a comparison of the physiological, growth, and reproductive characteristics of limnophila and hygrophila with those known for hydrilla should provide an indication as to whether the former two species are capable of duplicating the weed status of hydrilla in Florida waters.

Hydrilla is the most abundant aquatic plant in Florida (64), and the most problematic aquatic weed (20, 64). If limnophila and hygrophila appear likely to cause problems akin to those of hydrilla, then the expense of an eradication program at this stage of limited infestation could be worthwhile. Alternatively, if their spread in Florida waters appears to be self-limiting, then far less expensive, local, management techniques would be more desirable.

For the submersed aquatic macrophyte (SAM plant) hydrilla, the factors that contribute to its competitive success, and hence weed potential, are well established (8, 20, 21, 29, 67). The plant has several means of vegetative reproduction. It produces numerous tubers in the hydrosol that are resistant to present chemical treatments (20), and also winter buds or turions; both enable the plant to overwinter. The plant rapidly regrows from fragments (32) that survive adverse conditions and are easily dispersed. Natural populations of hydrilla do not reproduce sexually in Florida, as only the female flowers are found (20, 31). However, the presence of staminate (male) flowers in North Carolina (31) and other eastern states suggests that sexual reproduction via seeds could become a weed factor. Hydrilla has a canopy-type growth habit, with the biomass concentrated in

¹This study was supported in part through a research contract from the Florida Department of Natural Resources, Bureau of Aquatic Plant Research and Control. Published as Journal Series No. 5589 of the Florida Agricultural Experiment Station.

²Biological Scientist and Professor, respectively. Department of Botany, and the Center for Aquatic Weeds, 3157 McCarty Hall, University of Florida, Gainesville, Florida 32611.

the top 0.5 m of the water body, where interception of solar energy and shading of benthic species is greatest (7, 21, 67). This canopy structure of densely intertwined stems at the water surface is perhaps the major reason why hydrilla is a weed problem; benthic SAM plants are rarely aquatic weeds.

Physiologically, hydrilla has a low photosynthetic light compensation point and thus can fix CO₂ at light levels where many other SAM plants show net CO₂ loss through respiratory processes (8, 66). This benefits regrowth of tubers, in that it increases the depth from which tubers can sprout and still reach a light level that allows net CO₂ uptake (8, 67). Also it enables hydrilla to photosynthesize more rapidly during the early morning, when CO₂ levels are highest, but light intensity is still low (8, 67). Even though like other SAM plants hydrilla is a shade-adapted species (66), it seems to tolerate the potentially damaging effects of high irradiance at the air/water interface. At high irradiance the chloroplasts become concentrated in a narrow band around the margin of each leaf cell (Bowes, G. 1980, unpublished observation), which allows both excess light to be transmitted through the leaf without interception, and self-shading within the chloroplast population. This effect causes the silver-grey ("solarized") appearance of hydrilla leaves at the water surface on sunny days.

In high density vegetation conditions during the summer months, hydrilla switches its photosynthesis to a C₄-like system, utilizing phosphoenolpyruvate carboxylase (PEP-Case) as the major initial carboxylation enzyme (4, 28, 29, 54, 56). This environmentally-induced changeover enables the plant to reduce the inhibitory effect of oxygen on photosynthesis; reduce photorespiratory CO₂ loss; fix CO₂ at night, when it is more abundant; and have a relatively high temperature optimum for photosynthesis (29, 54). In short it is an effective carbon conservation measure. We have proposed that inorganic carbon is a major limiting nutrient for SAM plants in aquatic habitats (29, 54, 66), and from recent research the relevance of this concept is becoming increasingly evident (42).

In contrast to hydrilla, the literature describing limnophila and hygrophila is sparse, and is largely concerned with taxonomic relationships within the two genera (6, 10, 12, 17, 18, 23, 40, 43, 47, 48, 60, 63, 69, 70, 71, 72). The genus *Limnophila* belongs to the family Scrophulariaceae, while *Hygrophila* is in the Acanthaceae: both are dicotyledons. In addition to more classical methods of identification, attempts have been made to distinguish *Limnophila* species on the basis of protein bodies in the cell nucleus (63), and *Hygrophila* species by epidermal and cuticular characteristics of the leaves (2). The anatomical structure of *H. spinosa* has been described in recent literature (19), but not that of limnophila or hygrophila.

In terms of worldwide distribution, *Limnophila* and *Hygrophila* appear to be largely endemic to Asia, particularly Indochina and Malaysia (12, 17, 18, 23, 34, 43, 69, 71, 72). Both genera are found on the African continent (10, 51, 60), although not the particular species in question here. *Limnophila* is also present in the Philippines (45) and Japan (24, 62). Both genera are represented in Florida and the southeastern USA (33, 36, 37, 68). Of the approximately

80 species in the genus *Hygrophila*, most are in the Old World tropics, with only a few tropical American species (33). *Hygrophila lacustris* appears to be indigenous to the southeastern USA, and except for *H. polysperma*, it is the only other species of the genus found in Florida (33).

In India, *H. spinosa* seeds are used as a food source (61). *Hygrophila spinosa* and *H. polysperma* seeds also are used as a medication (5, 30); the *H. spinosa* seeds apparently have a diuretic effect (30). Oils can be derived from seeds of *H. spinosa* (22, 39) and *L. rugosa* (1, 53). Thus both genera do have some economic benefits in their indigenous countries.

Morphologically, neither limnophila nor hygrophila is extensively branched, but they can form dense mats of vegetation. Both plants can grow in over two meters of water (33, 37), and may place large amounts of biomass at the water surface. Because of their potentially emergent nature, they may outcompete benthic SAM plants, in a manner reminiscent of the hydrilla canopy structure.

The danger of both species becoming noxious weeds may be enhanced by the ability to propagate vegetatively (33, 37, 50, 68). *Hygrophila* especially forms many adventitious roots at nodes along the stem (33, 68) which aids the rooting of dispersed fragments. In contrast to hydrilla in Florida, both limnophila and hygrophila have the potential for sexual reproduction. *Limnophila* forms up to 150 seeds in each capsule (37); but the effectiveness of the seeds in propagation is unknown (37). *Hygrophila* also has been reported to produce seeds in Florida (33).

Limnophila species (including *L. sessiliflora*) are documented major weed problems in paddy rice fields of India, China, Japan, and the Philippines (24, 41, 45, 65). A hybrid between *L. indica* and *L. sessiliflora* also has been reported to be a new rice weed (48). In this context it should be noted that *L. indica* is currently being sold by the aquarium industry in Florida (37), and although it has not been reported growing as naturalized, the possibility for hybridization must not be overlooked. In Florida there are reports that both limnophila and hygrophila may outcompete hydrilla (37, 68). It is possible that chemical treatments for controlling hydrilla may leave an open niche for hygrophila invasion, and thus select for hygrophila. If this is the case, it is a matter for some concern.

With regard to control, the grass carp is reported to feed to a moderate extent on hygrophila (11), but there is doubt as to whether herbivorous fish will eat limnophila, because of a toxin supposedly present in the stem tissue (37). Chemical treatments using invert applications of endothal (7-oxabicyclo [2.2.1] heptane-2, 3, dicarboxylic acid) plus copper did not seem to be effective for hygrophila (68). In the case of limnophila, almost all chemicals registered for use in aquatic systems have been used with only limited success (37, 41). High levels of 2,4-D (2, 4-dichlorophenoxyacetic acid) and daily spraying for 8 days with 1,000 ppm paraquat (1, 1-dimethyl-4, 4' bipyridinium dichloride) have been reported to kill limnophila (37, 41).

The literature pertaining to the physiology of limnophila and hygrophila also is limited. Several species of *Limnophila* (but not *L. sessiliflora*) have been used in tissue

culture work for studying the regeneration of whole plants (49, 57), mainly because of their propensity for vegetative propagation (49). Hygrophila has been utilized in studies of apical dominance and in grafting experiments (13, 14, 15, 16). Some work has been published on the glandular hairs of *H. difformis* (52), and on the structure and development of stomata in limnophila (6). The only recently published work on photosynthesis in these two genera is for *L. gratiloides* (46), in which the influx of chloride and sulfate anions across the cell membrane was measured in conjunction with ATP levels and CO₂ fixation rates. It was reported that increasing concentrations of CCCP (carbonyl cyanide m-chlorophenylhydrazone), an electron flow inhibitor, reduced the ATP level and CO₂ fixation (46).

From an examination of the literature on limnophila and hygrophila, especially in regard to their placement of biomass at the water surface, their reproductive capacity, and their weed status in other tropical/subtropical areas, it appears there is reason to suspect that these plants could become weed problems in Florida. Consequently, and in light of their continued use by the aquarium industry, a more detailed, experimental investigation was undertaken.

MATERIALS AND METHODS

Seasonal standing crop measurements for limnophila and hygrophila were conducted in 1982 and 1983 in north, central, and south Florida. The limnophila sampling sites were: Lake Seminole (Georgia) off highway 253 (north site); Boggy Creek, Lake Tohopekaliga in Osceola County (central site); Loxahatchee River at the Jonathan Dickinson State Park in Martin County (south site); and Canal C-100 in Miami, Dade County (alternate south site). The hygrophila sampling sites were: Suwannee River at Turkey Island in Levy County (north site); Boggy Creek, Lake Tohopekaliga in Osceola County (central site); Sailfish canal in Lee County (south site); and Canal Road, Miramar in Broward County (alternate south site). At each of these locations, three to five replicate samples were taken with a 0.25 m² quadrat by removing all plant material (submersed and emersed) above the hydrosol. Samples were cleaned, their fresh weight determined, and then dried at 60 C to constant weight for dry weight determinations.

In order to compare the growth of limnophila and hygrophila with that of hydrilla under similar growth conditions, 25 cm long apical sections of each species were planted in wooden 930 cm² (1 ft²) boxes containing 10 cm of top soil, with 16 plants of a single species in each box. The boxes were placed into five concrete vaults (12 boxes per vault) each of which contained 1300 l of Bivens Arm Lake water which was replaced twice weekly. The vaults were located outdoors at the Bivens Arm Agronomy Field Station in Gainesville. For three of the vaults, only one species per vault was planted, while the remaining two vaults contained either limnophila with hydrilla or hygrophila with hydrilla in equal amounts. Prior to planting, samples were taken for fresh and dry weight determinations. After 10 weeks (April through June, 1983) the plants were harvested, cleaned, and fresh and dry weight determinations were made on the

standing crop. Subterranean tubers and leaf axil turions also were counted.

To determine the effect of pH on growth, 15 cm apical segments of limnophila, hygrophila, and hydrilla were planted in 6 cm of top soil overlain by 1 cm of sand in 180 ml styrofoam cups; three plants of a single species per cup. Fifteen cups of each species were placed into separate 20 l aquaria, with filtered Bivens Arm Lake water adjusted with 2 N NaOH or HCl to pH 5.0, 7.0, or 9.0. The water was changed weekly, and titrated daily to retain the pH at the appropriate treatment value. The aquaria were placed in a Conviron growth chamber where a 14-h/30 C photoperiod, 22 C night, and a quantum irradiance of 800 μmol/m²·s (400-700 nm) was achieved incrementally over a three hour equilibration phase. Fresh and dry weights were determined on samples at the start and after a growth period of 3 to 5 weeks.

The capacity for vegetative reproduction by fragmentation was compared for limnophila, hygrophila and hydrilla by determining regrowth from fragments with different numbers of nodes, utilizing a modification of the procedure described by Langeland and Sutton (32). Stem fragments containing 1, 3, or 6 nodes per fragment were placed in 250 ml culture tubes with 5% v/v Hoaglands solution and incubated in a growth chamber under a 14-h/30 C photoperiod, 22 C night, and a quantum irradiance of 400 μmol/m²·s (400-700 nm). The nutrient solution was replaced on alternate days, and regrowth recorded weekly.

Seed germination potential was evaluated for limnophila. Seeds were collected from mature ovaries, dried, and stored dry at room temperatures for approximately 9 months. The seeds were placed in 10 cm petri dishes on filter paper saturated with deionized water and then incubated in either the light or dark at 30 C in a growth chamber. Seeds also were placed under water, or under aerated water, or under water saturated with N₂ to exclude O₂, in 100 ml beakers. All treatments consisted of three replicates containing 25 seeds each.

Gas exchange measurements in the light and dark were determined with an ADC (Analytical Development Company Ltd, England) series 225, Mark III infrared gas analyzer incorporated into a closed system similar to that described by Van *et al* (66). Net photosynthesis and dark respiration rates were determined from the time required for the plants to decrease or increase the CO₂ concentration in the circulating gas mixture between 330 and 320 μl CO₂/l (gas phase). This CO₂ concentration was equivalent to ambient levels and gave a dissolved free CO₂ level of 9.2 μM, a value similar to that found in Florida lakes (66). All gas exchange measurements were made at 30 C and a saturating quantum irradiance of 700 μmol/m²·s (400-700 nm), unless otherwise stated. Oxygen levels were 21% (gas phase) unless otherwise indicated. The CO₂ compensation point values were determined in the closed IRGA system as described previously (66).

Ribulose biphosphate carboxylase/oxygenase (RuBP-Case) and PEPCase were extracted and assayed as described by Salvucci and Bowes (54) using the incorporation of ¹⁴C₂O into acid stable products. The chlorophyll concentration was determined by the method of Arnon (3).

RESULTS

The standing crop values for limnophila from various locations are presented in Figure 1. The northerly collection site for limnophila, in Lake Seminole, had a water depth of approximately 1.0 m, and a pH of 6.8. Although the site received full sun irradiance, numerous spatterdock (*Nuphar luteum*) [L.] Sibth. and Smith plants were scattered throughout the area. During the fall and early winter of 1982/83 the standing crop values declined by over 60%, and they remained low during the summer, possibly because of shading by a large increase in the spatterdock coverage. At the central Florida site (Boggy Creek) the water depth varied between 1.0 and 2.0 m. The pH was 6.2, and the location was exposed to full sun irradiance. The central Florida standing crop values were generally lower than those found in the other sites. During the winter, there was a 55% decline from the fall 1982 values, and they stayed low into the spring. In the summer the standing crop increased by 67% and remained at about this level through the fall of 1983. Two sampling locations were used in the south; both had a water depth of 1.0 to 2.0 m. The C-100 canal site received full sun during part of the day, while the Loxahatchee River site was more shaded. The southerly standing crop values decreased by 57% during the winter of 1982/83, and rose again by 67% in the summer, and stayed relatively high through the fall of 1983.

The standing crop values for hygrophylla from various locations in Florida are presented in Figure 2. The north Florida site (Suwannee River) had a water depth of 1.0 to 1.5 m, a pH of 7.5, and was partially shaded. At this site during the winter, the standing crop values dropped precipitously (by 87%) from the previous fall values. By the early summer of 1983 the plant was virtually absent from this site; however, by late summer the standing crop values had returned to about 25% of their original amounts and remained around this level through the early winter. The central Florida sampling location (Boggy Creek) for hygrophylla was in the same area as the site for limnophila, and thus it had the same characteristics. In contrast to the northerly sampling site, the standing crop values at this central Florida location remained relatively constant

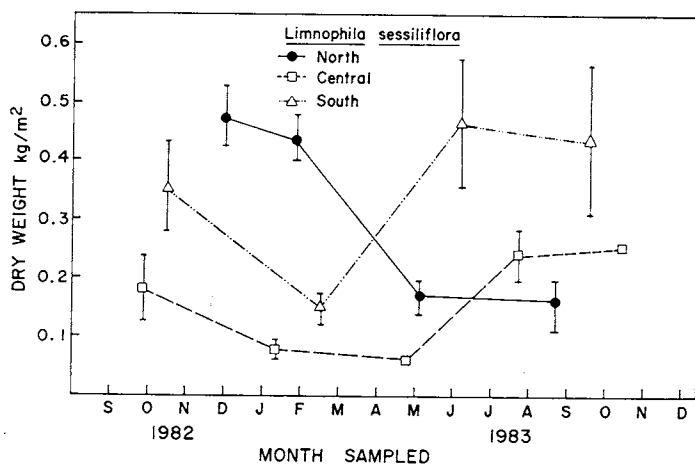


Figure 1. Seasonal standing crop values for limnophila from several locations in Florida during 1982 and 1983.

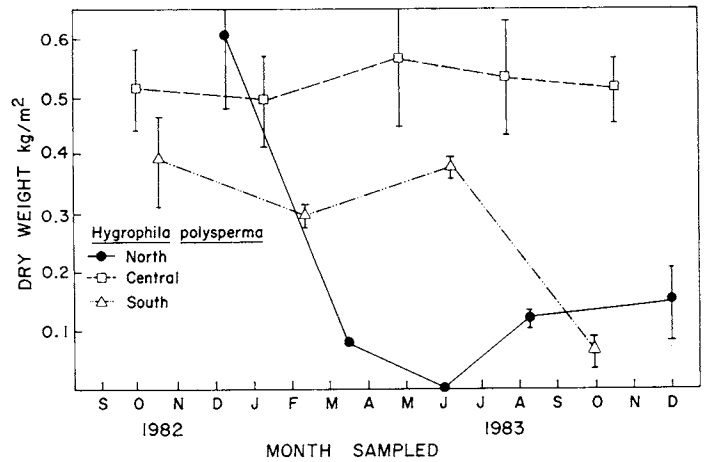


Figure 2. Seasonal standing crop values for hygrophylla from several locations in Florida during 1982 and 1983.

throughout the sampling period, with no decline in winter months. The values recorded for this site were among the highest found for either plant. The two south Florida sampling locations for hygrophylla (Sunfish and Miramar Canals) had water depths of 1.5 to 2.0 m, a pH of 6.5, and were exposed to full sun irradiance. From the fall of 1982 through the early summer of 1983, the hygrophylla standing crop values averaged between 0.3 and 0.4 kg/m², and showed little tendency to decline during the winter (Figure 2). However, by the fall of 1983 there was a decrease of 87% in the standing crop.

The standing crop values in Figures 1 and 2 are presented on a dry weight basis. Fresh weights also were determined and the mean fresh:dry weight ratios for limnophila and hygrophylla were 16.4 and 12.4, respectively.

In Table 1, standing crop data are presented for limnophila, hygrophylla, and hydrilla grown in outdoor vaults over a ten week period in the early summer of 1983. Both limnophila and hygrophylla exhibited a decline from the initial planting weight. In contrast, the hydrilla standing crop increased substantially, producing a weight increase of greater than 600% over the experimental period. Hydrilla, when grown with limnophila or hygrophylla increased its standing crop dry weight to a similar degree (737 and 574% respectively). No tubers or other hibernacula were

TABLE 1. GROWTH AND TUBER PRODUCTION OF LIMNOPHILA, HYGROPHILA, AND HYDRILLA IN OUTDOOR VAULTS.¹

| Plant | Final dry weight (g/m ²) | Tuber production (#/m ²) |
|------------------------|--------------------------------------|--------------------------------------|
| Limnophila | 8.6 ± 5.4 | 0 |
| Hygrophylla | 2.2 ± 2.2 | 0 |
| Hydrilla | 173.3 ± 1.1 | 253.0 ± 7.5 |
| Limnophila + Hydrilla | 230.4 ± 3.2 | 199.1 ± 129.2 |
| Hygrophylla + Hydrilla | 185.2 ± 12.9 | 220.7 ± 7.5 |

¹Limnophila and hygrophylla were either planted alone or in combination with hydrilla. Initial dry weights (g/m²): limnophila, 28.0 ± 3.8; hygrophylla, 7.5 ± 0; hydrilla, 27.5 ± 6.1.

²Each value is the mean of three replications ± the standard deviation.

produced by limnophila and hygrophila over this period, but hydrilla produced over 200 tubers/m², irrespective of whether it was grown in monoculture or in combination with limnophila or hygrophila (Table 1).

Table 2 compares the effects of three different water pH values on the growth rates of limnophila, hygrophila, and hydrilla in a controlled environment chamber. Limnophila and hygrophila at pH values of 5.0 and 7.0 increased their dry weight by a similar extent each week (approximately 15%). However, at pH 9.0, the growth rate was greatly retarded. The growth rate of hydrilla was markedly different from that of limnophila and hygrophila, at pH 5.0, the hydrilla growth rate was relatively low; at pH 7.0 it was over three times that exhibited by either of the other two plants; while at pH 9.0 it was almost five-fold greater than that achieved by limnophila or hygrophila at any pH.

In an investigation of the vegetative regrowth potential from stem pieces (Figure 3) limnophila fragments with one and three nodes showed no tendency to regrow, although 19% of the six node fragments formed new shoots. In contrast, hygrophila showed a substantial capacity for regrowth in that about half of the one node and all of the three and six node pieces showed regrowth. No hydrilla fragments with only one node regrew, but 38% and 61% of the three and six node fragments, respectively, were able to produce new shoots.

During the spring and summer months many seed-bearing capsules were found on limnophila plants throughout the State. However, for hygrophila no flowering, and hence no seed production, was observed. Each limnophila flower capsule was found to contain between 200 and 300 minute (approximately 450 μ m in length and 300 μ m in diameter) dark seeds. Table 3 presents a time course for germination of limnophila seeds under water and in the light at 30 C. Germination was rapid, with over 90% of the seeds germinating in 12 days. The germination requirements are presented in Table 4. When submersed, with or without aeration, limnophila seed germination was very high. However, when submersed in the absence of oxygen, no germination occurred. Seeds kept moist on filter paper, but not submersed, did not germinate to the same degree as those submersed. Similarly seeds held in total darkness did not germinate.

In Table 5, the light requirements for photosynthetic CO₂ fixation by limnophila and hygrophila taken from full

TABLE 2. EFFECT OF pH ON THE GROWTH OF SUBMERSED LIMNOPHILA, HYGROPHILA, AND HYDRILLA. GROWTH IS EXPRESSED AS THE CHANGE IN DRY WEIGHT PER WEEK.

| Plant ¹ | pH | | |
|--------------------|-------------------------|-------------|-------------|
| | 5.0 | 7.0 | 9.0 |
| | (% change/week) | | |
| Limnophila | 15.0 ² ± 6.2 | 14.1 ± 4.5 | 3.9 ± 3.1 |
| Hygrophila | 16.0 ± 6.3 | 13.6 ± 4.7 | -7.0 ± 5.5 |
| Hydrilla | 5.5 ± 8.7 | 55.5 ± 16.2 | 70.0 ± 24.7 |

¹Initial dry weights (g): limnophila, 0.16 ± 0.01; hygrophila, 0.11 ± 0.01; hydrilla, 0.24 ± 0.01. Growth period (wk): limnophila, 5.5; hygrophila, 3.5; hydrilla, 2.4.

²Each value is the mean of fifteen replications ± the standard deviation.

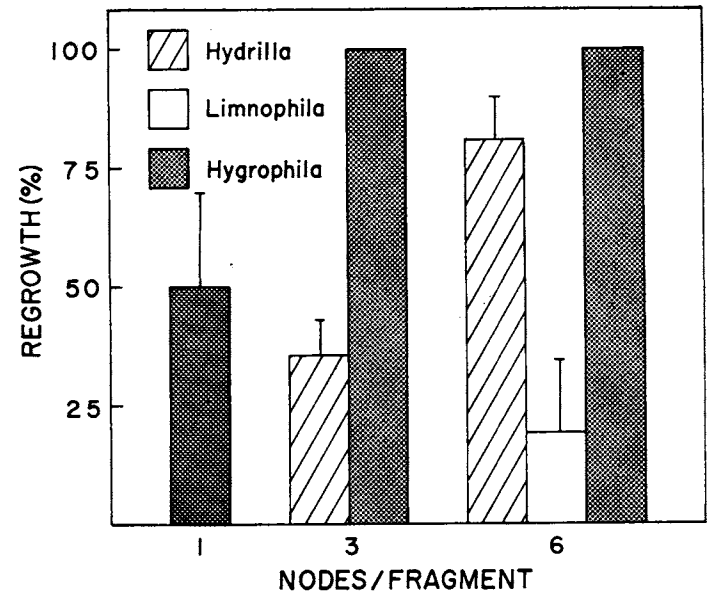


Figure 3. Comparative regrowth capacities of limnophila, hygrophila, and hydrilla from stem fragments with one to six leaf nodes per fragment.

sun field locations are listed. These data were determined at the ambient CO₂ levels prevailing in the natural habitat, and thus photosynthesis was not CO₂ saturated. In both plants the emerged portion was light saturated at irradiance levels equivalent to approximately one-third full sun. In contrast, the submersed portions required less light to saturate photosynthesis, with limnophila being the more shade-adapted of the two plants. The photosynthetic light compensation point is the irradiance at which no net carbon gain occurs because photosynthetic CO₂ uptake is just

TABLE 3. TIME COURSE FOR THE GERMINATION OF LIMNOPHILA SEEDS SUBMERSED AND IN THE LIGHT AT 30C.

| Time (days) | Germination (%) |
|-------------|-----------------|
| 0 | 0 ¹ |
| 5 | 18 ± 5 |
| 6 | 44 ± 19 |
| 7 | 65 ± 22 |
| 8 | 74 ± 28 |
| 9 | 82 ± 24 |
| 10 | 91 ± 16 |
| 12 | 96 ± 7 |

¹Each value is the mean of three replications ± the standard deviation.

TABLE 4. EFFECT OF VARIOUS ENVIRONMENTAL CONDITIONS ON THE GERMINATION OF LIMNOPHILA SEEDS.

| Treatment | | Germination (%) |
|---------------------|-------------|----------------------|
| Seeds submersed | Aerated | 94 ¹ ± 10 |
| | Non-aerated | 96 ± 4 |
| | Nitrogen | 0 |
| Seeds not submersed | Light | 22 ± 2 |
| | Dark | 0 |

¹Each value is the mean of three replications ± the standard deviation.

TABLE 5. PHOTOSYNTHETIC RESPONSE TO LIGHT OF FIELD-GROWN, SUN-ADAPTED LIMNOPHILA AND HYGROPHILA PLANTS.

| Plant | | Light saturation point ¹ | Light compensation point ¹ | Net photosynthetic rate |
|------------|-----------|---|---|---|
| | | ($\mu\text{mol}/\text{m}^2\cdot\text{s}$) | ($\mu\text{mol}/\text{m}^2\cdot\text{s}$) | ($\mu\text{mol CO}_2/\text{mg Chl}\cdot\text{h}$) |
| Limnophila | Emerged | 650 | 16 | 40.4 ± 2.7 |
| | Submersed | 250 | 8 | 7.8 ± 1.5 |
| Hygrophila | Emerged | 600 | 45 | 33.6 ± 7.5 |
| | Submersed | 400 | 9 | 4.4 ± 0.3 |

¹Data derived from quantum irradiance response graphs.

²Each value is the mean of three replications \pm the standard deviation.

balanced by photorespiratory and respiratory CO₂ losses. It provides some indication of the capacity of a plant to tolerate light-limited conditions. The light compensation point for submersed limnophila was similar to that measured for submersed hygrophila (Table 5). For both plants the emerged had higher light compensation points than the submersed parts; in the case of hygrophila the value was five-fold higher. Both plants showed light saturated net photosynthetic rates for the emerged leaves that were six or seven times greater than those of the submersed leaves, at the same ambient free CO₂ concentration.

In photosynthesis, the CO₂ compensation point is the CO₂ concentration at which photosynthetic CO₂ uptake in the light is equal to that lost by respiratory processes, especially photorespiration. It thus can be used as an indicator of photorespiration. For limnophila and hygrophila it was not a fixed value, but varied as a function of the conditions under which they were grown (Table 6). Under summer-like conditions, low CO₂ compensation points of 24 and 18 $\mu\text{l CO}_2/\text{l}$ (gas phase) occurred for limnophila and hygrophila, respectively. In contrast, both plants incubated in winter-like conditions had high CO₂ compensation points. Plants measured directly from the field usually showed high CO₂ compensation points, ranging from 40 to 110 $\mu\text{l CO}_2/\text{l}$ (data not shown). When measured at ambient CO₂ levels, the photosynthetic rates were inhibited by atmospheric levels of O₂ (21% as compared to 1%, gas phase), although the degree of inhibition for both species in the low CO₂ compensation point state was only about 12%. Hygrophila had a net photosynthetic rate that was almost

twice that of limnophila on a chlorophyll basis. The net photosynthetic rates of plants in the low CO₂ compensation point state were two to five times greater than those of high CO₂ compensation point plants.

The evolution of CO₂ into CO₂-free air in the light is largely of photorespiratory origin if net photosynthesis is inhibited by O₂, and it is thus considered to be an estimate of the photorespiratory capacity of a plant (44). For limnophila, the high CO₂ compensation point plants showed somewhat higher photorespiration than the low CO₂ compensation point plants (Table 6). Photorespiration in the low CO₂ compensation point state of hygrophila was not measured, though in the high state it was in the same range as that of limnophila. The rates of CO₂ evolution in the dark (an estimate of dark respiration) for limnophila and hygrophila (Table 6) were greater than the photorespiratory rates, and were higher in the low CO₂ compensation point state.

Figure 4 shows the effect of temperature on the net photosynthetic rate of submersed limnophila and hygrophila. In order to reflect the conditions in the natural environment, no attempt was made to compensate for the effects of temperature on CO₂ and O₂ solubility. Thus the response seen in Figure 4 includes some indirect effects due to changes in the concentration of CO₂ and O₂ in the water at different temperatures. The temperature optimum for

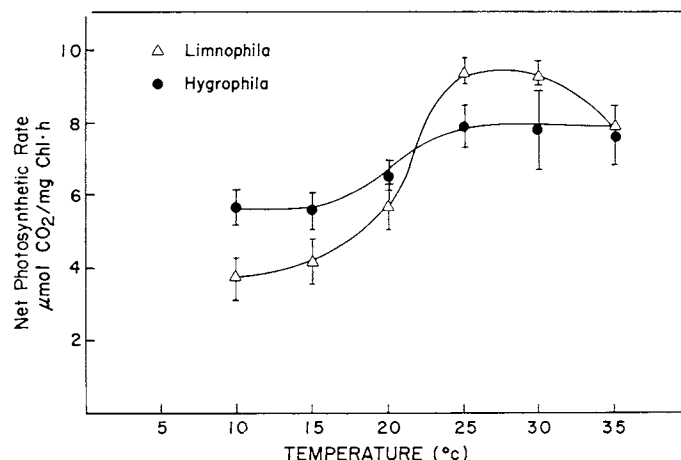


Figure 4. Effect of temperature on the net photosynthetic rate of submersed limnophila and hygrophila at ambient CO₂ and O₂ concentrations.

TABLE 6. CO₂ COMPENSATION POINTS, NET PHOTOSYNTHETIC, PHOTORESPIRATORY, AND RESPIRATORY RATES AND THE O₂ INHIBITION OF PHOTOSYNTHESIS OF CHAMBER-GROWN, SUBMERSED LIMNOPHILA, AND HYGROPHILA PLANTS.

| Plant | CO ₂ compensation point ($\mu\text{l CO}_2/\text{l}$) | Net photosynthetic rate | | Inhibition by 21% O ₂ (%) | CO ₂ evolution into CO ₂ free air in the light ($\mu\text{mol CO}_2/\text{mg Chl}\cdot\text{h}$) | Dark CO ₂ evolution ($\mu\text{mol CO}_2/\text{mg Chl}\cdot\text{h}$) |
|------------|--|--|-------------------|--------------------------------------|--|--|
| | | 21% O ₂ ($\mu\text{mol CO}_2/\text{mg Chl}\cdot\text{h}$) | 1% O ₂ | | | |
| Limnophila | 24 ¹ | 23.2 ± 4.2 | 26.5 ± 5.6 | 12.6 | 1.9 ± 0.6 | 6.0 ± 2.1 |
| | 65 ² | 11.9 ± 1.0 | 17.3 ± 1.9 | 31.3 | 2.2 ± 0.5 | 4.4 ± 1.1 |
| Hygrophila | 18 ¹ | 35.6 ± 5.1 | 40.8 ± 5.8 | 12.7 | — | 8.5 ± 2.2 |
| | 102 ² | 7.6 ± 2.1 | 9.5 ± 2.2 | 20.4 | 1.6 ± 0.2 | 3.1 ± 0.8 |

¹Grown under a 14-h, 30 C photoperiod (summer-like).

²Grown under a 10-h, 15 C photoperiod (winter-like).

³Each value is the mean of three replications \pm the standard deviation.

both plants was in the region of 25 to 30 C. At temperatures below 25 C, and to some extent over 30 C, limnophila exhibited a substantial decline in net photosynthetic rate. In contrast, hygrophila was far less temperature sensitive in regard to photosynthesis. A temperature decrease of 20 C (from 30 to 10 C) only reduced net photosynthesis in hygrophila by about 25%.

The activities of two major carboxylation enzymes were measured in plants taken directly from the field. RuBPCase activity was the highest of the two carboxylases in emerged and submersed limnophila and hygrophila (Table 7). The emerged portions of the plants exhibited higher RuBPCase activities than the submersed parts, particularly in hygrophila, where the emerged leaves had an almost three-fold greater activity of RuBPCase than the submersed leaves. Although RuBPCase predominated, PEPCase activity comprised a significant component of the total carboxylation potential, in that it ranged from 12 to 25% of the RuBPCase activity. As with RuBPCase, the emerged leaves showed greater PEPCase activity than did the submersed leaves. When compared to terrestrial plants, the enzyme activities were relatively low.

DISCUSSION

The standing crop values for limnophila and hygrophila are in the range reported for hydrilla (7). At the central and north Florida sites, hygrophila had higher values than those found for limnophila; suggesting that hygrophila has a greater biomass production potential than limnophila. The fresh:dry weight ratio indicates that hygrophila plants have a greater structural component than limnophila. However, the amount of biomass is only one factor contributing to weediness; of more importance is biomass distribution. The major portion of hydrilla biomass is restricted to the surface waters (7, 21), where it interferes most with human activities. The biomass of limnophila and hygrophila appears more evenly distributed, and even extends into the aerial environment. From field observations, the emergent photosynthetic parts of limnophila and hygrophila were generally produced somewhat later in the season, as the submersed parts became densely matted. The contribution of aerial photosynthesis to the overall carbon gain of amphibious plants has yet to be determined. The much higher photosynthetic rates of emerged limnophila and hygrophila leaves indicate a significant production potential, however, the maximum standing crop values belie this potential, as they were not much higher than those for totally submersed

plants such as hydrilla (7). Hygrophila was often found growing terrestrially along the shore, which suggests it has the capacity to be a ditchbank plant.

From the standing crop data, vegetative growth of limnophila appeared to be seasonal, with generally much lower standing crop values in winter and early spring. No correlation was evident between amount of biomass produced and the latitude. Hydrilla shows a similar seasonal fluctuation, except in some south Florida locations with more mild winter temperatures (7, 20). Hygrophila showed far less evidence of a seasonal effect on vegetative growth, especially at the central Florida sampling site. At the north Florida sampling site the hygrophila biomass declined during the spring of 1983 because of severe flooding by the Suwannee River, and it did not recover its pre-flooded biomass levels. The sensitivity of hygrophila to water level fluctuation requires investigation as a possible control methodology (20, 26, 27). The substantial hygrophila decline in the Miramar canal during the fall of 1983 occurred after a herbicide application of endothal on August 31, 1983 (R. Hooks, 1983, personal communication). This suggests that endothal can be effective against hygrophila.

The apparent seasonality of standing crop for limnophila, but not hygrophila, may be associated with the reduction in limnophila photosynthetic rate observed at temperatures below 20 C; by comparison, hygrophila photosynthesis was less influenced by temperature. From our data, hygrophila appears to have the potential to succeed in more northerly locations than it currently occupies. Although lack of seasonality is not necessarily a determinant of weediness (as evidenced by the fact that hydrilla exhibits seasonality throughout much of Florida), it would add to the potential weed problem.

The growth chamber studies show that although these three plants overlap in the pH range of water they tolerate, limnophila and hygrophila grow best at lower pH (5 to 7), whereas hydrilla growth is greatest at higher pH (7 to 9). In contrast to limnophila and hygrophila, hydrilla grew well at all pH values tested and must be regarded as more tolerant of pH than the other two plants. This wide pH tolerance is another factor contributing to the ability of hydrilla to exhibit weed characteristics in a variety of water bodies. The presence of limnophila and hygrophila at Boggy Creek, and hygrophila at Miramar Canal as significant components of the aquatic vegetation may be related to the lower pH values (between 6.2 and 6.5) found at these sites. Lower pH should improve the chances of limnophila, and especially hygrophila in competition against hydrilla.

Neither limnophila or hygrophila were able to become established when planted under a 1 m depth of relatively high pH, lake water. In contrast, hydrilla under these conditions rapidly produced a mat of vegetation and substantial numbers of tubers. Limnophila and hygrophila appear more limited than hydrilla in their ability to become established in deep water independently of an existing colony of plants. The capacity of hydrilla to invade and become established in new areas is well documented, and in this study it was evidenced by the fact that within 10 weeks hydrilla was permanently established in its boxes and had

TABLE 7. RuBP AND PEP CARBOXYLASE ACTIVITIES IN EMERGED AND SUBMERSED FORMS OF LIMNOPHILA AND HYGROPHILA.

| Plant | | Carboxylase activity | | RuBP PEP |
|------------|-----------|---|----------------|-------------|
| | | RuBP ($\mu\text{mol/mg Chl}\cdot\text{h}$) | PEP | |
| Limnophila | Emerald | 88.4 ¹ \pm 5.1 | 21.3 \pm 3.6 | 4.2 |
| | Submersed | 78.4 \pm 8.4 | 9.6 \pm 1.7 | 8.2 |
| Hygrophila | Emerald | 154.0 \pm 6.4 | 27.5 \pm 1.8 | 5.6 |
| | Submersed | 54.1 \pm 4.9 | 13.4 \pm 2.6 | 4.0 |

¹Each value is the mean of three replications \pm the standard deviation.

invaded neighboring boxes of limnophila and hygrophila in the same vault. Under the high pH conditions in this experiment limnophila and hygrophila apparently had a far less aggressive invasion potential.

Stem fragments can be major sources of inoculum material for the introduction of aquatic plants into new bodies of water (20, 59). Under growth chamber conditions hygrophila surpassed the substantial ability of hydrilla, to regenerate vegetatively from stem fragments. Thus as with hydrilla, stem fragments of hygrophila are probably an important factor influencing the spread and weed potential of this plant. This suggests that management practices should be selected to minimize hygrophila dispersion by fragmentation. Both limnophila and hygrophila lack the tuber and turion production capability of hydrilla, and in this respect cannot match the weed potential of hydrilla.

In contrast to hydrilla and hygrophila, the asexual reproductive capacity of limnophila appears to be poorly developed. However, this may be offset by the ability of limnophila to reproduce sexually via seeds; a characteristic apparently lacking, or at least uncommon, in hygrophila and hydrilla growing in Florida waters. Given the number (approximately 300) of seeds found in each limnophila flower and the high germination capacity (96%), each flower has the potential to produce about 300 seedlings. This is a large source of new plant material to contribute to the infestation of new water bodies. Furthermore, as the seeds were viable for at least nine months after maturity, they may substitute for the role of hydrilla tubers that enable the plant to survive a period of adverse environmental conditions. Hygrophila in Florida may not have such a well-developed survival mechanism. Limnophila seed germination should not be significant in water of limited light penetration or where anaerobic conditions exist. Germination also was low unless the seeds were submersed. Whether this means the seeds will not germinate on the bank is unclear, as it could simply reflect the need to leach inhibitors from the seed coat (38).

In the submersed state, limnophila and hygrophila plants have low light compensation and saturation points for photosynthesis similar to those of hydrilla (8, 66); which confirms the observation of other workers (Cobb, J., T. K. Van, and W. T. Haller, 1981, personal communication). They are thus shaded-adapted plants and are able to show net CO₂ uptake under very low light conditions. In this respect, like hydrilla, they are superior to some native submersed species, which although shade-adapted, do not possess such low light compensation points (66). This characteristic enables germinating hydrilla tubers to have a positive carbon balance at attenuated light levels in organic-stained Florida lakes (8). As limnophila and hygrophila do not produce tubers, this characteristic may be of less significance in their competitive success.

As has been reported for other amphibious aquatic plants (35, 55), the emersed portions of limnophila and hygrophila were less shade-adapted and had higher net photosynthetic rates than the submersed leaves. This reflects the fact that CO₂ is less limiting in an aerial environment, and also that the emergent leaves have a greater

carboxylation enzyme potential (54). Emergence seems to be one of several strategies utilized by SAM plants to enhance carbon gain, especially when dissolved inorganic carbon limitations become exacerbated by dense submersed vegetation. However, the potentially important role of emergence in seed production by limnophila must not be overlooked.

All the freshwater SAM plants we have examined show variable CO₂ compensation points, which depend on the growth conditions (7, 28, 29, 54, 55, 56). On this basis, we have proposed they belong to a new photosynthetic category (SAM), distinct from those applicable to terrestrial plants (7, 29, 56). From this study it is apparent that submersed limnophila and hygrophila also have variable (high through low) CO₂ compensation points, and thus are typical SAM plants. A low CO₂ compensation point generally reflects a state in which photosynthetic CO₂ uptake is elevated, while the apparently "wasteful" process of photorespiratory CO₂ release is reduced, and the inhibitory effect of O₂ on photosynthesis and growth is also moderated (44). It is apparent that these observations also apply to limnophila and hygrophila. The potential of SAM plants to change to a low photorespiration state (7, 54) is another strategy to enhance carbon gain or conserve carbon in aquatic environments where this substrate is severely limiting (28, 29, 42, 66). All submersed freshwater plants appear able to exhibit this state; but of the plants examined, including limnophila and hygrophila, hydrilla most readily changes to the low photorespiration condition. Thus this flexibility of hydrilla may be an important consideration in its weed potential.

Two biochemical mechanisms, appear to cause the low photorespiration state in submersed plants. One is based on a bicarbonate utilization system, as found in watermilfoil (*Myriophyllum spicatum* L.); while the other, exemplified by hydrilla, is based on a C₄ acid system (56). The measurement of carboxylation enzyme activities in limnophila and hygrophila show a somewhat elevated level of PEPCase (the initial carboxylation enzyme responsible for C₄ acid formation). However, the levels are not high, as those observed for hydrilla (4, 54), and unlike in hydrilla, RuBPCase remains the predominant carboxylase irrespective of the photorespiration state. It is still uncertain as to which biochemical system limnophila and hygrophila possess. More research is needed in this area. The possession of a C₄ acid CO₂ concentrating system undoubtedly adds to the weed success of hydrilla in tropical and subtropical regions and from our limited observations on limnophila and hygrophila it appears that neither can match the system found in hydrilla.

In conclusion, the success of hydrilla as a weed is due to a combination of characteristics that provide it with a competitive advantage over native plants in Florida (67). Some of these characteristics are present in limnophila and hygrophila. They include: amount and placement of biomass, substantial reproductive capacity, and potential for a low photorespiration state, and the ability to photosynthesize effectively under low light regimes, while tolerating exposure to high light. The more limited acid to neutral pH range for limnophila and hygrophila growth; the lack of tuber production; the apparent inability to become estab-

lished directly in deeper water; and also the less aggressive invasion capacity, all suggest that in Florida neither plant poses such a weed threat as hydrilla. Because of its year-round capacity for vegetative reproduction from stem fragments, and its apparently lower sensitivity to temperature and seasonality we suggest that *hygrophila* may be more of a potential problem than *limnophila*, and its northward expansion in the State might be anticipated to continue. As far as can be ascertained, this is the first comprehensive study to attempt in advance a physiological assessment of the weed potential of an introduced aquatic plant. To check the validity of this assessment and its applicability to other introduced species, it would be appropriate to monitor closely over the next few years the distribution of *limnophila* and *hygrophila* within the State.

ACKNOWLEDGMENTS

We wish to express our appreciation to Sally A. Berish, Paula T. Seamon, Warren J. Leow, and Daniel D. Thayer for their valuable assistance in this study. We would also like to thank the Florida Department of Natural Resources, Division of Recreation and Parks for access and permission to collect *limnophila* in the Jonathan Dickinson State Park.

LITERATURE CITED

- Agarwal, S. G., R. K. Thappa, V. N. Vashist, C. K. Atal, and R. Gupta. 1975. Chemical examination of the volatile oil of *Limnophila rugosa*. Indian J. Pharm. 37:99-100.
- Ahmad, K. J. 1976. Epidermal studies in some species of *Hygrophila* and *Dyschoriste* Acanthaceae. J. Indian Bot. Soc. 55:41-52.
- Arnon, D. I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. Plant Physiol. 24:1-15.
- Ascencio, J., and G. Bowes. 1983. Phosphoenolpyruvate carboxylase in *Hydrilla* plants with varying CO₂ compensation points. Photosyn. Res. 4:151-170.
- Baveja, S. K., and S. Kaur. 1974. Rheology of dispersion systems containing *Hemidelfis polyspermus*, *Hygrophila polysperma* seed mucilage. I. Effect of stirring storage and materials in suspension. Indian J. Pharm. 36:168.
- Bhatt, D. C., and J. A. Inamdar. 1975. Structure and development of stomata in some Scrophulariaceae. Botanique 6:209-218.
- Bowes, G., A. S. Holaday, and W. T. Haller. 1979. Seasonal variation in the biomass, tuber density, and photosynthetic metabolism of hydrilla in three Florida lakes. J. Aquatic Plant Manage. 17:61-65.
- Bowes, G., T. K. Van, L. A. Garrard, and W. T. Haller. 1977. Adaptation to low light levels by hydrilla. J. Aquatic Plant Manage. 15:32-35.
- Bruenner, G. 1970. A new giant aquatic plant *Limnophila aquatica* develops as a thankful guest. Aquarien Mag. 4:488-489.
- Brummitt, R. K. 1974. New combinations and three new Zambian species in Duosperma, Acanthaceae. Kew Bull. 29:411-414.
- Cassani, J. R. 1981. Feeding behavior of underyearling hybrids of the grass carp *Ctenopharyngodon idella* female and the bighead *Hypophthalmichthys nobilis* male on selected species of aquatic plants. J. Fish Biol. 18:127-134.
- Cramer, L. H. 1974. Notes on the Scrophulariaceae of Sri-Lanka. Ceylon J. Sci. Biol. Soc. 11:29-38.
- Cutter, E. G. 1972. A morphogeneticist's view of correlative inhibition in the shoot. Adv. Exp. Med. Biol. 18:51-73.
- Cutter, E. G. 1972. Regulation of branching in decussate species with unequal lateral buds. Ann. Bot. (London) 36:207-220.
- Cutter, E. G., and H. W. Chiu. 1972. Grafting experiments on correlative effects between lateral buds. Ann. Bot. (London) 36:221-228.
- Cutter, E. G., and H. W. Chiu. 1975. Differential responses of buds along the shoot to factors involved in apical dominance. J. Exp. Bot. 26:828-839.
- Dutta, N. M. 1975. A revision of the genus *Limnophila* of eastern India. Bull. Bot. Soc. Bengal 29:1-7.
- Dutta, N. M., and S. Chanda. 1979. A contribution to the taxonomy and palynology of Gratiolae Scrophulariaceae of eastern India. Trans. Bose Res. Inst. (Calcutta) 42:1-34.
- Furst, G. G. 1968. The anatomical structure of some aquatic plants. Byull. Gl. Bot. Sada 71:67-74.
- Haller, W. T. 1976. Hydrilla: a new and rapidly spreading aquatic weed problem. Circular S-245, Agric. Exper. Station, IFAS, University of Florida, Gainesville, Florida.
- Haller, W. T., and D. L. Sutton. 1975. Community structure and competition between hydrilla and vallisneria. J. Aquatic Plant Manage. 13:48-50.
- Haq, Q. N., and M. N. Nabi. 1978. Studies on oil from the seeds of *Hygrophila spinosa*. Bangladesh J. Sci. Ind. Res. 13:29-32.
- Hara, H. 1978. Comments on east Asiatic plants part five. J. Japan. Bot. 53:232-238.
- Harada, J., K. Shimotsubo, and H. Nakayama. 1975. Possible use of morphactin for reducing the amount of molinate, a paddy herbicide. Proc. Crop Sci. Soc. Japan 44:320-323.
- Hertel, I. 1971. Data on cultivation and reproduction of *Limnophila heterophylla*. Monatsschr. Ornithol. Viva. Ausg. B. Aquarien Terrarien 18:240-241.
- Hestand, R. S., and C. C. Carter. 1975. Succession of aquatic vegetation in Lake Ocklawaha two growing seasons following a winter drawdown. J. Aquatic Plant Manage. 13:43-47.
- Hestand, R. S., B. E. May, D. P. Schultz, and C. R. Walker. 1973. Ecological implications of water levels on plant growth in a shallow water reservoir. J. Aquatic Plant Manage. 11:51-54.
- Holaday, A. S., and G. Bowes. 1980. C₄ acid metabolism and dark CO₂ fixation in a submersed aquatic macrophyte (*Hydrilla verticillata*). Plant Physiol. 65:331-335.
- Holaday, A. S., M. E. Salvucci, and G. Bowes. 1983. Variable photosynthesis/photorespiration ratios in *Hydrilla* and other submersed aquatic macrophyte species. Can. J. Bot. 61:229-236.
- Kumar, G. S., and G. Y. N. Iyer. 1967. Preliminary studies on the diuretic effects of *Hygrophila spinosa* and *Tribulus terrestris*. Indian J. Med. Res. 55:714-717.
- Langeland, K. A., and D. Schillet. 1983. Hydrilla in North Carolina: a successful program begins. Aquatics 5(4):8-14.
- Langeland, K. A., and D. L. Sutton. 1980. Regrowth of hydrilla from axillary buds. J. Aquatic Plant Manage. 18:27-29.
- Les, D. H., and R. P. Wunderlin. 1981. *Hygrophila polysperma* (Acanthaceae) in Florida. Florida Scientist 44:189-192.
- Li, H. 1980. Lake vegetation of the Yunnan plateau China. Acta Bot. Yunnanica 2:113-141.
- Lloyd, N. D. H., D. T. Canvin, and J. M. Bristow. 1977. Photosynthesis and photorespiration in submerged aquatic vascular plants. Can. J. Bot. 55:3001-3005.
- Long, R. W. 1970. The genera of Acanthaceae in the southeastern USA. J. Arnold Arboretum Harvard Univ. 51:257-309.
- Mahler, M. J. 1980. *Limnophila*—a new exotic pest. Aquatics 2(1):4-7.
- Mayer, A. M., and Poljakoff-Mayber. 1963. The Germination of Seeds. Pergamon, London.
- Mazumder, U. K., and A. Sengupta. 1978. Triglyceride composition of *Hygrophila spinosa* seed oil. Indian J. Pharm. Sci. 40:119-120.
- Medus, J., and A. Sanokho. 1974. Palynological description of some species of the genera *Borreria* Rubiaceae and *Hygrophila* Acanthaceae. Bull. Inst. Fondam Afr. Noire Ser. A Sci. Nat. 36:379-391.
- Misra, G., and G. Tripathy. 1975. Studies on the control of aquatic weeds of Orissa India. 2. Effect of chemical herbicides on some aquatic weeds. J. Indian Bot. Soc. 54:65-71.
- Moore, P. D. 1983. Photosynthetic pathways in aquatic plants. Nature 304:310.
- Naik, V. N. 1969. On the identity and nomenclature of some Indian plants. Indian Forest. 95:413-417.
- Ogren, W. L., and R. Chollet. 1982. Photorespiration. In: Photosynthesis, vol. II. Development, Carbon Metabolism, and Plant Productivity. Govindjee, editor, Academic Press, New York.
- Pancho, J. V. 1976. Philippine aquatic weeds. Kalikasan 5:37-91.
- Penth, B., and J. Weigl. 1971. Anion influx, ATP level and CO₂ fixation in *Limnophila gratioloides* and *Chara foetida*. Planta (Berl.) 96:212-223.
- Philcox, D. 1970. A taxonomic revision of the genus *Limnophila* Scrophulariaceae. Kew Bull. 24:101-170.
- Piccoli, F. 1974. A previously unrecorded weed in rice fields *Limnophila indica* *Limnophila sessiliflora* hybrid. Riso (Milan) 23:181-190.
- Rao, S., and H. Y. M. Ram. 1981. Regeneration of whole plants from cultured root tips of *Limnophila indica*. Can. J. Bot. 59:969-973.
- Rataj, K., and T. J. Horeman. 1977. Aquarium Plants. T. F. H.

- Publications, Inc., Jersey City, New Jersey.
51. Raynal, A., and D. Philcox. 1975. *Limnophila ceratophylloides* and *Limnophila fluviatilis*, two heteromorphic African species. *Adansonia* 15:225-238.
 52. Rohr, R., J. Dexheimer, and M. Kieffer. 1980. Etude tridimensionnelle du complexe sécréteur-plastes-reticulum endoplasmique dans les poils glandulaires d'*Hygrophila difformis* (Acanthacées). *Can. J. Bot.* 58: 1859-1871.
 53. Ruecker, G., and R. K. Baslas. 1974. Phenylpropane derivatives of the essential oil from *Limnophila rugosa*. *Planta Med.* 25:253-257.
 54. Salvucci, M. E., and G. Bowes. 1981. The induction of reduced photorespiratory activity in submersed and amphibious aquatic macrophytes. *Plant Physiol.* 67:335-340.
 55. Salvucci, M. E., and G. Bowes. 1982. Photosynthetic and photorespiratory responses of the aerial and submerged leaves of *Myriophyllum brasiliense*. *Aquatic Bot.* 13:147-164.
 56. Salvucci, M. E., and G. Bowes. 1983. Two photosynthetic mechanisms mediating the low photorespiratory state in submersed aquatic angiosperms. *Plant Physiol.* 73:488-496.
 57. Sangwan, R. S., B. Norreel, and H. Harada. 1976. Effects of kinetin and gibberellin A₃ on callus growth and organ formation in *Limnophila chinensis* tissue culture. *Biol. Plant. (Prague)* 18: 126-131.
 58. Schoepfel, H. 1969. New aquatic plants. A review of the period from 1964-1968. *Monatsschr. Ornithol. Viva. Ausg. B. Aquarien Terrarien* 16:230-233.
 59. Sculthorpe, M. A. 1967. *The Biology of Aquatic Vascular Plants*. St. Martin's Press, New York.
 60. Sebald, O. 1972. Contribution to Ethiopian floristics. 3. Ericaceae to Campanulaceae. *Stuttg. Beitr. Naturkd.* 244:1-41.
 61. Sengupta, S. R., and B. Pal. 1969. Studies on less familiar foods part 3. *Sci. Cult.* 35:111.
 62. Shibayama, H. 1981. Aquatic weeds in creeks and their control in Japan. *FFTC Book Series No. 20, Weeds and Weed Control in Asia*, pp. 240-256.
 63. Speta, F. 1972. On protein bodies in the cell nuclei of Scrophulariaceae. Occurrence, form and systematic value. *Oesterr. Bot. Z.* 120: 117-136.
 64. Schardt, J. D., and L. E. Nall. 1982. *Aquatic Flora of Florida Survey Report*. Florida Department of Natural Resources, Bureau of Aquatic Plant Research and Control, Tallahassee, Florida.
 65. Takematsu, T., M. Konnai, Y. Takeuchi, and N. Ichizen. 1976. Weeds of cultivated fields and herbicides in China. *Bull. Coll. Agric. Utsunomiya Univ.* 9:91-107.
 66. Van, T. K., W. T. Haller, and G. Bowes. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. *Plant Physiol.* 58:761-768.
 67. Van, T. K., W. T. Haller, and G. Bowes. 1978. Some aspects of the competitive biology of hydrilla. *Proc. EWRS 5th Symp. on Aquatic Weeds*, pp. 117-126.
 68. Vandiver, V. V. Jr. 1980. *Hygrophila*. *Aquatics* 2(4):4-11.
 69. Varma, S. K. 1978. New plant for Bihar State India. *Geobios (Jodhpur)* 5:293-294.
 70. Yamazaki, T. 1978. On *Limnophila aromatica* and *Limnophila chinensis*. *J. Japan. Bot.* 53:312-313.
 71. Yamazaki, T. 1979. New or noteworthy plants of Scrophulariaceae from Indochina. 3. New taxa of *Limnophila*. *J. Japan. Bot.* 54: 15-21.
 72. Yamazaki, T. 1980. New or noteworthy plants of Scrophulariaceae from Indochina. *J. Japan. Bot.* 55:328-336.
 73. Zimpel, H. 1972. *Hygrophila polysperma* a hard plant. *Monatsschr. Ornithol. Viva. Ausg. B. Aquarien Terrarien* 19:99.

J. Aquat. Plant Manage. 23: 16-20

A Preliminary Study of the Efficacy of Hybrid Grass Carp For Hydrilla Control¹

JOHN A. OSBORNE²

ABSTRACT

Hydrilla biomass was monitored between November, 1980 and September, 1982 in six central Florida lakes to determine the efficacy of hybrid grass carp for hydrilla control. Hybrid grass carp from the 1979, 1980 and 1981 spawns (J. M. Malone and Sons, Enterprises) were used. Fish from the 1979 spawn were stocked in Lake Sybelia and Lake Wildermere at 14 and 16 fish mt⁻¹-FW hydrilla. Fish from the 1980 spawn were stocked at rates between 6 and 118 fish mt⁻¹-FW hydrilla and fish from the 1981 spawn were stocked at rates between 11 and 37 fish mt⁻¹-FW hydrilla. Hydrilla biomass increased in all of the lakes immediately after the fish were stocked. Some of the lakes had vegetation biomass increases of several orders of magnitude. The lack of control by the hybrid grass carp was probably due to

several factors; the time of stocking, multiple stockings, the number of fish stocked, the low feeding rate of the hybrid grass carp relative to the growth rate of hydrilla, and losses of fish due to predation and mortality from hybridization. It was concluded that the hybrid grass carp was not effective as a hydrilla control agent at the stocking rates used in this study and since much higher stocking rates would probably be needed, the cost of the fish would severely limit their use in submersed aquatic weed management programs.

Key words: Aquatic weeds, biomass, growth, Florida, stocking rate, biomass sampling, *Ceratophyllum*, *Najas*, *Vallisneria*.

INTRODUCTION

The primary objective of this research project was to determine the efficacy of the hybrid grass carp (*Ctenopharyngodon idella* X *Aristichthys nobilis*) at controlling hydrilla (*Hydrilla verticillata* (L.f.) Royle) in central Florida freshwater lakes.

The hybridization of the bighead carp (*Aristichthys nobilis*) and the grass carp (*Ctenopharyngodon idella*) was first performed in 1968 in Szarvas, Hungary which resulted in triploid (2N = 72) hybrid grass carp as reported by

¹Primary funding for this research was provided by the Office of Research and Development, U.S. Environmental Protection Agency, under grant number R-807961010. Additional funding was provided by the University of Central Florida. The U.S. Environmental Protection Agency does not necessarily endorse any commercial products used in the study and the conclusions represent the view of the author which do not necessarily represent the opinions, policies or recommendations of the U.S. Environmental Protection Agency.

²Professor, Department of Biological Sciences, University of Central Florida, P.O. Box 25000, Orlando, Florida 32816.