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Effects of drawdowns and dessication on tubers of hydrilla, an exotic aquatic weed

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Subterranean turions (tubers) of hydrilla lose viability when desiccated. Experimental data showed that freshly collected tubers had a moisture content between 50 and 60% and more than 90% viability. When desiccated, there was an approximate 2% increase in tuber mortality with each percent decline in moisture content. However under field conditions, the tuber bank within the exposed sediments of a northern Texas reservoir showed no decline in number or tuber viability throughout a 12-mo continuous drawdown. Apparently, the buried tubers were never subject to sufficient dessication to damage them. Finally, an experimental pond with an extensive hydrilla tuber bank was manipulated through six flood/drawdown cycles to determine the effects of short-term drawdowns on tuber survival and quiescence. Initially, the pond had a tuber bank of about 676 and 305 tubers m^{-2} in the shallow and deep zones, respectively. Although the tuber number was reduced to fewer than 15 to 30 tubers m^{-2} by these repetitive drawdowns, hydrilla tubers were not eradicated from the pond.

Nomenclature: Hydrilla, *Hydrilla verticillata* (L.F.) Royle HYLLI.

Key words: Aquatic weeds, submersed plants, physical control, dewatering, drawdown, HYLLI.

Hydrilla (*Hydrilla verticillata*) is a nuisance exotic aquatic plant species introduced to North America about 1960 (Pieterse 1981). This invasive plant has been described as the "perfect aquatic weed" (Langeland 1996) because of its ability to colonize disturbed aquatic environments. These adaptations include formation of a dense canopy at the water surface, low light and CO_2 compensation points, C_4-type photosynthetic mechanism that results in lowered photorespiration, and production of enormous quantities of various types of vegetative propagules, including stem fragments, axillary turions, and tubers (subterranean turions) (Langeland 1996; Haller and Sutton 1975; Bowes et al. 1977; Miller et al. 1993; Van et al 1976).

Although extensive studies have been conducted on the mature plant and on tubers removed from the sediments, there is less information available on the ecology of undisturbed subterranean tubers (Netherland 1999). However, it is known that the tubers form under short-day conditions (Steward 1997; Thakore et al. 1997; Van et al. 1978), rapidly accumulate to high densities, and may be relatively long-lived in undisturbed sediments. The tubers provide the species with an effective means of recovery from natural or man-induced disturbances to the aquatic system. After only a few years of hydrilla growth, the tuber density within sediments is often reported to be in the range of 200 to 1,000 tubers m^{-2} (Haller and Sutton 1975; Harlan et al. 1985; Sutton and Portier 1985). Undisturbed sediments retain viable tubers of monoecious hydrilla for at least 4 yr (Van and Steward 1990). Observation in the field following herbicide or grass carp (*Ctenopharyngodon idella*) treatments have demonstrated that tubers of the dioecious biotype may persist for 2 to 5 yr (Langeland 1993; Sutton 1996).

Long-term control of hydrilla is made difficult by the prolific formation of tubers in the sediments (Haller and Sutton 1975; Langeland 1996; Netherland 1999). In this respect, hydrilla resembles more conventional agriculture weeds such as nutsedges (*Cyperus* spp.) that are also difficult to control because of the formation of underground tubers. Hydrilla tubers that remain undisturbed in the sediments remain viable for several years but sprout at relatively low annual rates (apparently $< 10\%$ per year), ensuring a continuous supply of new plants to the system (Netherland 1999). Although effective herbicides are available to treat the mature plant and reduce production of new tubers (Haller et al. 1992; Langeland and LaRoche 1992) these do not control pre-existing, quiescent tubers, which remain protected within the sediments. Insects that feed on tubers and fungi that infect tubers are being studied as possible control mechanisms (Balciunas and Purcell 1991; Benhart and Duniway 1986; Godfrey and Anderson 1994).

To date the only control measure that has been demonstrated to have an effect on the quiescent tubers within the sediments is drawdown. Even short drawdowns may stimulate tuber sprouting in excess of 80% of the tuber bank in sediments that drain quickly (Netherland 1999). Because of the sprouting stimulation of drawdowns, multiple drawdowns may be useful to deplete a hydrilla tuber bank. The first drawdown may induce most of the tubers to sprout, and the subsequent drawdown may kill the maturing plant before new tubers can be produced.

The three studies reported here focus on the effects of drawdowns and dessication on the survival and viability of dioecious hydrilla tubers. The first study documents the effect of 12 mo of continuous drawdown on the size and viability of the tuber bank within the sediments of a northern Texas reservoir. The second study quantifies the degree of dessication needed to affect survival of hydrilla tubers. The third study is a controlled pond study that quantifies the effects of multiple drawdowns on the sprouting, survival, and quiescence of hydrilla tubers.

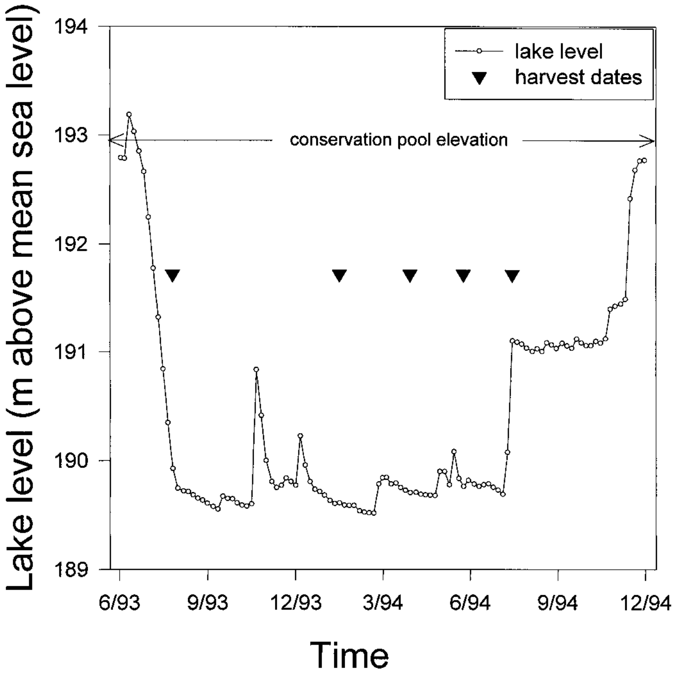

FIGURE 1. Water level of Lake Ray Roberts (open circles) and timing of hydrilla tuber harvests (closed triangles) during the 1993–1994 drawdown.

Materials and Methods

Effect of Extended Drawdowns on Hydrilla Tuber Bank

The hydrilla tuber bank in Lake Ray Roberts was monitored during a 12-mo drawdown. Lake Ray Roberts is a 15,000-ha reservoir located 50 km north of Dallas, TX, that was impounded in 1987. Small colonies of hydrilla were first observed in Lake Ray Roberts during the summer of 1992, and aerial reconnaissance revealed that the total area of infestation was about 2 ha. In the summer of 1993, the population had expanded modestly but was still confined to two sites on the lake with a total areal coverage of less than 5 ha. In June 1993, the lake level was reduced from the conservation level by about 3 m to permit repairs and modifications to the dam (Figure 1). The drawdown was not intended for management of the hydrilla, but expectations were high that this fortuitous event would control the outbreak of the weed.

This study was designed to monitor the effect of the extended drawdown on the size and viability of the hydrilla tuber bank present in the sediments where the initial hydrilla colony had been observed in 1992. This site had been colonized by hydrilla for two summers, and at the time of drawdown was heavily infested. The sediments were predominantly sand down to a depth of about 25 cm, where a heavy clay layer was present. At normal pool, these sediments were at a depth of approximately 1 to 1.25 m.

In July 1993, 5 wk following the drawdown, a site visit was made to determine the area of highest hydrilla density and to select a site for continued tuber monitoring. Two areas of dense hydrilla measuring 30 by 30 m were selected and marked by driving T-posts at the corners of the plot. The aboveground mass of hydrilla remaining on the sediment surface at that time was determined to be 700 to 800 g dry weight m^{-2}. The size of the hydrilla tuber bank was quantified at this time and then monitored an additional four times during the next 12 mo (Figure 1). At each sampling time, 12 random samples were collected from within each of the marked plots by excavating 28-cm diameter holes. Each hole extended through the sandy sediment and about 2 cm into the clay layer beneath. Most tubers were observed at the interface of the sandy sediments with the denser clay layer beneath. The sediments from each excavated hole were collected and washed through a wire mesh to separate tubers from the sediments.

On three occasions (July 1993, January 1994, May 1994), the viability of the tubers collected was determined. After enumeration, all the tubers were composited and placed in an aerated container of filtered pond water under greenhouse conditions (25 C). The tubers were observed until all tubers had sprouted or rotted.

Effect of Dessication on Tuber Viability

The effect of dessication on tuber viability was investigated in a laboratory experiment. Tubers were collected by harvesting pots of actively growing hydrilla plants maintained in culture at the Lewisville Aquatic Ecosystem Research Facility (LAERF), Lewisville, TX. Tubers (195) selected for this study were washed, blotted dry, and individually weighed to determine fresh weight. Initial moisture content of the tubers was determined by drying 15 randomly selected tubers to constant weight. This value was used to determine the dry weight equivalent of the tubers used in the study. The tubers used for the study were fully developed and ranged in size from 0.089 to 0.275 g dry weight with an average weight of 0.188 g dry weight. Each tuber was randomly placed on a grid marked on a laboratory counter top and left exposed to the air to desiccate (23 C, 30 to 40% relative humidity). Three groups of 15 tubers each were randomly selected from the grid at time intervals of 0 (within 15 min of setup), 8, 24, and 48 h. Five of the tubers from each group were used to determine the mean moisture content of that group. Moisture content was determined by reweighing the tubers immediately after taking them from the grid and again after drying them to constant weight at 60 C. The remaining 10 tubers from each group were tested for viability (i.e., ability to sprout). These tubers were placed in a 500-ml container of filtered pond water in a greenhouse (25 C) and observed daily until all tubers had sprouted or rotted. The average tuber dry weight of the 12 groups varied between 0.165 and 0.206 g, but they were not significantly different from one another ($P = 0.55$).

Effect of Multiple Drawdowns on Survival and Quiescence of Hydrilla Tubers

The hydrilla tuber bank in a pond at LAERF was sampled eight times over six flood/drawdown cycles (Figure 2). The pond was initially flooded for three consecutive years, during which time hydrilla covered the entire surface area of the pond. Following this long flood period, the pond was repeatedly drained and flooded to determine the effects of the water level fluctuations on the survival and quiescence of the tuber bank. Flood periods ranged from 3 to 10 wk, and drawdown length ranged from 1 to 20 mo.

The pond used for this study had a surface area of 0.35 ha and a maximum depth of 2.0 m. A full description of

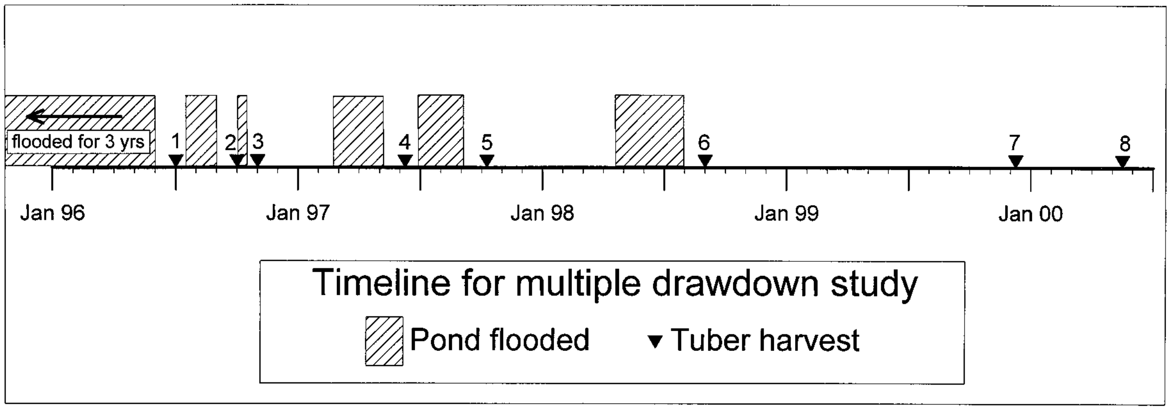

FIGURE 2. Timeline of flood/drain cycles and harvest of tubers within the monitored LAERF pond. Flood periods indicated by hatched polygons, and harvest times shown as arrows intersecting the timeline.

the ponds at LAERF is provided by Smart et al. (1995) and is briefly summarized here. The ponds are lined with compacted clay and covered with 15 to 30 cm of sediments consisting of approximately equal parts sand, silt, and clay. Bulk density of the pond sediments ranged from 1.1 to 1.3 g dry mass cm^{-3} and organic content ranged from 4 to 6%. These sediment characteristics are within favorable ranges for rooted, submersed, aquatic macrophytes (Barko and Smart 1986). Water was provided to the ponds from Lake Lewisville, a large water supply reservoir located adjacent to LAERF. Daily average pond temperatures typically ranged from about 30 C in the summer to less than 10 C in the winter. Ice did not occur on this pond during the study.

At each harvest, 20 samples were collected from the pond. Samples were collected after the sediments had dried for 2 to 4 wk, except for the seventh and eighth harvests, which took place 16 and 21 mo following the last flood period. On each harvest date, 10 samples were collected from deeper zone of the pond. When the pond was flooded, water depth over these samples ranged from 1.5 to 1.9 m and averaged about 1.7 m. Ten additional samples were collected from the shallow zone of the pond. The water depth here averaged 0.5 m when flooded. For each sample, a 28-cm-diam hole was dug into the pond extending through the fine-textured sediment and about 2 cm into the clay liner. The sediment samples were carefully washed through a wire mesh to separate tubers from the sediments, while not breaking the sprouted stem (if present) from the tuber. Tubers were quantified as being quiescent, rotted, or sprouted. Sprouted tubers were identified by their attachment to a growing shoot or by a hole in the tuber where it had formerly been attached to a shoot apex (Netherland 1999). Tubers that had not sprouted and that appeared turgid and healthy were counted as quiescent. Tubers that were soft or partially decomposed were classified as rotten and discarded. The dry weight of each quiescent tuber collected was determined. Partial tubers (cut by the digging process) were counted only if the portion collected contained the growth apex of the tuber; otherwise, they were discarded. Partial tubers were not used to determine the size frequency or sprouting viability of quiescent tubers. During the 10-wk flood period between late February and early May (see Figure 1), there were a few (< 3 m^{-2}) new tubers produced by the plants that themselves had regrown from tubers. These tubers were identified by their attachment to the tips of hydrilla rhizomes and by their small, undeveloped nature. These newly formed tubers were not viable and were removed from the analysis.

Statistical Analysis

One-way analysis of variance (ANOVA) followed by mean separation tests (LSD, $\alpha = 0.05$) was used to identify differences among the five sampling dates on Lake Ray Roberts and among the eight harvest dates of the pond study. Linear regression analysis was used to identify the linear relationship between tuber viability and tuber moisture content in the dessication study.

Results and Discussion

Effect of Extended Drawdown on Hydrilla Tuber Bank

Tubers collected from exposed sediments during short-term drawdowns are generally found to be in excellent condition and to have very high viability (Miller et al. 1976). Upon reflooding after a drawdown, it is commonly observed that a high proportion of the tuber bank germinates (Netherland 1999). However, the effects of long-term (1 yr) drawdowns do not appear to have been investigated previously. In this study, the hydrilla tuber bank on Lake Ray Roberts, TX, remained undiminished throughout 12 continuous months of drawdown (Figure 3). The tuber bank at the beginning of the drawdown averaged about 85 tubers m^{-2}, and 95% of these tubers sprouted under greenhouse conditions, indicating most were viable. Through the next 12 mo, there was no evidence of decline in any of the four sampling periods, and the means of the five sampling efforts were not significantly different from each other (one-way ANOVA, $P = 0.97$ and $P = 0.50$, plots 1 and 2 in Figure 3, respectively). In addition, more than 95% of the tubers collected in January and May 1994 sprouted under greenhouse conditions, indicating continued high viability. Throughout the drawdown period, the clay layer beneath the sandy layer remained moist and pliable, and apparently enough moisture was present to maintain tuber viability. Ten tubers collected in May 1994 were analyzed for moisture content and showed a mean moisture content of 51%. In the year following the drawdown, when the reservoir was

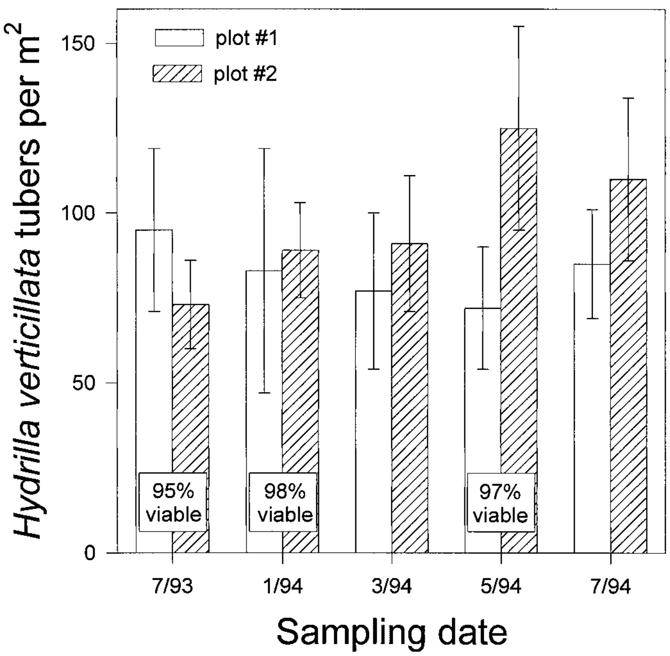

FIGURE 3. Number of hydrilla tubers m^{-2} collected in the two permanent plots during the extended drawdown of Lake Ray Roberts, TX. The percentage of the tubers that sprouted when placed in filtered lake water under greenhouse conditions is shown where available. Error bars represent ± SE, $n = 12$.

returned to normal levels, we observed that the hydrilla population at the study site quickly recovered to predrawdown levels. In the years since, the hydrilla population has expanded dramatically on Lake Ray Roberts and is now widely distributed throughout the eastern arm of the lake.

Effect of Dessication on Tuber Viability

Because of continued viability of the tubers collected during the extended drawdown at Lake Ray Roberts, the dessication study was initiated to determine the degree of moisture loss needed to affect the viability of hydrilla tubers. Exposure to air drying reduced the moisture content of the tubers from 50 to 60% when fully hydrated to about 10% after 48 h exposure. The fully hydrated tubers showed near 100% survival, whereas the most desiccated tubers had no survival (Figure 4). The two intermediate dessication periods showed intermediate survival. Linear regression shows a strong relationship between the two factors ($r^2 = 0.96$). The slope of the relationship indicates that for each 1% decline in moisture, there was an approximately 2% decline in tuber viability.

These results help explain why there was no decline in the tuber bank on Lake Ray Roberts, despite the prolonged drawdown. The tubers collected from Lake Ray Roberts following almost a year of drawdown (May 1994) still had a moisture content of 51%, a value that falls within the range observed for the fully hydrated tubers at the beginning of this study. This indicates that despite a year-long drawdown, there had been no significant dessication stress to the tubers within the sediments.

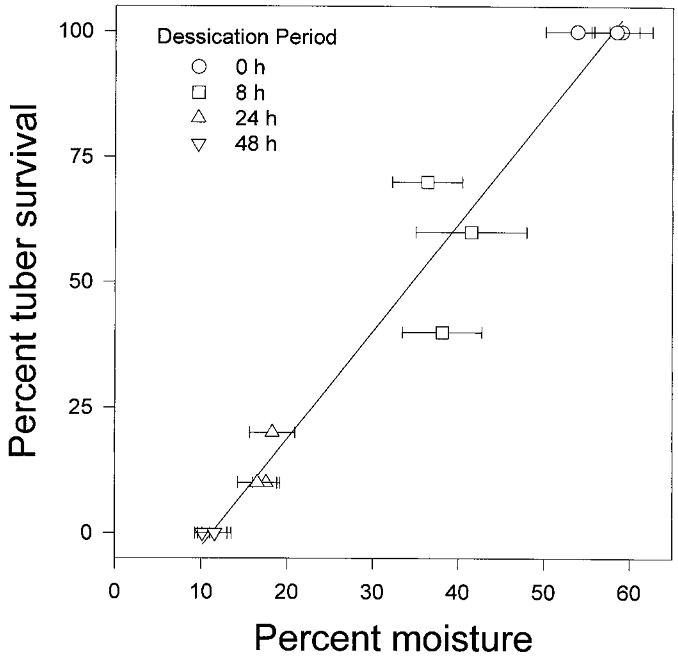

FIGURE 4. Hydrilla tuber survival as a function of tuber moisture content.

Effect of Multiple Drawdowns on Survival and Quiescence of Hydrilla Tubers

At the beginning of the study, the shallow zone of the pond had more, but somewhat smaller, tubers than the deeper zone. Initially, the shallow zone had about 676 ± 96 tubers m^{-2} (mean ± SE, $n = 10$), averaging 249 ± 5 mg dry weight ($n = 409$), whereas the deeper zone had only about 305 ± 72 tubers m^{-2} ($n = 10$), averaging 286 ± 8 mg dry weight ($n = 184$). The difference in mass was significant (t test, $P < 0.01$). Information on the role of water depth on the production of hydrilla tubers has been somewhat contradictory. Miller et al. (1976) and Miller (1975) suggest that tuber number and size increase with depth. However in a review of these data, Netherland (1999) suggested that the shallower water sites may have been periodically dominated not by hydrilla but by emergent and floating vegetation, thereby accounting for the lower numbers observed in shallow water. Our data indicate that tuber number declined significantly (> 50%) between 0.5 and 1.7 m depth, while tuber size increased modestly (ca. 15%).

Depletion of the tuber bank within the sediments of a reservoir appears to be key for long-term control of hydrilla. However to date, such depletion has been elusive and has been achieved in only a few cases where herbicides have been used to control established plants and grass carp have been present to eat any hydrilla regrowing from tubers. For example, in the North New River Canal, FL, Sutton (1996) reported that following 5 yr of herbicide treatments and the accidental introduction of grass carp in the system, the hydrilla tuber bank was depleted from about 600 to 0 tubers m^{-2} in the 3 to 4 yr following removal of the parent plants with herbicides.

The use of drawdowns as a control method for hydrilla has long been recommended, especially if the drawdown is timed to minimize or prevent tuber production and to stimulate subsequent sprouting of quiescent tubers (Haller et al. 1976; Netherland 1999). The idea behind the multiple

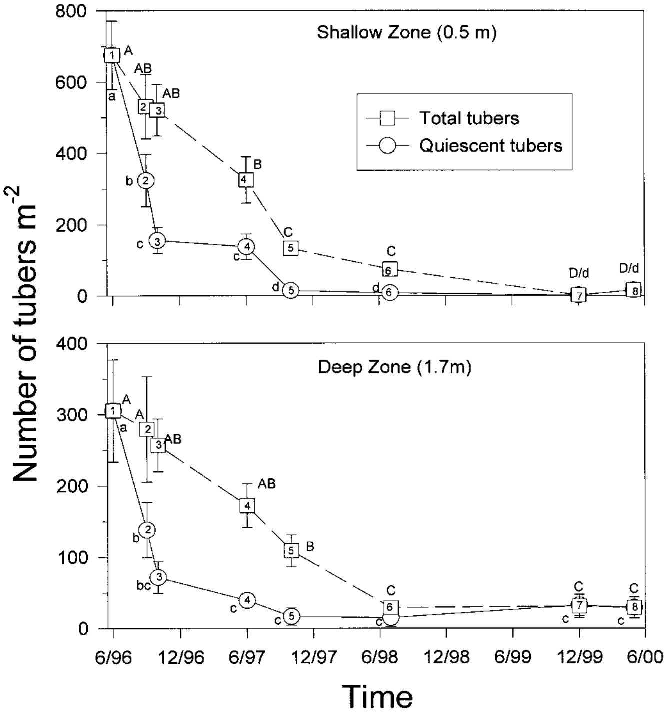

FIGURE 5. Hydrilla tuber bank in the shallow zone (top) and deep zone (bottom) of the LAERF pond. The total number of viable tubers collected are shown by the circles, whereas the number of quiescent (viable but unsprouted) tubers at the time of harvest are shown as squares. Letters indicate significant differences in means among sample dates for quiescent (small letters) or total number of tubers (capital letters) at $P \leq 0.05$.

flood/drawdown cycles used in this study was to draw the pond down and stimulate sprouting of the quiescent hydrilla tubers upon reflooding. Then, before substantial development could take place and new tubers formed, the pond would be drained to kill the sprouted plants. The tuber bank in the pond at LAERF was substantially diminished by repetitive drawdowns, but even after 2 yr of water level manipulation, followed by another 2 yr of continuous drawdown, a small number of viable tubers was still present within the sediments (Figure 5).

The results of this study support the findings of Netherland (1999) that show that short-term drawdowns stimulate sprouting of up to 90% of quiescent tubers in well-drained soils and almost 70% sprouting in poorly drained clay soils. In the present study, the two short initial drawdowns that occurred during the summer/fall of 1996 promoted the sprouting of 75 to 80% of the tubers in both the shallow and deep zones of the pond (Figure 5). The first drawdown cycle (6-wk drawdown followed by 6-wk flood) stimulated 56 and 58% of the tubers in the shallow and deep zones, respectively, to sprout. The second cycle (4-wk drawdown followed by 2-wk flood) stimulated an additional 25 and 20% of the quiescent tubers to sprout in the shallow and deep zones, respectively.

Although the short drawdowns stimulated tubers to sprout, they were relatively ineffective at killing the sprouted tubers that had not yet broken through the sediment–water interface. The hope that once a tuber sprouted it would be killed during the next short drawdown appears to be unfounded. During the first four harvests, the total number of tubers collected at a given harvest exceeded the number of quiescent tubers during the previous harvest, indicating that some of the previously sprouted tubers had survived (see Figure 5). For example, at the third harvest (October 1996) the shallow and deep zones had only 156 ± 45 and 72 ± 22 quiescent tubers in the shallow and deep zones, respectively. However, the four-month winter drawdown that followed harvest (October 1996–February 1997) apparently did not kill all of the previously sprouted tubers because at the next harvest (June 1997) the tuber bank was found to have a total of 390 ± 75 and 200 ± 30 tubers in the shallow and deep zones, respectively (total of quiescent and sprouted tubers). The damp conditions created by frequent winter rains appear to have allowed sprouted tubers that had not yet broken the sediment surface to survive. Likewise, even the more extensive drawdown between September 1997 and April 1998 did not remove all previously sprouted tubers from the tuber bank.

The flood/drawdown strategy for depleting the tuber bank of the pond appears to have been more successful in the shallow zone of the pond. In the shallow zone, the tuber bank was reduced from an initial density of 676 tubers m^{-2} to fewer than 15 quiescent tubers m^{-2} by the final harvest (ca. 2%). In the deeper zone of the pond, the tuber bank was reduced from an initial density of 305 tubers m^{-2} to a density of about 30 tubers m^{-2} (ca. 10%). Although this represents a substantial reduction, it certainly did not completely eliminate the tubers from the sediments of the ponds. In this deeper portion of the pond there was no significant decline in the quiescent tuber bank after the third harvest.

The higher persistence of quiescent tubers in the deep zones of the ponds is likely due to the difficulty in completely drying out the deeper portions of the pond. We observed that the deeper portion was always slower to dry following a drawdown and, even during the extended drawdowns, was frequently wet because of rainfall. The shallow zone, which quickly drained, was observed to be much drier than the deep zone. Netherland (1999) likewise observed increased stimulation to sprout in well-drained soils relative to more poorly drained soils.

The failure of the drawdown strategy to completely eliminate hydrilla tubers from the pond sediments, even under ideal conditions and complete hydrologic control, indicates that although drawdowns may be used to manage hydrilla, there is little chance that eradication can be achieved with this method alone.

Hydrilla tubers lose viability upon dessication. Our data indicate that once moisture content drops below 50%, there is an approximate 2% decline in viability for each percent drop in moisture content. Unfortunately, dessication to this level does not appear to be achieved often under field conditions in northern Texas. The drawdown on Lake Ray Roberts appeared to offer ideal conditions for tuber damage: the hydrilla was growing in sandy sediments, and the area was continuously exposed for more than 12 mo. Even there, however, there was no evidence in decline in the tuber bank size or the viability of the tubers. Multiple drawdowns offer hope that a hydrilla tuber bank might be depleted. Even short-term drawdowns, which do not result in completely dry sediments, were sufficient to stimulate the tubers to sprout upon reflooding. However, even following six drawdown/flood cycles, the tuber bank within the pond had not been completely exhausted. The deeper zone, which was less effectively dried during the drawdowns, still had about 10% of the original tuber bank present after 4 yr of intensive water level management.

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