

Influence of Water Depth on the Rate of Expansion of Giant Cutgrass Populations and Management Implications

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ABSTRACT

Giant cutgrass (*Zizaniopsis miliacea* (Michx.) Doell. & Asch.), a tall emergent grass native to the southeastern United States, was studied in Lake Seminole where it formed large expanding stands, and Lake Alice where it was confined to a stable narrow fringe. In Lake Seminole, the production of functional stolons which were able to become rooted in the substrate resulted in stand expansion of 1 to 3 m per year, depending upon water levels. Once flowering stems became decumbent in Lake Alice they were likely to break, with few nodes attached to the parent plant becoming rooted in the substrate, which resulted in a limited rate of stand expansion in Lake Alice. Sections of flowering stems bearing axillary shoots that were detached from the parent plant and free-floating could become rooted on reaching shallow water and produce robust new flowering plants. The reproductive biology of giant cutgrass is well-adapted to promote stand expansion and downstream dispersal, and is related to predicting potential areas of colonization, managing nuisance populations, and the use of giant cutgrass in revegetation projects.

Key words: functional stolons, reproductive strategy, colonization, invasive, distribution, revegetation, *Zizaniopsis miliacea*, Poaceae.

INTRODUCTION

Giant cutgrass is a rhizomatous perennial grass which is found as a fringing emergent or in large dense stands in marshes, ditches, creeks and along the edges of lakes, rivers

and streams. A native of the southeastern U.S. (Figure 1a), giant cutgrass has been identified from herbarium samples, surveys of state park and other water management personnel, and from the 1990 aquatic plant survey of the Florida Department of Natural Resources, in at least 50 waterbodies throughout Florida (Figure 1b).

Despite being described as a good indicator species for open cypress-gum swamp communities in southeastern Louisiana (Penfound and Hathaway 1938), there have been few reports of other plant species commonly found in association with giant cutgrass. In fact, the monospecific nature of dense giant cutgrass stands (Penfound 1952, Martin 1953, Holmes and Stalling 1990) in which “. . . no herbaceous plants, not even cattail (*Typha latifolia* L.), seem able to compete with it effectively” (Steenis and Cottam 1945) have given this species an undesirable reputation in wildlife reserves.

This reputation has been further tarnished by the ability of giant cutgrass to aggressively invade shallow waters and cause problems by limiting species diversity, narrowing river channels, and reducing storage capacities of reservoirs (Deiler 1957, Kight 1980). The deposition and accumulation of sediments from rivers, the velocities of which have been reduced in giant cutgrass stands, not only reduces water depth and surface area but may provide substrate for the succession of woody species.

Although seeds of giant cutgrass have been found in the stomachs of waterfowl, their proportion in relation to other plant seeds was small (Mabbot 1920). Its insignificance as waterfowl food, combined with the poor species diversity in giant cutgrass stands and its ability to inflict painful wounds has made this plant a less desirable species in waterfowl reserves (Uhler 1944, Martin 1953). Giant cutgrass also reportedly provided suitable habitat for malaria-carrying mosquitoes (*Anopheles quadrimaculatus*; Hess and Hall 1945) thus making this species a prime target for management in

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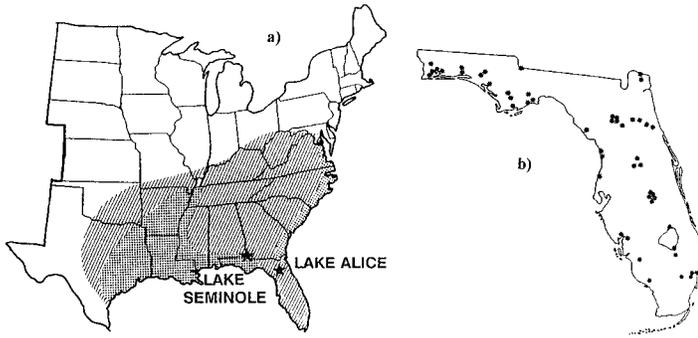


Figure 1. Distribution of giant cutgrass in: a) the southeastern United States showing principal abundance (dots) and lesser abundance (right hatch) compiled from Fassett (1969), Martin (1953), Correll and Correll (1975), and Godfrey and Wooten (1979); b) waterbodies of Florida (from sources listed in text and Schardt 1991).

malaria control programs in the 1940s and 1950s (Steenis and Cottam 1945, Goodrum and Gray 1958).

Mechanical removal of giant cutgrass in Lake Seminole was unsuccessful (Kight 1980, Smart and Barko 1982). However, investigations in Reelfoot Lake, Tennessee, and freshwater tidal marshes of the lower Savannah River valley, Georgia, indicated that late summer or fall harvests, followed by flooding or cutting again the following year, could substantially reduce biomass (Steenis and Cottam 1945, Birch and Cooley 1983). Among the most important of the few quantitative studies of the species are the productivity and biomass study of Birch and Cooley (1982) and Odum et al. (1983).

However, management of giant cutgrass is not always directed toward its control. It has been suggested that giant cutgrass marshes could be managed to provide sustainable yields of biomass, either for use in energy production, or for the purpose of nutrient removal (Birch and Cooley 1983). With its ability to rapidly colonize sites and stabilize sediments, giant cutgrass has been evaluated in Louisiana for its potential for controlling shoreline erosion in freshwater impoundments (Holmes and Stalling 1988, Cutshall et al. 1989, Good 1989). Establishment of giant cutgrass in field sites has met with varying degrees of success. Survival problems included damage caused from crowding by water hyacinth and feeding by the aquatic rodent nutria (*Myocaster coypus*) (Good 1988).

The aggressive colonizing potential of giant cutgrass in shallow waterbodies has been documented in Lake Seminole, a 15,176-ha reservoir formed by the Jim Woodruff Dam on the lower Chattahoochee and Flint Rivers, on the Florida, Georgia, Alabama borders. At the time of impoundment in 1957, giant cutgrass was only known to grow upstream of the flooded area on the Flint River, but by 1960, 1.2 ha were found within the reservoir (Kight 1980). This was the beginning of a period of colonization between 1963 and 1976 that was described as "phenomenal expansion" by local biologists (Gholson 1984a, 1984b; Figure 2).

Although the total area of giant cutgrass coverage in Lake Seminole did not increase greatly in the decade preceding 1992 (Figure 2), localized expansion continued. For example, aerial photographs taken in 1986 and 1990 of the 5.1 ha Fox Island (1.5 km south of Sealy Point Landing) showed that giant cutgrass had increased its coverage around the is-

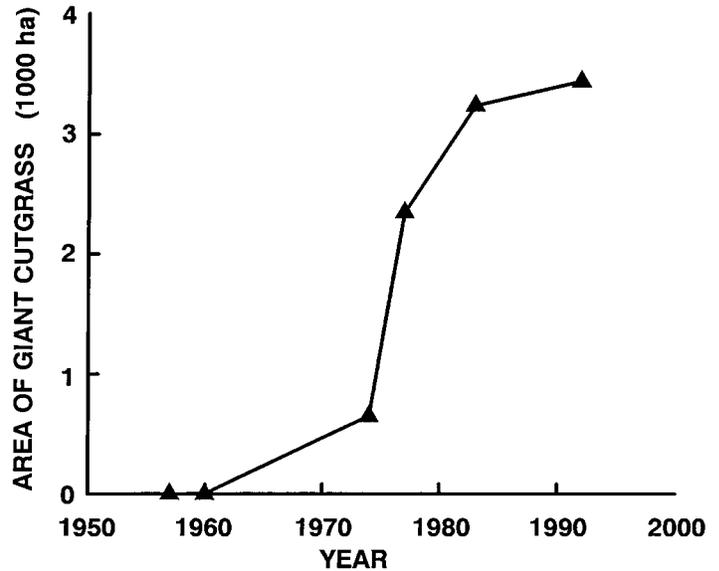


Figure 2. Changes in areal coverage of giant cutgrass in Lake Seminole since impoundment in 1957. Compiled from Gholson (1984a, 1984b) and 1992 estimate from Joe Kight (pers. comm.).

land by 2.0 ha in 4.25 years, producing a nearly 50% increase in island size (Figure 3).

By contrast, some waterbodies in Florida have long established populations of giant cutgrass that have not significantly expanded in area for many years. For example, Lake Alice is a 9 ha lake on the University of Florida campus in Gainesville, Florida. The lake receives secondary-treated wastewater which has passed through a 21 ha marsh on its east side (Korhnak 1996). Lake water is pumped into the Florida aquifer by two injection wells at the west edge of the lake, which are regulated to maintain water levels. Giant cutgrass first appeared in Lake Alice in the 1970s (W. T. Haller, pers. comm.) and the 3- to 10-m-wide fringe around the lake has not noticeably expanded in the 1980s.

Rapid stand expansion has been attributed to the production of 'stolons' or 'runners' up to 4 m long from which axillary shoots and adventitious roots develop (Steenis and Cottam 1945, Martin 1953, Kight 1980, Cutshall et al. 1989). A mechanism whereby decumbent flowering stems produce sequential inflorescences at their distal nodes to become functional stolons has been described (Fox and Haller 1990, Fox 1993). This process was observed to potentially expand the range of a stand by 2 to 3 m annually in shallow water conditions in Lake Seminole. Because the stability and local colonizing potential of a functional stolon is dependent upon the ability of adventitious roots at some nodes to become rooted in the substrate, a relationship between functional stolon length, adventitious root length, and water depth might be suggested.

The purpose of this study was to quantify a relationship between water depth and the colonizing potential of giant cutgrass. Specific objectives were to quantify rates of stand expansion over a two year period and compare these rates from two sites known to have contrasting histories of stand establishment, and to determine how environmental factors, such as water depth, influence these expansion rates. These

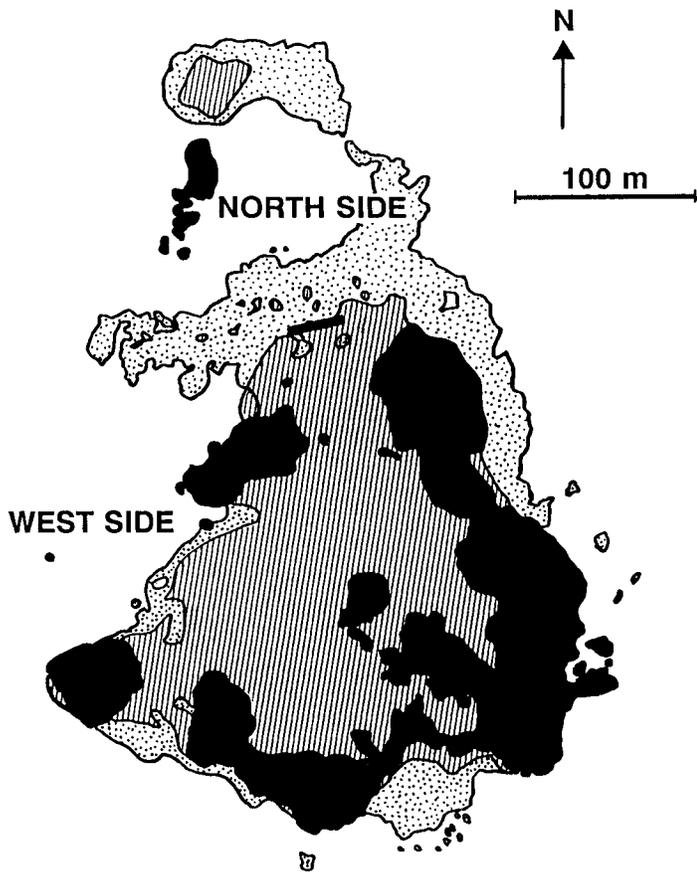


Figure 3. Map of Fox Island, Lake Seminole, compiled from aerial photographs showing tree cover (black shading; principally *Taxodium* sp.), island boundaries in 1986 (right hatch; principally *Zizaniopsis miliacea*, *Typha* sp., *Salix* spp. *Colocasia esculenta* (L.) Schott.), giant cutgrass expansion to 1990 boundaries (dots).

results would then be related to the long-distance dispersal of giant cutgrass, prediction of potential areas of giant cutgrass colonization within a waterbody, methods of controlling nuisance populations, and the suitability of this species for various types of revegetation projects.

MATERIALS AND METHODS

Five poly-vinyl-chloride (PVC) poles were permanently established in April 1989 around the south and west shorelines of Lake Alice and five each on the north and west edges of Fox Island (Figure 3). At approximately two month intervals throughout 1989 and 1990, a 4-m-wide baseline was established, centered on a PVC pole and parallel to the to the edge of the giant cutgrass stand (Figure 4). A 4-m-wide swath was then delineated lakeward from the baseline and perpendicular to the stand edge. Within this swath, the furthest shoot from the stand edge was determined, regardless of whether it was produced from a functional stolon node or rhizome. The distance from this shoot back to the baseline (perpendicular to the stand edge) was measured. If this shoot was rooted in the substrate, this counted as both the furthest shoot and the furthest rooted shoot. If it was not rooted, the same measurements were made at the shoot that

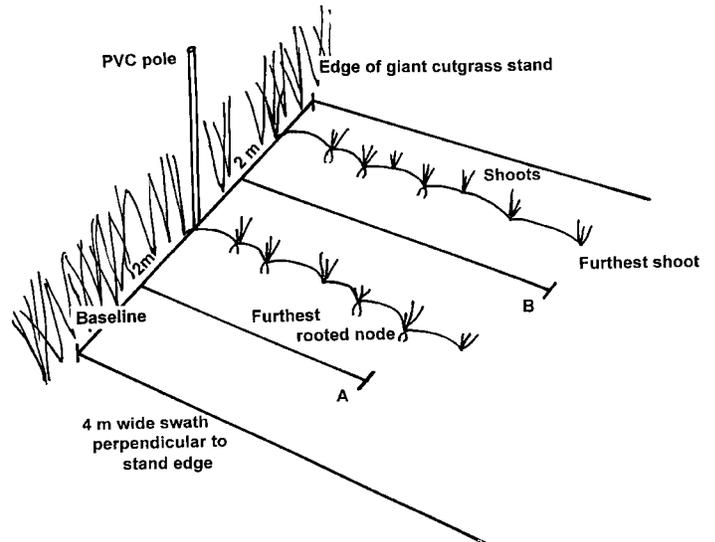


Figure 4. Diagram of how actual (distance baseline to A) and potential (distance baseline to B) stand expansion were estimated from permanent poles at the stand edge.

was rooted furthest from the stand edge. Water depth was measured at the furthest rooted node. These procedures were repeated at all PVC poles.

Actual stand expansion was calculated at any time by subtracting the distance to the furthest rooted node at the beginning of the study from the distance to the furthest rooted at the sampling time. Annual estimates of actual stand expansion were calculated by subtracting distances to the furthest rooted node at, or before, the beginning of the growing season from the comparable distance at, or after, the end of the year. No new nodes were observed on functional stolons after November or prior to May. Although the actual months in which these data were collected varied between sites and years, the latest sampling time between November and May was designated as the end of one growing season and the beginning of the next. In this study the 1989 and 1990 growing seasons were, respectively, April 1989 to November 1989; and November 1989 to February 1991 in Lake Alice. In Lake Seminole they were from April 1989 to February 1990; and February 1990 to February 1991. Of all distances from the baseline to the furthest node recorded during each year, the maximum value for each pole was designated as the potential stand expansion for that pole in that year. Analyses of variance (ANOVA) were applied to data on actual and potential stand expansion in all sites, and were applied to water depth data within each lake using SAS statistical programs (Littell et al. 1991).

RESULTS AND DISCUSSION.

Estimation of rates of stand expansion. Actual stand expansion during 1989 and 1990, as indicated by distances from the permanent pole baselines to the furthest rooted shoots, was much less in Lake Alice than in Lake Seminole (Figure 5). Annual changes in actual stand expansion were also estimated for each year (Table 1). Actual and potential stand expansion were both significantly less in Lake Alice than in

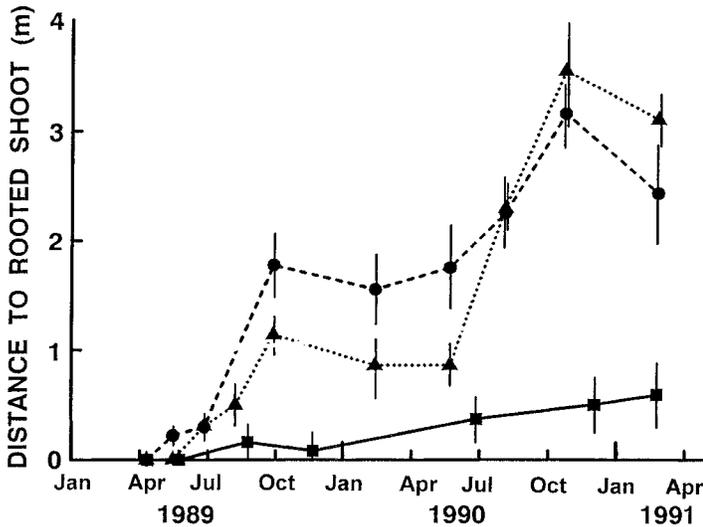


Figure 5. Estimates of actual stand expansion as indicated by distances from permanent poles to furthest rooted shoots in Lake Alice (solid line), west side of Fox Island (dashed line) and north side of Fox Island (dotted line). Error bars = ± 1 SE.

Lake Seminole (ANOVA of sites in Table 1). This correlates with the lower average number of functional stolon nodes that survived from one season to the next in Lake Alice compared to Lake Seminole (0.3 and 3.2 nodes, respectively from 1989, Fox and Haller, unpubl. data).

Although actual stand expansion appeared to be greater in Lake Alice in 1990 than in 1989 (51 cm and 8 cm, respectively), this difference was not significant, due to the great variation between replicates (Table 1). Potential for stand expansion was almost identical for the 2 years (1.04 m and 1.00 m in 1989 and 1990). When data from each year were analyzed separately, there were significant differences between actual and potential stand expansion in 1989 but not in 1990. This supports the hypothesis that actual expansion in 1989 was reduced from its potential by factors that influenced the rate of nodes becoming rooted in the substrate or likelihood of functional stolon detachment. Since only a single node was observed to become rooted in the substrate in Lake Alice in 1988 and none in 1989, out of approximately 20 plants tracked per year (Fox and Haller, unpubl. data), the very limited rate of stand expansion in 1989 is not surprising.

It is also possible that some stand expansion in Lake Alice resulted from shoots derived from rhizomes rather than rooted nodes, since shoot origins were not distinguished at this site. In Lake Seminole all of the furthest rooted shoots were identified as being attached to functional stolons, and so were derived from rooted nodes not rhizomes.

In Lake Seminole, actual stand expansion was greatest in late September to October of each year, declined slightly by February, and subsequently increased again with the next year's growth (Figure 5). As in Lake Alice, the potential for stand expansion appeared to vary less between sites and years than did actual stand expansion (Table 1), suggesting that factors influencing the ability of nodes to become rooted were perhaps more variable than the growth rates of the plants.

On the north side of Fox Island there was significantly greater actual stand expansion in 1990 than in 1989 (Figure 5) and actual stand expansion in 1989 was significantly less than its potential (Table 1). Quantitative data on node production collected from tagged plants in Lake Seminole showed that fewer nodes had roots and a lower percentage became rooted in 1989 than in 1988. One of the likely reasons for such annual differences in the ability of nodes to become rooted was that the water at the tagged plants was deeper in June/July 1989 than the maximum lengths of adventitious roots. Reductions in water elevations in September, which would have allowed nodes with roots to become rooted, were only temporary.

Node production data were not collected in 1990. However, water elevations in Lake Seminole during 1990 were on average significantly lower during the functional stolon growing season (May to November), and especially in the important rooting period of June/July, compared to 1989 (Table 2). ANOVA comparisons of water depths at the furthest rooted nodes also showed significantly shallower water in 1990 than 1989 (Table 2). Such reductions in water depth at the stand edge in 1990 are very likely to have allowed greater rooting of nodes in the substrate and hence the increased rate of actual stand expansion in 1990. This is supported by the fact that actual stand expansion was not significantly different from its potential in 1990, but was reduced from its potential in 1989 (Table 1).

On the west side of Fox Island annual differences were not significant (Table 1). These data are based on distances to furthest rooted nodes in February (the new stand edge for the following growth season). The reduced stand expansion

TABLE 1. ACTUAL STAND EXPANSION BY THE END OF EACH YEAR AND MAXIMUM POTENTIAL STAND EXPANSION IN 1989 AND 1990 IN LAKE ALICE, AND ON THE NORTH AND WEST SIDES OF FOX ISLAND IN LAKE SEMINOLE.

	Actual Stand Expansion (m)			Potential Stand Expansion (m)				
	1989	1990	Sites ¹	1989	1990	Sites ¹		
Lake Alice	8.0 a ²	— ³	51.0 b	I	104.0 A	—	100.0 b	I
North side	85.6 c	***	210.0 d	II	193.6 C	—	242.5 d	II
West side	155.0 e	—	88.0 f	II	209.0 e	—	172.0 F	II
Average all sites and years		95.8 z					167.7 Z	

¹Sites with same Roman numerals were not significantly different when compared by ANOVA averaged over both years.

²Comparisons were made by ANOVA between data with the same letter; data were not significantly different if same letter case.

³Comparisons by ANOVA within sites and between years; — = no significant difference, *** = significant difference between years.

TABLE 2. LAKE ELEVATIONS AND WATER DEPTH AT FURTHEST ROOTED NODE IN LAKE SEMINOLE. ELEVATIONS AND DEPTHS WITHIN EACH ROW ARE SIGNIFICANTLY DIFFERENT IN STUDENT'S T-TESTS.

	n	1989	1990
Lake water elevations (m)			
Annual average	365	23.48	23.42
Growing season (May to November)	214	23.51	23.37
June + July	61	23.58	23.31
Water depth at furthest rooted node (cm)			
Annual average (north and west sides) ¹	40	54.4	43.4
August average (north side only)	5	55.0	33.2
		North	West
All sampling times average ¹	40	52.6	45.2

¹Unmatched data from west side in August 1989 omitted.

in 1990 compared to 1989 actually arises because of a substantial loss in distance to the furthest rooted node between October 1990 and February 1991 (Figure 5). This reduction is greater than for the north side or preceding year. Had this reduction been similar to the preceding year, or that observed on the north side, the overall annual rates of stand expansion on the west sides of Fox Island would have been closer for the two years (Figure 5).

The question still remains as to why annual differences in stand expansion on the north side of Fox Island correspond to changes in water elevation in Lake Seminole but stand expansion on the west side of the Island appears to be unaffected by water depth? Water depths measured in the stand expansion study have to be compared with caution because for each pole they were measured at different places each sampling time, wherever the furthest rooted shoot occurred. Thus, both temporal variations in lake water elevations and spatial variations in the position of the furthest rooted shoot are included in these water depth data.

When average water depths at the furthest rooted shoots were compared by ANOVA, water depths were found to be 7.4 cm deeper on the north side compared to the west (Table 2). As small as this difference between the sides may seem, it may have been important in relation to the significant average difference in water depth between 1989 and 1990 of 11 cm (Table 2). Thus, perhaps the shallower west side would not have been as affected by the rise in water levels in 1989 as was the north side. In August, a critical time for the rooting of nodes in the substrate, the annual difference on the north side was 21.8 cm. Data were not collected on the west side in August 1989.

Relationship between water depth and stand expansion. To investigate the relationship between water depth and stand expansion in more detail, water depths at the furthest rooted node were averaged for each pole over all sampling times, and this value was regressed against the distance to the furthest rooted node at the final sampling time in February 1991 (Figure 6). The regression coefficient (r^2) for Lake Alice data was 0.93, showing a strong relationship between water depth and stand expansion. The x intercept indicated that stand expansion in Lake Alice would not occur in water deeper

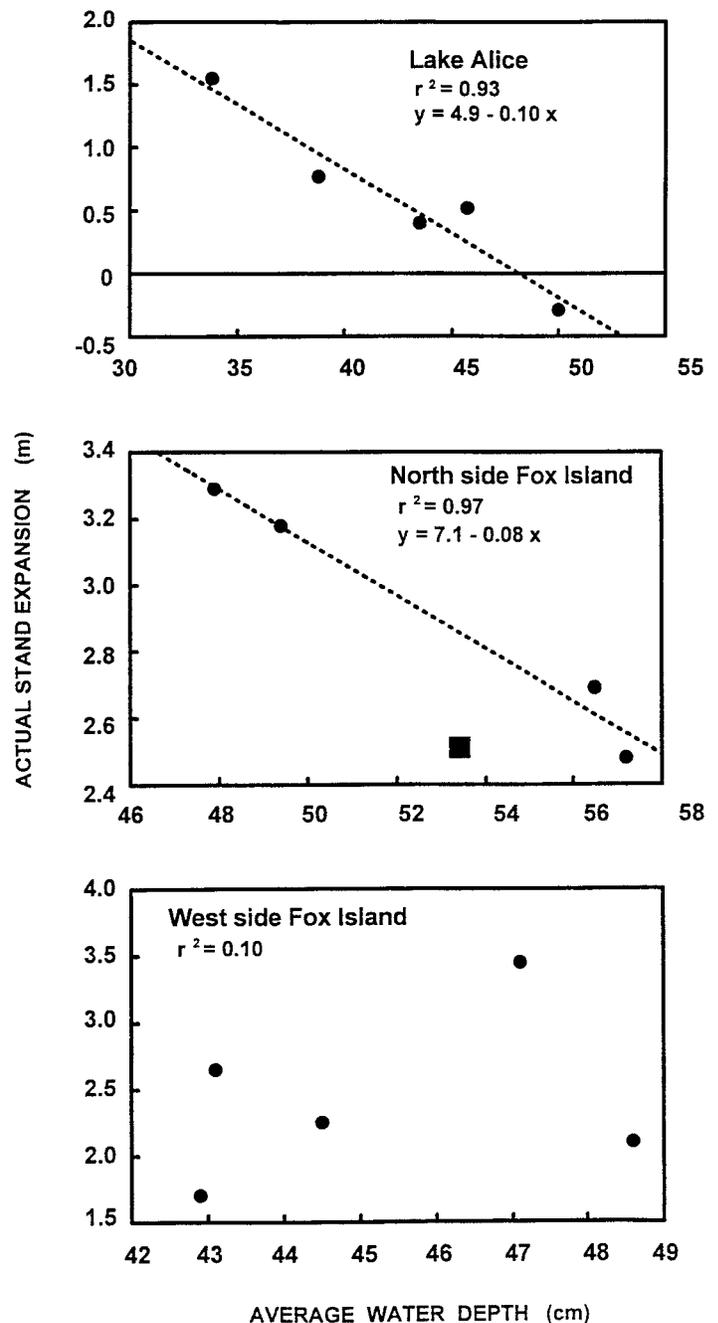


Figure 6. Regression of actual stand expansion by February 1991, against average water depth at the furthest rooted shoots for Lake Alice, North side of Fox Island, and west side. (Square symbol = Pole No. 4 which was excluded from the regression on the north side of Fox Island).

than 48.2 cm (Figure 6a). This depth is 1.7 times the maximum adventitious root lengths measured in Lake Alice in 1989 (29.6 cm; Fox and Haller 2000a). Several factors could account for this discrepancy. 1) Root lengths measured in 1989 could have been underestimated; 2) the root length/water depth relationship depends upon minimum water depths in June-October (when most nodes will have roots) rather than annual or growing season averages; 3) some, or all, furthest rooted shoots in Lake Alice arose from rhizomes

rather than from axillary shoots, and the production or survival of shoots from rhizomes is also influenced by water depth. Whichever of these factors may be influential, these data indicate a relationship between stand expansion and water depth at the limiting depths for stand expansion in Lake Alice and this explains why giant cutgrass has maintained a stable fringe around the lake, given the relatively stable water levels maintained in this system.

Data from only four poles on the north side of Fox Island were used for the water depth/expansion regression because by August 1990 the plants associated with one pole (No. 4) had met plants growing from an opposite stand edge. By the following February it was difficult to be sure where the furthest rooted shoot from the pole side was, and the measurement made here was most likely an underestimate (Figure 6b; 1990 data from this pole were omitted from all other analyses). Regression of data from the remaining poles had an r^2 value of 0.97 and an x intercept of 89 cm of water depth (Figure 6b). Again, this potential depth for the limit of stand expansion was considerably greater than the maximum lengths of adventitious roots measured in 1989 (46.5 cm; Fox and Haller, unpubl. data). The first two possible explanations listed above for Lake Alice may relate to this discrepancy, especially since the average water depths for all plants on the north side of Fox Island were greater than the measured root lengths and yet significant stand expansion continued. Also, the relationship between water depth and stand expansion may not remain linear in water depths greater than those measured here, so the x intercept cannot be used with great confidence.

Although regression equations for Lake Alice and the north side of Fox Island had different y intercepts (Figure 6a and b), a statistical test comparing the slopes (Mead and Curnow 1983) showed that these were not significantly different. Thus, regression lines from the two lakes were parallel and indicated that, within certain limits along gradually sloping shorelines, a 10 cm reduction in average water depth at the plant base could result in approximately 1 m increase in stand expansion.

These correlations showed that there was a relationship between water depth and stand expansion within, and between, sites. However, differences in the water depths at which no expansion was predicted (x intercepts) suggested that other factors were important in determining the maximum depth of water into which expansion could occur at each site. In addition to the longer adventitious roots observed in Lake Seminole, the PVC poles on the north of Fox Island tended to be at sites sheltered from wave action and floating debris (Figure 3). Sites in Lake Alice were prone to both wave damage and floating material, especially rafts of broken giant cutgrass stems which can form in mid-summer and are blown around the lake.

Data from the west side of Fox Island did not show a clear correlation between water depth and maximum stand expansion (Figure 6c). This was probably because of differences between the poles in exposure to the open water and prevailing winds (southwesterly in summer and northwesterly in winter). The shallowest pole (No. 3) had the least expansion but was in an exposed position, while one of the deeper poles (No. 5), which was sheltered from wave action, showed the greatest expansion (Figure 6c). Thus, in this area if water

depths are not deep enough to limit the ability of axillary shoots to root in the substrate (water depths for most poles were less than the average adventitious roots lengths) it may be that exposure of functional stolons to damage has greater influence over stand expansion. This may also explain the lack of significant differences in actual stand expansion between 1989 and 1990 on the west side (Table 1), despite annual differences on the north side that appeared to relate to differences in lake water elevations between these years.

Indices can be devised to estimate exposure of shorelines to wind action and wave fetch and these might be useful in comparing overall stand expansion rates at different sites. The exposure of individual plants to damage from waves and floating debris, however, is difficult to quantify, and can vary throughout the season as neighboring plants expand to provide shelter. In general the west side of Fox Island was more exposed to prevailing winds and hence wave action, than the north of the island (Figure 3) which was evidenced by tagged plants being lost on the west side in 1988 due to coverage by piles of uprooted hydrilla (*Hydrilla verticillata* (L.f.) Royle) or damage from floating logs. Although plants were less exposed on the north side, it is not possible from these data to quantitatively distinguish between influences of exposure and slight differences in water depth on these two sides of Fox Island. It is likely that both of these factors are important and that they interact, since plants that can more readily root in the substrate in shallow water will be able to survive greater exposure than plants that struggle to root in deeper water.

Prediction of potential areas for giant cutgrass colonization. Stand expansion resulting from axillary shoots produced on functional stolons appears to be limited by summer water depths. The limiting depth at a particular site is influenced by exposure to wave action and other mechanical stresses that would tend to break the flowering stem prior to the rooting of its nodes in the substrate. Maximum length and rate of adventitious root growth, which can vary with environmental conditions and plant populations, will interact with water depth and plant exposure. Such site-specific variables make generalized predictions of potential stand expansion difficult and inaccurate. Knowledge of summer water depths, extent of exposure to mechanical stresses, and adventitious root growth potential for plants in a given waterbody, however, should allow fairly accurate predictions of stand expansion to be made there.

Of these three factors, estimates of exposure to waves and floating debris are likely to be the most difficult to evaluate. The influence of these factors should be indicated by one growth season's observations of node and secondary flower production (c.f., Lake Alice compared to Lake Seminole). Changes in plant exposure may occur over time, resulting from variations in wind conditions or growth of surrounding vegetation. Shelter could be afforded by other parts of a giant cutgrass stand, by other emergent species, or by the effects of submersed plants in reducing wave action.

The extent of stand expansion will vary annually, chiefly depending upon the frequency of low summer water levels. Thus, stands in a site such as Lake Alice that have shown little expansion for many years, could suddenly enlarge if water levels in the critical month or two after flowering were unusually low, especially if coincident with reduced wave action.

The effects of exceptionally low summer water levels are not restricted to contiguous lateral stand expansion. Floating sections of giant cutgrass stems that have broken from a parent plant can become rooted during low water conditions at a site that would usually be too deep for such colonization. Once rooted and sufficiently established, such a plant may survive long periods of higher water levels without much change in lateral size. Clump size would increase by rhizome growth or by the rooting of nodes during subsequent summers with low water levels.

An isolated giant cutgrass plant of this type was photographed for a period of two years on the east side of Fox Island. Growing in water that was typically 1.2 to 1.3 m deep, this plant produced several flowering stems, nodes, and secondary flowers each summer. None of the adventitious roots grew long enough to reach the substrate in 1988 or 1989 and eventually the flowering stems broke off, so that only a few leaves (mostly submersed) survived each winter. During the summer this plant was surrounded by dense hydrilla, protecting it from wave action. The hydrilla died back far enough during winter to not shade the submersed giant cutgrass leaves prior to the regrowth of emergent leaves in the spring.

This plant was able to survive in water deeper than the commonly cited maximum depth for giant cutgrass growth of 1 m (Steenis and Cottam 1945, Martin 1953, Smart and Barko 1982) for several reasons. It was protected from mechanical stresses by hydrilla, water temperatures did not fall so low as to kill the plant back to the rhizome in winter, and water was clear enough to allow regrowth in the spring which was not necessarily totally dependent upon rhizome energy reserves. Under such conditions, areas of Lake Seminole over 1 m deep have the potential to be colonized by giant cutgrass if individual plants become established there during summers with exceptionally low water levels.

Stand expansion resulting from only lateral rhizome growth will not be as dependent upon low summer water levels and shelter from mechanical stresses. Water depth will be limiting if shoots from the rhizome cannot reach sufficient light for photosynthesis prior to exhaustion of rhizome energy reserves (i.e., depth will be more limiting in turbid water).

In view of the lake sites studied, these discussions are inevitably limited to the consideration of non-tidal habitats. How daily variations in water level experienced in tidal marshes influence the rooting of axillary nodes is not evident from these studies nor the literature. The daily occurrence of low water levels may either increase the likelihood that axillary shoots could root, or the stresses of daily water level fluctuations may encourage stem fracture and the production of floating stem fragments. Since giant cutgrass commonly occurs in, or is being transplanted to, tidal marshes (Odum et al. 1983, Good 1989), this is an important question worthy of further investigation.

Water level management of giant cutgrass. The expansion of giant cutgrass stands could be limited in regulated waterbodies by the manipulation of water levels. High water levels in summer would prevent axillary shoots from taking root, resulting in the eventual breakage and loss of flowering stems. This technique was reported to be quite effective in Reelfoot Lake in the 1940s (Steenis and Cottam 1945). In addition, high water levels in winter appear to encourage flower for-

mation and reduce rhizome growth (Fox and Haller, unpubl. data). A strategy of maintaining high water levels in winter and summer could only be used in sites where the production of floating stems fragments, or seeds, is not likely to increase giant cutgrass dispersal to new areas for colonization (i.e., in an isolated waterbody with no uncolonized shallow shoreline). If downstream dispersal in the watershed is a potential problem, then low water levels in winter would reduce flower production and hence reduce potential floating functional stolon sections during summer, but possibly at the expense of encouraging shoot production from rhizomes (Fox and Haller, unpubl. data).

In reality, there are few sites in which such complete water level manipulation would be possible and even less in which it would be practical. In some regulated systems, however, a degree of water level manipulation could be combined with other management methods. For example, raising water level after late summer herbicide use or cutting was found to reduce regrowth from rhizomes (Steenis 1950, Birch and Cooley 1983).

While these studies have not specifically addressed the use of herbicides and cutting as control methods for giant cutgrass, some of their conclusions can be related to management priorities. If the expansion of existing giant cutgrass is to be prevented in a waterbody, then control of plants growing in shallow, sheltered areas should be of high priority. If the dispersal of floating stem fragments to uncolonized areas is to be prevented, then early season control of flowering plants in deeper and more exposed sites should take precedence.

Long-distance dispersal of giant cutgrass. The dominant role of vegetative reproduction in the propagation and expansion of giant cutgrass, is typical of many aquatic plant species (Grace 1993). In addition to rapid stand expansion by functional stolons, longer-distance dispersal of axillary shoots that break and float away from the parent plant may be significant within a waterbody or watershed. The perenniating function of the rhizomes allows giant cutgrass to survive temporary adverse above-ground conditions. Creeping rhizome growth enables stand expansion and consolidation to continue even under conditions that are not favorable to flower formation or the rooting of axillary shoots.

It should be acknowledged that the importance of sexual reproduction in the field has not been thoroughly investigated, but it has been shown in the laboratory that giant cutgrass seeds can germinate in both moist and submersed conditions (Holmes and Stalling 1991). Redwing blackbirds and waterfowl have been reported to feed on giant cutgrass seeds (Steenis and Cottam 1945), which could aid its dispersal, but only occasional observations of seedling growth, always on exposed mud flats, have been recorded (Steenis and Cottam 1945, Smart and Barko 1982). Seedlings were never observed on Fox Island nor in Lake Alice during these studies. Naturally-shed seedlings were observed on exposed mud in an experimental pond when water levels were unusually low in July 1988, but less than 3% survived until the following growing season.

Although over 3,000 seeds can be produced from each inflorescence, their total weight is less than 10 g. The biomass of a single flowering stem comprises approximately 19% of

the total biomass of a typical giant cutgrass plant (excluding roots). However, since all of this stem except the seed head itself can contribute to vegetative propagation, less than 4% of the total biomass of a plant is dedicated to sexual reproduction. Thus, it appears that seedling production may be important when giant cutgrass stands are exposed to specific environmental conditions or after avian dispersal of seeds, but only a small proportion of plant resources are allocated for these possibilities and such proliferation has rarely been observed.

Little is known about how giant cutgrass is disseminated over long distances, particularly between watersheds. It is certainly not as wide-spread as highly fecund plants with wind dispersed seed, such as *Typha* spp., and the occurrence of giant cutgrass in a wide variety of habitats indicates that it is not as likely to be limited by environmental conditions as it may be by its ability to reach new sites.

Revegetation using giant cutgrass. The ability of robust plants of giant cutgrass to develop from axillary shoots on single flowering stem nodes (as was seen in the experimental tanks by Fox and Haller 2000b) is of great value to revegetation projects. By eliminating the need to germinate seeds and establish seedlings, or to dig up rhizomes, the timing and cost of transplantation can be much reduced. If new transplants can be protected from wave damage, competition and herbivory, then this species is a good candidate for providing a hardy fringe of emergent vegetation that can stabilize shorelines and reduce erosion.

Such fringe development is most likely along shorelines with steep drop-offs, an extreme example being plants found along the banks of canals south of Lake Okeechobee, Florida. Because of the disadvantages of low species diversity and increased sediment deposition associated with dense stands of giant cutgrass, extreme caution should be used in shallow sites where, once established, giant cutgrass could expand rapidly, should low water levels and reduced exposure occur.

It should not be assumed that because vegetation is needed to stabilize a shoreline, the erosive forces will always be maintained to keep the spread of giant cutgrass in check. Subsequent invasion of a canopied submersed species, such as hydrilla or Eurasian watermilfoil (*Myriophyllum spicatum* L.) could dampen wave action sufficiently to reduce breakage of horizontal flowering stems prior to rooting. Until more is known about the influence of tidal water level fluctuations on the rooting of axillary shoots, it cannot be assumed that stand expansion by flowering stems is necessarily limited in tidal marshes.

Perhaps of greater concern should be the potential consequences if giant cutgrass is to be distributed to new sites. If plants can be established in erosive sites there is a high likelihood that floating stem fragments with viable shoots will be detached and dispersed to other parts of the waterbody, or to other waterbodies downstream (Holmes and Stalling 1990).

If long-distance dispersal is the weakest element of the reproductive biology of giant cutgrass, then more frequent transplantation of this species to new watersheds by human activities could significantly increase its rate of dissemination. As the number of watersheds containing giant cutgrass increases so will the chance that some sites will develop nuisance populations. Thus, the reproductive biology of giant

cutgrass that makes it such a successful vegetative colonizer of waterbodies, and hence an attractive revegetation tool, must also be carefully considered with respect to the possible infestation of adjoining non-target sites.

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