

Seasonal Biomass and Starch Allocation of Common Reed (*Phragmites australis*) (Haplotype I) in Southern Alabama, USA

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Common reed (*Phragmites australis*) is a nonnative invasive perennial grass that is problematic in aquatic and riparian environments across the United States. Common reed often forms monotypic stands that displace native vegetation which provide food and cover for wildlife. To help maintain native habitats and manage populations of common reed in the United States, an understanding of its life history and starch allocation patterns are needed. Monthly biomass samples were harvested from sites throughout the Mobile River delta in southern Alabama, USA from January 2006 to December 2007 to quantify seasonal biomass and starch allocation patterns. Total biomass of common reed throughout the study was between 1375 and 3718 g m⁻² depending on the season. Maximum aboveground biomass was 2200 ± 220 g m⁻² in October of 2006 and 1302 ± 88 g m⁻² in December of 2007. Maximum belowground biomass was seen in November of 2006 and 2007 with 1602 ± 233 and 1610 ± 517 g m⁻² respectively. Biomass was related to ambient temperature, in that, as temperature decreased aboveground biomass ($p = 0.05$) decreased. Decreases in aboveground biomass were followed by an increase in belowground biomass ($p < 0.01$). Starch comprised 1 to 10% of aboveground biomass with peak temporary storage occurring in July and August 2006 and September to November of 2007. Belowground tissues stored the majority of starch for common reed regardless of the time of year. Overall, belowground tissues stored 5 to 20% of total starch for common reed with peak storage occurring in December 2006 and October 2007. Starch allocation to belowground tissues increased as temperatures decreased. Understanding seasonal life history patterns can provide information to guide management strategies by identifying the vulnerable points in biomass and starch reserves in common reed.

Nomenclature: Common reed, *Phragmites australis* (Cav.) Trin. ex Steud PHRCO.

Key words: Carbohydrate, invasive species, life history, haplotype.

Common reed [*Phragmites australis* (Cav.) Trin. ex Steud.] is an invasive aquatic and riparian grass that is expanding throughout the continental United States. This expansion has been attributed to multiple introductions of a nonnative strain from Europe in the late 1700s (Saltonstall 2002) as well as anthropogenic effects (Roman et al. 1984), and hyper-eutrophication of wetland habitats (Chambers et al. 1999). Multiple introductions of common reed over the last 200 years have resulted in a

loss of native common reed and an increase in nonnative haplotypes (Saltonstall 2002). Of the 29 total haplotypes of common reed identified throughout the world (Saltonstall, personal communication), thirteen are native to North America; five of these are native to the northeastern portion of North America. Haplotypes I and M are the most abundant throughout the United States (Saltonstall 2002).

Haplotype I is thought to have originated from South America and parts of Asia and is the most prevalent haplotype along the Gulf Coast of the United States (Hauber et al. 1991; Saltonstall 2002). Haplotype I is unique in that previous studies have found evidence of its presence along the Gulf Coast since the late 1800s (Saltonstall 2002). Genetic analysis of both pre-1910 herbarium samples as well as current samples indicate genetic autonomy as well as geographic isolation of this haplotype along the Gulf Coast of the United States (Hauber et al. 1991; Pellegrin and Hauber 1999; Saltonstall 2002) from all other populations of common reed

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Management Implications

Common reed is an invasive grass that continues to spread across the United States. The genetic haplotype I is the dominant form of this species along the Gulf Coast of the United States. During this two year study, common reed biomass fluctuated seasonally, though maximum biomass exceeded 3700 g m^{-2} . Biomass allocation was influenced by seasonal temperatures in that aboveground biomass peaked in early fall, followed by a peak in belowground biomass. The peak in belowground biomass allocation corresponded to increased starch allocation to underground tissues. Understanding these seasonal life history patterns can provide information to guide management strategies by identifying the vulnerable points in biomass and starch reserves in common reed. Based on these data it may be beneficial to implement management techniques in early spring when starch reserves in belowground tissues are being used to support shoot growth. Aboveground biomass during this time would be reduced as plants would be small, and therefore, may be more susceptible to management.

in North America. In addition, haplotype I's introduction to North America is unclear as its closest taxonomic relative is only found in Asia, and it could be possible that haplotype I is originally from Asia (Saltonstall 2002).

Taxonomically, common reed is a perennial, rhizomatous monocot from the Poaceae family (Clayton 1967). Common reed is described as a tall, coarse perennial with stout rhizomes, deeply seated in the substrate (Godfrey and Wooten 1979). In general, aboveground growth begins in the spring when soil and ambient temperatures trigger growth from belowground tissues. Growth continues throughout summer until seed set, after which plants begin to senesce during fall and shift resources to belowground tissues. By winter, in most temperate locations, aboveground biomass is gone with the exception of dead culms. The rhizomes of common reed function as the primary means of reproduction (Kilmeš et al. 1999) and serve as a storage organ for total nonstructural carbohydrates (TNC) and water soluble carbohydrates (WSC) (Fiala 1976; Kilmeš et al. 1999). However, seasonal allocation patterns of biomass and carbohydrates have not been well established for this species or haplotype and phenological studies are needed.

An understanding of the phenological patterns of a target plant can identify optimum times during the plant's life cycle in which to apply management techniques for the most efficacy. Phenological studies of alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb], waterhyacinth [*Eichhornia crassipes* (Mart.) Solms], Eurasian watermilfoil [*Myriophyllum spicatum* L.], hydrilla [*Hydrilla verticillata* (L.f.) Royle], curlyleaf pondweed [*Potamogeton crispus* L.], Brazilian elodea [*Egeria densa* Planch.], and parrotfeather [*Myriophyllum aquaticum* (Vell.) Verdc.] have all examined carbohydrate allocation patterns, and suggest that increases in management efficacy can be achieved by timing management to low

points of carbohydrate availability during a plant's life cycle (Madsen 1993, 1997; Madsen and Owens 1998; Pennington and Sytsma 2009; Weldon and Blackburn 1968; Wersal et al. 2011; Woolf and Madsen 2003). Therefore, the objectives of this study were to: (1) document phenology (biomass allocation) over a 2-yr period as it related to temperature and plant tissues, and (2) quantify seasonal starch allocation patterns within above and belowground tissues of common reed.

Materials and Methods

Seasonal Biomass Collection. The study was conducted in the Mobile-Tensaw River Delta, near Mobile, AL from January 2006 through December 2007. All common reed harvested during this study was haplotype I as determined by PCR-RFLP assays (Cheshier et al. 2012). Forty eight biomass samples were taken monthly from four sites (12 samples per site, $n = 1152$) located throughout the Mobile River Delta. The four sites were Polecat Bay ($30^{\circ}42'36''\text{N}$, $88^{\circ}0'40''\text{W}$), Crab Creek ($30^{\circ}43'49''\text{N}$, $87^{\circ}58'32''\text{W}$), Graving Island ($30^{\circ}46'36''\text{N}$, $87^{\circ}55'34''\text{W}$) and Sardine Pass ($30^{\circ}40'13''\text{N}$, $87^{\circ}56'11''\text{W}$). Biomass samples were randomly collected using a 0.1 m^2 (31.5 cm by 31.5 cm) PVC quadrat (League et al. 2006). The quadrat was constructed so that one side could be removed to allow it to slide around plants prior to harvesting. The side that was removed was reattached to complete the sampling square. The area inside the quadrat was harvested by cutting aboveground biomass at the sediment line. Belowground biomass was harvested by digging sediment from the quadrat to a depth of 30 cm to collect roots and rhizomes (Cížková et al. 2001; League et al. 2006). Belowground biomass refers to all underground plant tissues (rhizomes and roots) as no differentiation was made during collection or processing.

Above- and belowground tissues were put into appropriately labeled mesh bags and transported to Mississippi State University for processing. Aboveground plants were washed and cut to fit into paper bags for drying. Belowground samples were washed to remove sediment and to collect plant tissues for each sample. All plant tissues were dried at 70 C (158 F) for 72 h to determine dry mass. Temperature data for the Mobile, AL, area were obtained from the National Oceanic and Atmospheric Administration during each sampling event to relate plant growth with temperature.

Starch Determination Procedure. Biomass harvested during the life history evaluation was used to assess seasonal starch allocation in common reed. For each set of 12 samples at each location in a given month, and for both above and belowground tissues, dried biomass was combined into three bulked samples comprising four

samples each (i.e. life history biomass samples one through four were combined into tissue sample one, and so on). Combining samples ensured that adequate tissue mass was available for analytical techniques, and reduced the number of tissue analyses required (Wersal et al. 2011; Woolf and Madsen 2003). Bulked samples were stored in paper bags at room temperature until all biomass sampling had concluded.

Beginning in May 2008, the bulked samples were sent through a commercial shrub chipper to break down the large biomass samples into smaller pieces. The chipped samples were then ground using a Cyclone Sample Mill (UDY Corporation, Fort Collins, CO) to pass through #40 mesh screen (0.42 mm). Approximately 100 mg of the ground sample was transferred into plastic whirl-pak bags for storage at room temperature and preparation for starch analysis. Starch extraction and determination began in January 2009 and was conducted using the STA20 starch assay kit (Sigma Aldrich, St. Louis, MO) (Wersal et al. 2011). A total of 576 samples were assayed for starch content. Duplicate samples were included to monitor assay precision. Standard curves were also developed to ensure that our starch data were within the range of what the kits could detect, and to assess the relative accuracy of our data. The precision of our assays as determined by the percent difference of our duplicate samples was 11.3%. Accuracy as determined by our standard curves was $\pm 1\%$ ($r^2 = 0.99$).

Data Analysis. Mean biomass values for above and belowground tissues were determined for each site and month, and were combined for analyses. A three point moving average was calculated by taking a biomass value in the series of values with the previous and next number in the series and averaging the three of them. The moving average was then shifted until averages for the entire study period were calculated. For example, a series could include 100, 200, 300, 400, 500, and 600; the first average would include the numbers 100, 200, and 300, the second average would include 200, 300, and 400 until all averages are computed. A three point moving average was used to reduce variability of mean biomass data over time to better show seasonal trends. Data were analyzed by fitting mixed models using the Mixed Procedure in SAS (SAS Institute, Inc., Cary, NC) to determine potential relationships between ambient temperature and above and belowground biomass of common reed (Littell et al. 1996; Wersal et al. 2011). Above- and belowground biomass were included as dependent variables. Ambient temperature and year were included as the independent variables in all models. Site and site-year interaction terms were included as random effects in the model to account for their influence on the results. All terms included in the analyses were linear. Data are reported as means (± 1 SE) and analyses were conducted at a $p \leq 0.05$ significance level.

Results

Biomass of common reed was greater in 2006 than in 2007 ($p < 0.01$). Total biomass of common reed throughout the study was between 1375 and 3718 g m^{-2} depending on the season. Maximum aboveground biomass was $2200 \pm 220 \text{ g m}^{-2}$ in October of 2006 and $1302 \pm 88 \text{ g m}^{-2}$ in December of 2007 (Figure 1). Aboveground biomass constituted 36 to 62% of the total biomass of common reed depending on the season. Maximum belowground biomass was seen in November of 2006 and 2007 with 1602 ± 233 and $1610 \pm 517 \text{ g m}^{-2}$ respectively (Figure 1). Belowground biomass constituted 37 to 63% of total common reed biomass depending on the season.

Low points in above and belowground biomass occurred from March to May in both years. Biomass was related to ambient temperature, and as temperature decreased aboveground biomass decreased followed by an increase in belowground biomass. In general, there appears to be a lag in aboveground biomass production that corresponds to a peak in temperature. That is, when ambient temperature peaked in July and August it was followed by a peak in common reed aboveground biomass.

Starch content in aboveground tissues followed a similar trend as biomass. Aboveground tissues were comprised of 1 to 10% starch with peak storage occurring in July and August 2006 and September to November of 2007 (Figure 2). The later peak in 2007 may have been because of warmer temperatures observed later in the year (Figure 2). Ambient temperatures in 2006 began to decrease rapidly in September, whereas, temperatures in 2007 remained warmer until November (Figure 2) This could have been enough to prolong common reed growth and shift life history stages later in the growing season. In general, peaks in starch storage occurred prior to common reed attaining maximum aboveground biomass. Belowground tissues stored the majority of starch for common reed regardless of the time of year. Overall, belowground tissues stored 5 to 20% of total starch for common reed with peak storage occurring in December 2006 and October 2007, which also corresponded to maximum belowground biomass.

Discussion

Previous research has demonstrated high variability in common reed biomass (Rolletschek and Hartzendorf 2000; Rolletschek et al. 1999); however, biomass values in this study were similar to those found by Soetaert et al. (2004). Biomass, most notably aboveground, was influenced by ambient temperatures throughout the year most likely as a cue to begin senescence during the fall or to begin growth in the spring. This is supported by the lag in aboveground biomass production with respect to ambient temperature,

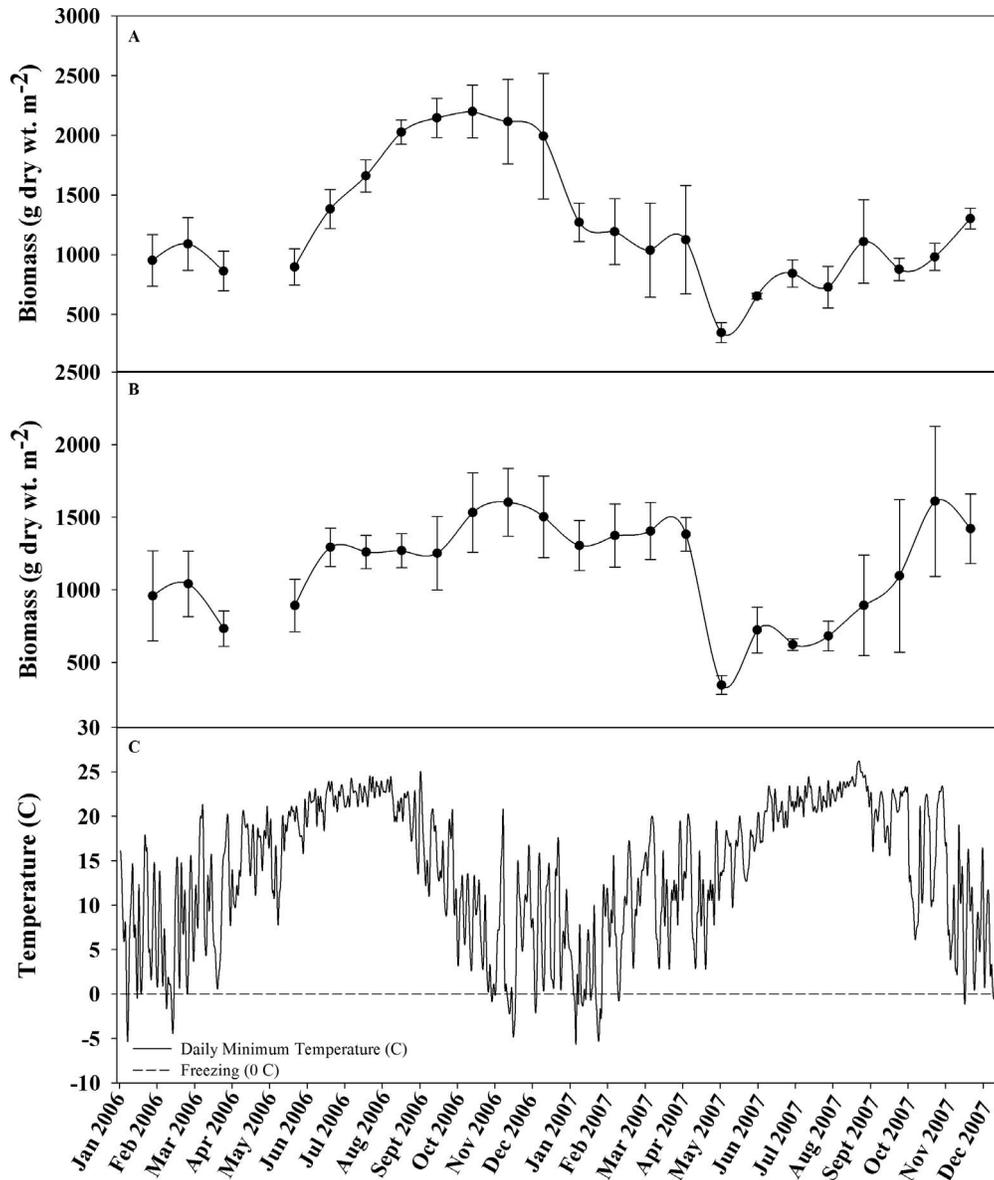


Figure 1. Mean (\pm 1SE) aboveground biomass (A), mean (\pm 1SE) belowground biomass (B) of common reed, and ambient temperature (C) collected in the Mobile River Delta, AL during 2006 and 2007.

though other factors undoubtedly influence the phenology of common reed. In fact, salinity can affect common reed growth, in that salinity levels approaching 22.5% of sea water can cause complete mortality of seedlings (Lissner and Schierup 1997). Flooding duration has also been examined in Europe and the United States and have demonstrated some reductions in common reed colonization, seedling survival, and overall biomass if water levels are maintained at least 10 to 20 cm over the existing water table (Cross and Fleming 1989; Hellings and Gallagher 1992; Mauchamp et al. 2001).

In addition to variable biomass production, carbohydrate allocation patterns in common reed can be affected

by plant age, nutrients in the sediment, location, trophic status, and time of year (Čížková and Bauer 1998; Čížková et al. 1996; Fiala 1976; Kilmeš et al. 1999; Tylová et al. 2008). Total carbohydrates within common reed tend to decrease during spring growth, sometimes by as much as 60% (Čížková et al. 2001), then rapidly increase from July to September, and then decrease again during winter (Asaeda et al. 2006; Čížková et al. 1996, Čížková et al. 2001; Granéli et al. 1992). In some instances, the carbohydrate reserves were restored as early as June (Granéli et al. 1992). In the populations of common reed sampled in the Mobile River Delta, greater than 80% of the total aboveground starch content was achieved by

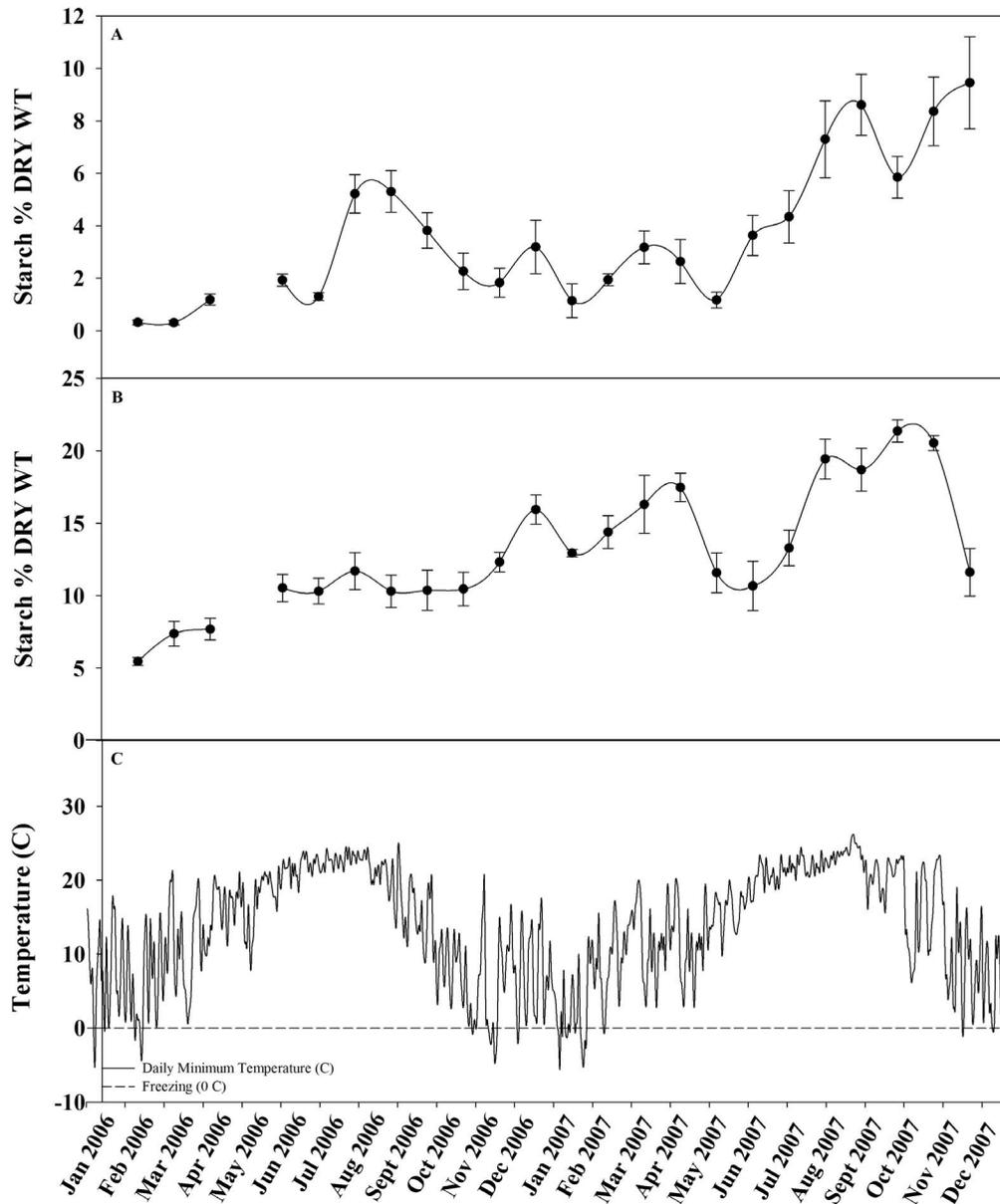


Figure 2. Mean (\pm 1SE) aboveground percent starch (A), mean (\pm 1SE) belowground percent starch (B) of common reed, and ambient temperature collected in the Mobile River Delta, AL during 2006 and 2007.

August 2006 and September 2007 respectively, which corresponds to patterns observed in previous studies. Belowground starch allocation peaked after aboveground biomass senesced and represents a shift in resource allocation to belowground tissues.

Common reed growth is related to ambient temperature as shown by both biomass and starch concentrations in this study, though other factors such as salinity, nutrient availability, inundation duration, and sediment will also influence growth. Aboveground biomass was present throughout the year albeit at reduced levels over winter. This is due in large part to the location where the plants are growing. Although, minimum temperatures did go below

freezing a few times during the winter months, there was never a prolonged period of freezing temperatures to cause complete plant mortality. It is not uncommon in the Mobile Bay area to see daytime temperatures during winter months exceed 25 C. Given the higher daytime temperatures and bare mudflats where these plants are growing, there are likely increases in soil temperature and an insulating effect from the water as tides come in to keep plants growing through winter; however, additional studies are needed to confirm this.

Starch was predominately stored in belowground tissues, though temporary storage in stems and leaves can be as much as 10%. Reductions in carbohydrate concentrations

in aquatic plants in temperate regions typically occur during spring regrowth when plants are relying on stored energy to initiate growth of plant tissues until photosynthesis can begin (Madsen 1997). Understanding the seasonal variation in biomass and starch allocation of common reed may serve as a vital tool for long-term management.

Current management strategies include applying herbicides in the fall in an attempt to get better translocation of the herbicides into belowground tissues as common reed reallocates its resources from aboveground to belowground tissues. However, there are concerns with herbicide coverage and plants being missed during fall applications, as common reed biomass and stem densities are typically higher during this time as opposed to spring. Management during the early spring and summer (March through June) could target low points in starch reserves in common reed, and target smaller plants. Pursuant to this, it was reported that applications of glyphosate and imazapyr can be made earlier in the season when common reed is shorter and easier to spray and still maintain the same level of efficacy as observed in fall treatments (Derr 2008).

By targeting this point in the life cycle, it is presumed there would be little stored energy remaining to re-initiate growth, or it would remove the plants' ability to produce and reallocate new carbohydrate stores. Understanding the life history and carbohydrate storage dynamics has been beneficial in managing other aquatic plants. Carbohydrate depletion in Eurasian watermilfoil as it relates to frequent harvesting has been used to predict long-term success of management programs (Kimbel and Carpenter 1981; Perkins and Sytsma 1987; Painter 1988; Painter and Waltho 1985). Herbicides were reported to be more efficacious against sago pondweed and alligatorweed when they were applied during times of low carbohydrate storage (Hodgson 1966; Weldon and Blackburn 1968). In a small scale study it was reported that spring treatments of diquat and endothall provided better control of curlyleaf pondweed than herbicide applications made later in the season (Poovey et al. 2002). Waterhyacinth leaf damage caused by *Neochetina* weevils reduced leaf carbohydrate content (Center and Van 1989), and likely the ability of plants to recover.

Although some of the aforementioned studies were small scale, they do provide evidence that targeting weak points in a species' life history or carbohydrate cycle can impact the effectiveness of management techniques. However, in practice, the application of specific management techniques will depend upon location and environmental factors in that it may not always be possible to target a specific species early in its life history, and alternative timings will need to be determined. Life history data are needed for more aquatic plant species so that new management strategies can be developed.

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