J. Aquat. Plant Manage. 56: 35–38

Phenology of curlyleaf pondweed (*Potamogeton crispus* L.) in the southeastern United States: A two-year mesocosm study

GRAY TURNAGE, JOHN D. MADSEN, AND RYAN M. WERSAL*

ABSTRACT

Curlyleaf pondweed (*Potamogeton crispus*) is a submersed invasive aquatic plant that first appeared in the U.S. in the 1840 s and has since been distributed throughout the lower 48 states. In northern populations, curlyleaf has the growth cycle of a winter annual, however, little is known about the phenology of curlyleaf in the southern U.S. Therefore, research was conducted to better understand the phenology of curlyleaf pondweed in the southern U.S. In this study, total plant biomass and turion production peaked ($>$3,000 individuals [N] m^{-2}) in winter, which coincided with minimum annual water temperature and photoperiod. Unlike northern populations, plant growth occurred throughout the year. Turion production occurred year round, but was lowest in summer months and in excess of 1,000 N m^2 of substrate. Turion and biomass production were positively correlated with photoperiod and water temperature. This study indicates that southern populations of curlyleaf pondweed have altered their phenology to climatic conditions present in the southeastern U.S. Knowing that curlyleaf pondweed can grow as an evergreen perennial is both beneficial and detrimental to management efforts. When working with perennial evergreen curlyleaf pondweed populations, resource managers have a longer period to utilize control measures such as herbicides. However, as these populations produce turions year round, they will likely require multiple herbicide applications per year to reduce the turion bank in infested waterbodies, thus increasing management costs. Systemic herbicides should be a larger component of control measures for perennial evergreen curlyleaf pondweed because these herbicides translocate readily to belowground structures.

Key words: Phenology, life cycle, invasive species, submersed plant species.

INTRODUCTION

One of the most problematic invasive aquatic plants in the northern United States and Canada is curly-leaf pondweed (*Potamogeton crispus* L.). Curlyleaf is a submersed aquatic plant that is native to Eurasia, Africa, and Australia (Catling and Dobson 1985). It was introduced to the United States in the 1840s and has since spread to all states except Alaska and Hawaii (Stuckey 1979, Les and Mehrhoff 1999). Long-distance dispersal was initially attributed to fish hatchery activities, and in many states the first observance of curly leaf pondweed was in hatchery ponds (Stuckey 1979). Curlyleaf pondweed is capable of outcompeting native species and forming large monospecific beds (Tobiessen et al. 1992). This submersed species can impact ecological balance by altering habitat structure, lowering species diversity, changing nutrient cycles, lowering dissolved oxygen, and affecting pH and temperature gradients (Tobiessen et al. 1992, Cheruvelil et al. 2002, James et al. 2003). However, these effects are generally more problematic in the northern states (Parsons 2006). It is listed as a class C noxious weed in Alabama and Washington and class B in Vermont and as invasive in Connecticut and Maine, and it is prohibited in Massachusetts (USDA 2016). The life cycle and reproductive process of northern populations has been more thoroughly studied and documented than southern populations (Woolf and Madsen 2003).

In northern populations, curlyleaf pondweed has an atypical growth cycle (Figure 1A); in mid- to late fall turions sprout and plants begin to grow but slow their growth during winter months when water bodies are frozen over. When ice melts the following spring, plants start to grow again and produce turions prior to senescence in early summer. After senescence, turions fall to the substrate and are dormant through the summer (Woolf and Madsen 2003).

Curlyleaf pondweed primarily reproduces vegetatively via turion production or rhizome elongation (Bolduan et al. 1994, Woolf and Madsen 2003, Wells and Sytsma 2006). Turions are vegetative structures capable of surviving extreme conditions (e.g., drought, herbicide treatments) and producing a viable plant capable of reproduction (Madsen 2000). These are typically produced in the weeks before the plant senesces (Bolduan et al. 1994, Woolf and Madsen 2003, Wells and Sytsma 2006).

In northern states, most chemical control efforts target curlyleaf pondweed in the early spring before the formation of turions (Netherland et al. 2000, Woolf and Madsen 2003, Johnson et al. 2012). This strategy targets the maximum number of plants in a population, reduces or eliminates curlyleaf pondweed turion production and recruitment into the local turion bank, and consequently reduces the number of new curlyleaf pondweed plants the following fall (Nether-

---

*First author, Research Associate, Geosystems Research Institute, Mississippi State University, 2 Research Blvd., Starkville, MS 39759; Second author, Research Biologist, USDA ARS EIWRU, University of California–Davis, Plant Sciences Department, Mail Stop 4, 1 Shields Ave., Davis, CA 95616. Third author, Aquatic Plant Scientist, Lonza, Water Treatment, 1200 Bluegrass Parkway, Alpharetta, GA 30004. Corresponding author's E-mail: Gturnage@gri.msstate.edu. Received for publication ____________ and in revised form ____________.

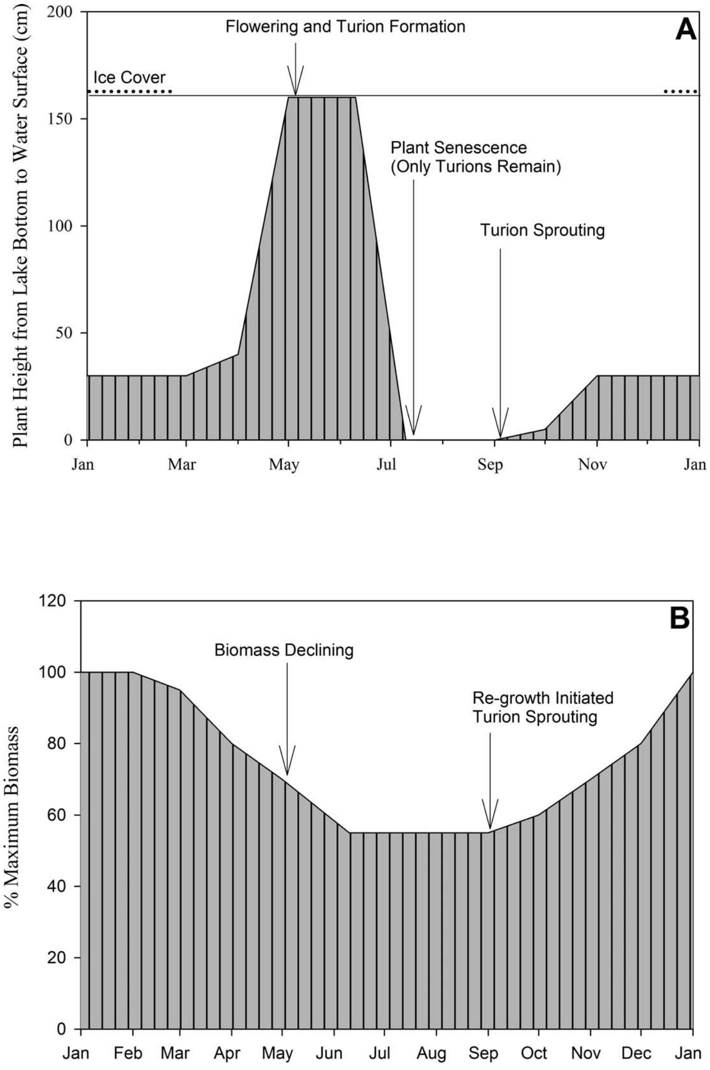

Figure 1. Conceptual descriptions of phenology of northern (A) and southern (B) populations of curlyleaf pondweed (Figure 1A adapted from Woolf and Madsen 2003).

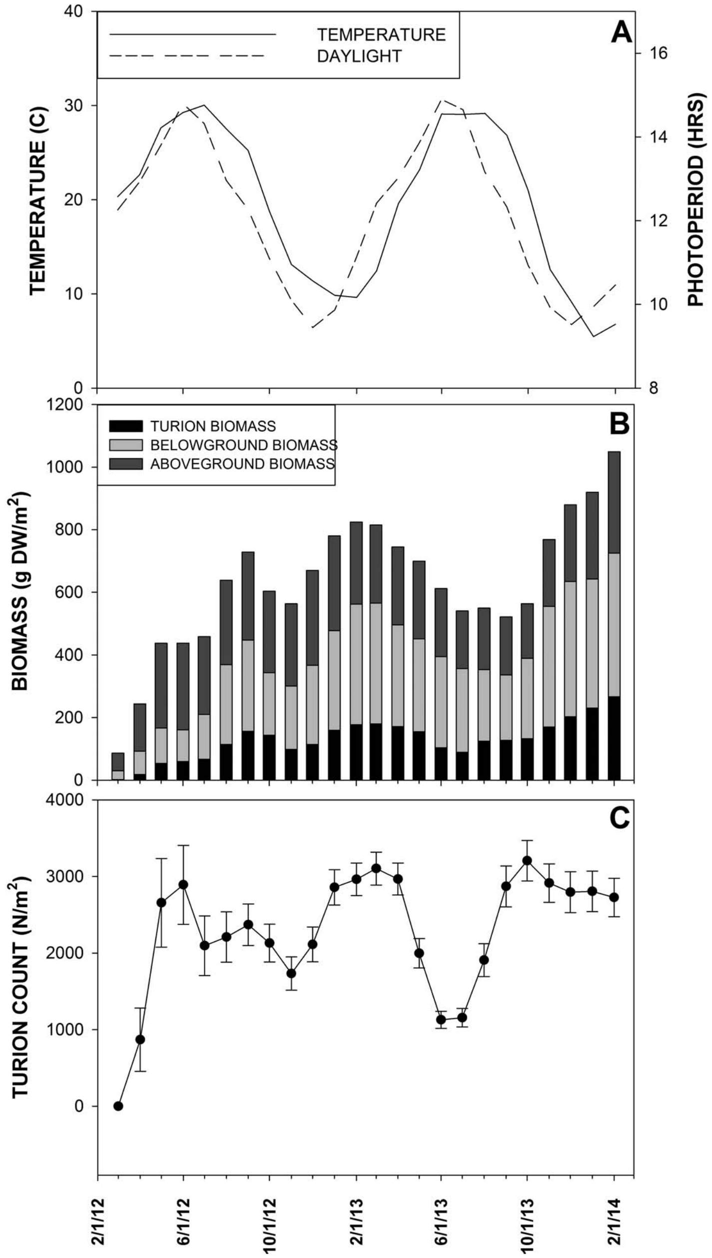

Figure 2. Comparisons between (A) water, temperature, and photoperiod (hr), (B) biomass (gDW m^{-2}), and (C) turion count (N m^{-2}). In middle panel, standard error was less than 80 for all plant structures. Error bars are one standard error of the mean for the bottom panel.

land et al. 2000, Woolf and Madsen 2003, Skogerboe et al. 2008, Johnson et al. 2012). Implementing control strategies in early spring also selectively controls curlyleaf pondweed because most other plants are not actively growing at this time (Netherland et al. 2000, Woolf and Madsen 2003, Skogerboe et al. 2008, Johnson et al. 2012).

In the southeastern United States, curlyleaf is present in every state but has been less studied than more problematic species such as hydrilla (*Hydrilla verticillata* (L.f.) Royle). Consequently, little is known about the growth and control of curlyleaf populations in this region. In general, southeastern populations were assumed to have the same life history as northern populations. Since little is known about these populations, research was conducted to better understand the phenology of curlyleaf pondweed in the southern United States, specifically biomass allocation, turion production, and their correlation with environmental factors. This new information will provide data on curlyleaf pondweed growth habits in the South and may help to guide effective management of southern populations where they become problematic.

MATERIALS AND METHODS

The study was conducted at the R. R. Foil Plant Science Research Center (Mississippi State University, Starkville, MS) in three 5700-L (1500-gal) outdoor mesocosms from February 2012 through February 2014. Curlyleaf pondweed was propagated from stock cultures at Mississippi State University. Turions were collected from the bottom of propagation tanks and placed in a 20-L (5-gal) plastic

Table 1. *R* values from Pearson's correlation analysis of curlyleaf pondweed plant metrics from the southern United States and environmental variables.[1]

Plant Metric	Water Temperature				Photoperiod			
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Belowground biomass	0.66				0.70			
Aboveground biomass	0.81				0.82			
Turion biomass	0.73				0.75			
	0.73	0.69	0.85	0.89	0.66	0.68	0.85	0.89
Turion density	0.69				0.72			

[1] All plant metrics were analyzed within year except turion biomass, which was analyzed within year and within season. *P* values < 0.0001 for all.

container filled with pond water for 7 d to stimulate sprouting. Once sprouted, two turions were planted in 3.8-L (1-gal) containers filled with sand amended with Osmocote®[1] (19-6-12) fertilizer at rate of 2 g L^{-1} of soil to maintain plant growth. Seventy-two potted containers of curlyleaf were placed into each of the mesocosms filled with pond water to a depth of 0.7 m. Plants were allowed to grow for 1 mo before the first harvest. Photoperiod and water temperature were recorded for the duration of the study using HOBO pendant®[2] data loggers (Figure 2A). Three containers were harvested each month from each tank throughout the duration of the trial (2 yr). If present, the number of turions per plant was recorded. Harvesting consisted of collecting aboveground, belowground, and turion plant tissues. Plant tissues were washed to remove dirt and debris, placed into labeled paper bags, and dried at 70 C for 5 d. After drying, plant tissues were weighed.

Pearson's correlation analysis was used to evaluate correlations between mean monthly plant metrics (aboveground and belowground biomass, turion biomass, and turion number) and mean monthly water temperature or photoperiod. All statistical analyses were conducted with Statistix 9.0 software (Analytical Software 2009).

RESULTS AND DISCUSSION

Mean total biomass peaked in February 2013 and 2014 (Figure 2B); however, plant growth was observed year-round (Figure 2B). In contrast to northern curlyleaf pondweed populations (Woolf and Madsen 2003), belowground biomass structures in our populations contributed a larger component of total biomass than did turion biomass (Figure 2B). Belowground biomass had a significant positive correlation to water temperature and photoperiod (Table 1; Figure 2A). Mean belowground biomass peaked in February of each year similarly to that of total biomass. This is a very different growth pattern than seen in northern populations of curlyleaf, which form large floating mats of plants as belowground structures degrade and plants break free from the bottom sediments. Our populations did not have a complete loss of belowground plant structures. The plants continued to grow year-round even though some loss of belowground biomass did occur after the peak.

In the current study, mean aboveground biomass peaked in January and February, declined through June, remained constant through September, and then started to increase again in the fall. Aboveground biomass was positively correlated to water temperature and photoperiod (Table 1). This correlation is different from reported by Woolf and Madsen (2003) in northern populations where aboveground biomass increased with water temperature during spring months, peaked in June, but then declined in summer months as water temperature continued to increase.

Turion number (Figure 2C) was positively correlated to water temperature and photoperiod (Table 1; Figure 2). Similarly, turion biomass had significant positive correlations with water temperature and photoperiod (Table 1). This is an unexpected correlation given that, while turion production occurred year-round, it was lowest in the warmer months and highest in cooler months (Figure 2C). However, in northern populations turion production occurs in spring and early summer.

When analyzed seasonally rather than annually, these correlations with water temperature (Table 1) and photoperiod (Table 1) still existed, thus suggesting that turion production, while lower in the summer, was still positively influenced by photoperiod and water temperature. These data suggest that curlyleaf pondweed in southern populations produce turions continuously instead of seasonally as with northern populations (Woolf and Madsen 2003), which could affect management costs and strategies utilized. Turion count peaked in the spring and fall of each year (Figure 2C); however, mean turion biomass peaked in the winter, suggesting that the fall peak comprised smaller turions. Plants yielded similar numbers of turions per square meter (3,093 m^{-2} at peak production) of substrate as in other parts of curlyleaf pondweed's North American distribution (Figure 2C; Bolduan et al. 1994, Woolf and Madsen 2003) but had lower turion numbers than that reported by Kunii (1989) at peak production (7000 m^{-2}) in a Japanese population.

Kunii (1989) noted continuous growth and turion production throughout the year, which is similar to the current research. However, Kunii noted two distinct peaks in biomass, one in the spring and another in the late summer/fall, whereas the southern population showed only one peak (Figure 1B). Woolf and Madsen (2003) similarly showed a single peak in total biomass, but the peak in our study was approximately five times greater (1000 g m^{-2} vs. 190 g m^{-2}) and occurred in February rather than June. Our findings are similar to those of Kunii, who found that turion biomass was a minor component of total biomass in an evergreen perennial curlyleaf population in Japan. In contrast, Woolf and Madsen found that in northern populations, peak turion biomass (120 g m^{-2}) appeared to be the majority (63%) of total biomass, whereas our peak turion biomass (266 g m^{-2}) was not (25% of total, Figure 2B).

Our findings highlight the need for additional studies to investigate stimuli of curlyleaf pondweed phenology other than water temperature and photoperiod at different locales. Maximum water temperature in our study was greater than that (30 C vs. 25 C) reported by Woolf and Madsen (2003), and yet southern specimens did not undergo full senescence as did their northern field populations. Kunii (1989) reported a maximum temperature of 24.7 C, and field specimens did not undergo senescence. Other factors (turbidity, lotic vs. lentic waters, pH, sediment characteristics) that are known to affect aquatic plants (e.g., pH and *Cabomba caroliniana* Gray; Jacobs and MacIsaac 2009) may influence curlyleaf pondweed phenology in an as yet undescribed way.

Understanding that curlyleaf pondweed can behave as an evergreen perennial plant in southern populations rather than as a winter herbaceous perennial as in northern populations is the first step in determining suitable management options for perennial populations. Knowing that curlyleaf pondweed can grow as an evergreen perennial is both beneficial and detrimental to management efforts in those populations. When working with perennial evergreen populations, resource managers have a much longer period to utilize control measures such as herbicides because they do not senesce to a propagule in summer months. Since this plant species produces turions throughout the year, it will likely require multiple herbicide applications per year to reduce the turion bank in infested waterbodies. As a result, increased management costs will occur. Finally, systemic herbicides should be a larger component of control measures used to manage evergreen perennial populations of curlyleaf pondweed rather than on herbaceous evergreen populations since these herbicides translocate readily throughout the plant to control belowground structures (Vencill 2002).

SOURCES OF MATERIALS

[1] Osmocote 19-6-12 fertilizer, Scotts-Sierra Horticultural Products Company, 14111 Scottslawn Rd., Marysville, OH 43041.

[2] HOBO pendant® temperature/light data logger, Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532.

ACKNOWLEDGEMENTS

We would like to thank Julie Gower, Trey Higginbotham, John Mark Curtis, John Perren, and Cody Cotton for assistance in carrying out this study. Mention of a manufacturer does not constitute a warranty or guarantee of the product by the U.S. Department of Agriculture or an endorsement over other products not mentioned.

LITERATURE CITED

Analytical Software. 2009. Statistix 9. User's Manual Analytical Software. Florida State University Tallahassee, FL.

Bolduan BR, Van Eeckhout CG, Wade HW, Gannon JE. 1994. *Potamogeton crispus*—The other invader. Lake Reserv. Manage. 10:113–125.

Catling PM, Dobson I. 1985. The biology of Canadian weeds. 69. *Potamogeton crispus* L. Can. J. Plant Sci. 65:655–668.

Cheruvelil KS, Soranno PA, Madsen JD, Roberson MR. 2002. Plant architecture and epiphytic macroinvertebrate communities: The role of an exotic dissected macrophyte. J. North Amer. Benth. Soc. 21:261–277.

Jacobs MJ, MacIsaac HJ. 2009. Modelling the spread of the invasive macrophyte *Cabomba caroliniana*. Freshwater Bio. 54:296–305.

James WF, Barko JW, Eakin HL, Sorge PW. 2003. Phosphorus budget and management strategies for an urban Wisconsin lake. Lake Reserv. Manage. 18:149–163.

Johnson JA, Jones AR, Newman RM. 2012. Evaluation of lake-wide, early season herbicide treatments for controlling invasive curlyleaf pondweed (*Potamogeton crispus*) in Minnesota lakes. Lake Reserv. Manage. 28:346–363.

Kunii H. 1989. Continuous growth and clump maintenance of *Potamogeton crispus* L. in Narutoh river, Japan. Aquat. Bot. 33:13–26.

Les DH, Mehrhoff LJ. 1999. Introduction of nonindigenous aquatic vascular plants in southern New England: A historical perspective. Bio. Invas. 1:281–300.

Madsen JD. 2000. Advantages and disadvantages of aquatic plant management techniques. Final report, ERDC/EL MP-0001. U.S. Army Engineer Research and Development Center, Vicksburg, MS. 31 pp.

Moore E. 1913. The Potamogetons in relation to pond culture. Bull. Bur. Fish. 33:251–291.

Netherland MD, Skogerboe JD, Owens CS, Madsen JD. 2000. Influence of water temperature on the efficacy of diquat and endothall versus curlyleaf pondweed. J. Aquat. Plant Manage. 38:25–32.

Parsons J. 2006. The worst submersed weeds in the western US. In: Proceedings of the 25th Annual Meeting of the Western Aquatic Plant Management Society, 27–29 March, San Diego, CA. Western Aquatic Plant Management Society, www.wapms.org. Accessed November 9, 2017. 17 pages.

Skogerboe JD, Poovey AG, Getsinger KD, Crowell W, Macbeth E. 2008. Early season, low-dose applications of endothall to selectively control curlyleaf pondweed in Minnesota lakes APCRP Technical Notes Collection. ERDC/TN APCRP-CC-08. U.S. Army Engineer Research and Development Center, Vicksburg, MS. 14 pp.

Stuckey RL. 1979. Distributional history of *Potamogeton crispus* (curly pondweed) in North America. Bartonia 46:22–42.

Tobiessen P, Swart J, Benjamin S. 1992. Dredging to control curly-leaved pondweed: A decade later. J. Aquat. Plant Manage. 30:71–72.

[USDA] United States Department of Agriculture. 2016. *Potamogeton crispus* L. curlyl pondweed. http://plants.usda.gov/core/profile?symbol=POCR3. Accessed December 13, 2016.

Vencill WK, ed. 2002. Herbicide handbook. 8th ed. Weed Science Society of America, Champaign, IL. 503 pp.

Wells S, Sytsma M. 2006. Phenology of *Potamogeton crispus* L. in Blue Lake, Oregon: Timing of turion formation and sprouting. In: Proceedings of the 26th Annual Meeting of the Aquatic Plant Management Society, 16–19 July, Portland, OR. Aquatic Plant Management Society, Gainesville, FL. 54 pp.

Woolf TE, Madsen JD. 2003. Seasonal biomass and carbohydrate allocation patterns in southern Minnesota curlyleaf pondweed populations. J. Aquat. Plant Manage. 41:113–118.