Survival of parrotfeather following simulated drawdown events

RYAN M. WERSAL, J. D. MADSEN, AND P. D. GERARD*

ABSTRACT

Non-native aquatic plants can often invade and rapidly outgrow native species in shallow water bodies resulting in the establishment of monotypic populations of the invading plant. Parrotfeather (Myriophyllum aquaticum Vell. Verdc.) is a non-native species that can be a nuisance in shallow water bodies. Therefore, we simulated a 0, 2, 4, 6, 8, and 12 wk winter and summer drawdown under controlled mesocosm conditions to evaluate the survival of parrotfeather with respect to seasonal and durational effects of drawdown events. The winter drawdowns did not affect (P = 0.89) parrotfeather survival. Parrotfeather survival was 68 to 80% between winter drawdown events. Conversely, summer drawdowns were much more effective (P < 0.01) with the exception of the 2-wk duration. Parrotfeather survival was 75% following a 2-wk drawdown and 18% following a 12-wk drawdown. The survival of parrotfeather in this study indicates that summer drawdowns may offer short-term suppression, as this species can withstand drawdowns of 12 wk. Longer drawdown durations or an integrated approach is required for complete control.

Key words: management, invasive species, exotic species, water level, soil moisture.

INTRODUCTION

Parrotfeather [*Myriophyllum aquaticum* (Vell.) Verdc.] is an herbaceous perennial aquatic plant that is not native to the United States. This species readily invades shallow water bodies that are prone to disturbance. Dense beds of parrotfeather have resulted in reductions in dissolved oxygen in the water column, which may be detrimental to fish (Fonseca 1984, Moreira et al. 1999). Parrotfeather growth can inhibit the growth of more desirable plant species such as pondweeds and coontail (Ferreira and Moreira 1994), which are readily utilized by waterfowl as food items (Wersal et al. 2005). A strong correlation was also determined between the density of parrotfeather growth and the presence of mosquito eggs and larvae (Orr and Resh 1989), which may lead to increases in mosquito-borne diseases that could infect wildlife and humans.

Survival and spread of parrotfeather depends solely on vegetative reproduction via fragmentation, as this species does not produce any specialized reproductive structures such as seeds, tubers, or turions (Sytsma and Anderson 1993a). Parrotfeather is a dioecious species however, pistillate flowers are most common in all naturalized populations including its native range, with staminate flowers rarely observed (Orchard 1979). During a comprehensive study of Myriophyllum species, Orchard (1981) found only a few staminate flowers, and two plants with immature fruits, on specimens collected from South America. Therefore, little is known regarding the appearance of staminate flowers, fruit, or seed; and no information is available on factors affecting pollination, fruit development, and seed germination since staminate flowers are rare (Sutton 1985). The paucity of staminate flowers indicates that seed production likely does not occur and therefore this species would rely on vegetative means for reproduction and survival.

The lack of specialized reproductive structures may allow drawdown events to be efficacious against parrotfeather if the sediment can be dried sufficiently and over long enough duration to cause desiccation of plant tissues. Parrotfeather relies on stolon and submersed shoots to store the bulk of its starch (Wersal et al. 2011); and management techniques that target these storage tissues would eliminate the stored energy that would be utilized for regrowth. Furthermore, parrotfeather can survive on water column nutrients alone (Wersal and Madsen 2011a), likely as a result of adventitious roots, and these roots may be the primary site for nutrient acquisition for this species (Sytsma and Anderson 1993b). Parrotfeather growth did not reduce sediment nutrient concentrations over the course of a controlled study when adventitious roots were present (Sytsma and Anderson 1993b). In fact, the water column provided 98% of the water transpired by parrotfeather, which suggests that the majority of nutrients used for growth would also come from the water column (Sytsma and Anderson 1993b).

Drawdowns would remove overlying water, thereby reducing nutrient availability, and exposing stolons and the adventitious roots to desiccation. Though, the duration of exposure and degree of sediment drying would be important factors influencing plant mortality. In a study conducted in a 2 ha palustrine wetland in the Sinos River Basin, Brazil, parrotfeather was collected during both a flooded period and a drawdown period, but was more associated with wet growing conditions (Maltchik et al. 2007). Maltchik et al. (2007) suggested that parrotfeather may be tolerant of drawdown events lasting 9 mo, through

^{*}First and second authors, Geosystems Research Institute, Mississippi State University, Box 9627, Mississippi State, MS 39762-9652. Third author, Department of Mathematical Sciences, Clemson University, 291 Barre Hall, Clemson, SC 29634. Current address of first author: Lonza, Specialty Ingredients - Water Technology, Alpharetta Innovation and Technology Center, 1200 Bluegrass Lakes Pkwy., Alpharetta, GA 30004. Corresponding author's E-mail: ryan.wersal@lonza.com. Received for publication February 13, 2012 and in revised form January 15, 2013.

changes in growth habit, if the sediment remains saturated. There are data describing changes in leaf form of parrotfeather in response to water regimes (Sculthorpe 1967, Wersal and Madsen 2011b), though currently there are little quantitative data regarding the seasonal effects of drawdowns on parrotfeather. Therefore, our objectives were to examine the efficacy of winter and summer drawdown events lasting 2 to 12 wk under controlled mesocosm conditions.

MATERIALS AND METHODS

Experiments were conducted at the R.R. Foil Plant Science Research Center, Mississippi State University, Starkville, MS from June 2008 through September 2009. Both the winter and summer drawdown experiments were conducted in 24, 1,100 L mesocosms (experimental unit) arranged in a completely randomized experimental design. Drawdown durations (treatments) were 0, 2, 4, 6, 8, and 12 wk. All drawdown durations were replicated in 4 mesocosms during both experiments.

Planting

Parrotfeather was harvested from a local pond and transported to Mississippi State University for planting. Planting consisted of placing two apical shoots of parrotfeather, approximately 20 cm in length, into each of 240, 3.78 L (15.5 cm diameter, 20.5 cm height) pots containing a top soil, loam, and sand mixture (3:2:1) (Wersal and Madsen 2010, Wersal and Madsen 2011b). Sediment was amended at a rate of 2 g L pot⁻¹ with Osmocote¹ 19–6–12 fertilizer. Ten pots of planted parrotfeather were placed into each mesocosm. All mesocosms were filled with water so that the water level was approximately 12 cm above the plants. Water was supplied to each mesocosm from an irrigation reservoir adjacent to the mesocosm facility. Air was continuously supplied to all mesocosms during the growth phase of each experiment by a regenerative air blower using 2.5 cm stone diffusers and a PVC lift pipe placed in each mesocosm. Once the drawdowns were initiated air was removed with the exception of the reference tanks, which had continuous air. Air was resupplied to all mesocosms during the refill (recovery) stage of both experiments to circulate water in the mesocosms.

Winter and summer drawdown experiments

Planting for the winter drawdown occurred on 8 September 2008 followed by a 4-mo growth period. The growth period was used to establish a mature population of parrotfeather in each mesocosm. The winter drawdown was initiated on 16 January 2009 with the final biomass harvest on 8 May 2009. Planting for the summer drawdown occurred on 2 February 2009 followed by a 4-mo growth period. The summer drawdown was initiated on 15 June 2009 and final biomass harvest on 28 September 2009.

At the conclusion of the 4-mo growth periods plants had completely covered the water surface in all mesocosms and there were plants in every pot. The water in all mesocosms, with the exception of the 0-wk treatment, was removed to simulate a drawdown. After the specified drawdown duration (for example 2 wk) had been reached, mesocosms were refilled with water. A 4-wk recovery period following the water refill was used to evaluate regrowth after each drawdown period. Following the recovery period, the pots in each mesocosm were assessed for survival by assigning a 0 for no living plants or a 1 for pots with living plants. This sequence was followed for each drawdown duration during both the winter and summer seasons.

Environmental monitoring

Weather data were recorded in 1-hr intervals over the duration of both experiments by a HOBO Weather Station². The weather station was located on site within 15 m of the mesocosms. Soil moisture probes $(EC-5)^3$ were placed into one pot for each mesocosm to monitor soil moisture. The EC-5 model probes were chosen because they perform better at high soil moisture contents and are field ready for most soils with no calibration while maintaining a $\pm 3\%$ accuracy (Decagon Devices 2006). Soil moisture was also measured in an air-dried sample to validate moisture measurements in treatment mesocosms.

Statistical analyses

The proportion of pots in each mesocosm that survived (i.e., the percentage of 1's) was calculated for all mesocosms and drawdown durations. Data were then transformed using the arc sine square root of each calculated survival to stabilize variances. Transformed survival data were analyzed by fitting mixed models using the Mixed Procedure in SAS[®]. Survival was included as the dependent variable in the model, and treatment, time, and the treatment by time interaction term were included as independent variables.

The tank (treatment by time) term was included as a random effect to account for its influence on the results. The 0-wk treatment was removed from the analyses, though data are reported, as perfect survival was observed which hindered model convergence. There were significant treatment, time, and treatment by time interaction (P < 0.01 for all) effects. Treatment means were separated using least squares means, and because the interaction was significant, slice tests were used to determine differences in time and treatment simple effects. Untransformed data are presented for ease of interpretation. All analyses were conducted at a P < 0.05 level of significance. Soil moisture data were averaged within drawdown duration and reported as the mean (\pm 1 SE) percent for each duration across both experiments. Similarly, weather data were averaged across months and the means (± 1 SE) are reported.

RESULTS

Environmental monitoring

Soil moisture during the winter drawdowns never fell below the complete soil saturation line and therefore did not approach dry soil (Figure 1). In contrast, soil moisture

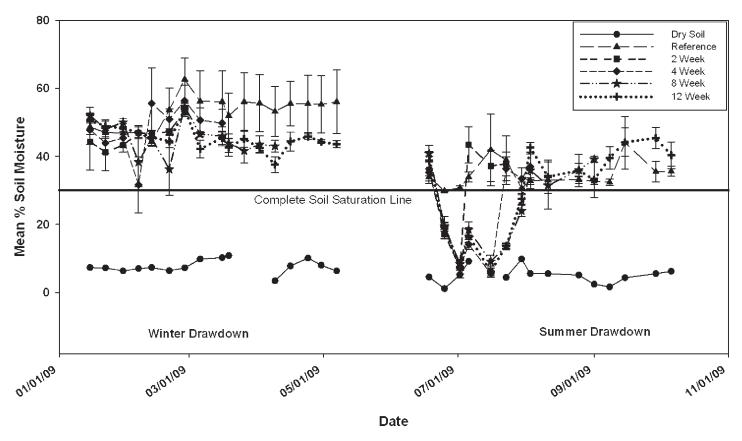


Figure 1. Mean (\pm 1 SE) percent soil moisture for both the winter and summer drawdown durations. One soil moisture probe was placed into a pot in each mesocosm to monitor soil moisture. The complete soil saturation line represents the value reported by the probe manufacturer for complete soil saturation. The dry soil line refers to soil that was kept under ambient conditions with no addition of water. The reference soil moisture line refers to measurements taken from mesocosms that remained full of water during the experiments (0-wk drawdown).

during the summer drawdowns immediately fell below complete soil saturation upon draining the mesocosms with the exception of the reference mesocosms in which the soil remained completely submersed and thus saturated. Complete saturation for the ECH₂O probes are typically 40 to 50% soil moisture (Decagon Devices 2006), but some of our completely submersed pots gave readings as low as 30% during summer months; therefore 30% soil moisture was considered complete saturation for this study. Temperature, humidity, and photosynthetically active radiation (PAR) are summarized for both experiments in Table 1. Average temperatures during the winter drawdown never fell below freezing.

Winter and summer drawdown survival

Survivability of parrotfeather to winter drawdowns was not different (P = 0.89) among the durations used in this study (Table 2). Parrotfeather survival was 70, 80, 68, 68, and 78% for the 2, 4, 6, 8, and 12-wk drawdown durations respectively. Conversely, summer drawdowns impacted parrotfeather survival (P < 0.01) with the exception of the 2-wk duration when compared to winter drawdown survival (Table 2). Parrotfeather survival was 75% following a 2-wk drawdown, which was not a significant (P = 0.96) decline in survival. Parrotfeather survival was 18% following the 12-wk drawdown.

DISCUSSION

The use of drawdowns during winter in Mississippi did not adversely affect parrotfeather survival which is due in large part to soil moisture, warmer temperatures, and the insulating effect that emergent biomass had on the sediment once the water was removed. Soil moisture during winter drawdowns never fell below complete saturation, and thus plants were able to survive better under these conditions. Conversely, when drawdown events were initiated in summer, soil moisture rapidly fell to levels near that of dry soil. Soil moisture over summer closely tracked that of the dry soil until the refill occurred at 2, 4, and 8 wk after initial drawdown, resulting in greater plant mortality. After the refill, soil moisture rose quickly to complete saturation. The soil moisture in the 12-wk mesocosms increased abruptly after only 8 wk drawdown exposure. The increase in soil moisture at this time corresponds to increased amounts of rain received during late summer.

Total rainfall from July through September 2009 was 14.5 cm greater than the same time period in 2008. It rained 35 out of 61 days from August through September 2009, which kept soil saturated and allowed parrotfeather to survive where mortality was expected. These results corroborate those reported from a field trial where parrotfeather was found to be more associated with the wet phase of the hydrologic cycle in Brazil (Maltchik et al. 2007). Although

Table 1. Summary of mean (\pm 1 SE) monthly environmental data collected for the duration of both the winter and summer drawdown experiments. Rainfall data are totals for each month.

| Date | Rain (cm) | Temperature (C) | Min | Max | Relative humidity (%) | Min | Max | $\begin{array}{c} \text{PAR} \\ (\mu\text{mol } \text{m}^{-2} \text{ sec}^{-1}) \end{array}$ | Min | Max |
|----------|-----------|-----------------|----------------|----------------|--------------------------|----------------|-----------------|--|---------------|---------------------|
| Date | Kam (em) | Temperature (C) | MIIII | max | number (70) | MIIII | max | (µmor m see) | MIII | Max |
| Jul 2008 | 5.9 | 27.1 ± 0.4 | 23.3 ± 0.4 | 32.4 ± 1.0 | 86.3 ± 1.7 | 62.4 ± 3.2 | 99.9 ± 0.1 | 463.3 ± 61.5 | 1.2 ± 0.0 | $1,615.7 \pm 187.9$ |
| Aug 2008 | 24.6 | 25.4 ± 0.3 | 21.5 ± 0.3 | 30.3 ± 0.6 | 85.8 ± 1.6 | 63.5 ± 3.2 | 99.9 ± 0.1 | 627.1 ± 182 | 1.2 ± 0.0 | $1,510.5 \pm 87.9$ |
| Sep 2008 | 13.2 | 22.8 ± 0.5 | 18.8 ± 0.7 | 28.1 ± 0.5 | 86.3 ± 1.6 | 64.7 ± 2.8 | 99.9 ± 0.0 | 404.4 ± 24.5 | 1.2 ± 0.0 | $1,390.1 \pm 80.5$ |
| Oct2008 | 5.9 | 16.4 ± 0.8 | 10.9 ± 1.0 | 22.8 ± 0.7 | 81.1 ± 2.0 | 54.8 ± 2.8 | 98.1 ± 1.1 | 371.1 ± 18.1 | 1.2 ± 0.0 | $1,421.8 \pm 64.9$ |
| Nov 2008 | 7.5 | 10.1 ± 0.7 | 4.4 ± 0.8 | 16.3 ± 0.9 | 77.1 ± 2.5 | 53.5 ± 4.0 | 95.1 ± 1.5 | 257.0 ± 22.0 | 1.2 ± 0.0 | $1,023.4 \pm 76.4$ |
| Dec 2008 | 31.8 | 8.2 ± 1.1 | 3.6 ± 1.1 | 13.5 ± 1.1 | 81.7 ± 2.7 | 64.3 ± 4.1 | 94.7 ± 1.8 | 180.4 ± 17.6 | 1.2 ± 0.0 | 806.8 ± 64.3 |
| Jan 2009 | 17.9 | 6.5 ± 1.0 | 1.4 ± 1.1 | 12.2 ± 1.1 | 75.5 ± 2.9 | 56.2 ± 3.9 | 90.5 ± 2.3 | 232.1 ± 91.0 | 1.2 ± 0.0 | 972.7 ± 68.2 |
| Feb 2009 | 4.9 | 9.3 ± 1.1 | 2.9 ± 1.1 | 15.6 ± 1.0 | 68.4 ± 2.9 | 42.9 ± 3.7 | 90.5 ± 2.2 | 314.6 ± 23.1 | 1.2 ± 0.0 | $1,261.0 \pm 74.8$ |
| Mar 2009 | 19.9 | 13.4 ± 1.0 | 8.3 ± 1.0 | 18.8 ± 1.0 | 76.7 ± 2.8 | 54.1 ± 3.9 | 95.7 ± 1.5 | 365.3 ± 26.4 | 1.2 ± 0.0 | $1,410.3 \pm 78.6$ |
| Apr 2009 | 9.7 | 16.9 ± 0.9 | 10.7 ± 0.9 | 29.6 ± 6.9 | 73.0 ± 2.0 | 47.9 ± 2.5 | 94.9 ± 1.6 | 485.4 ± 27.8 | 1.2 ± 0.0 | $1,703.4 \pm 65.0$ |
| May 2009 | 27.4 | 21.1 ± 0.6 | 18.0 ± 0.6 | 24.9 ± 0.9 | 94.3 ± 1.6 | 80.8 ± 4.4 | 100.0 ± 0.0 | 355.1 ± 41.8 | 1.2 ± 0.0 | $1,378.3 \pm 129.3$ |
| Jun 2009 | 10.4 | 27.1 ± 0.6 | 20.2 ± 1.2 | 32.6 ± 1.4 | 64.8 ± 3.2 | 36.3 ± 4.0 | 96.2 ± 3.9 | 870.0 ± 145.9 | 1.2 ± 0.0 | $2,026.2 \pm 2.5$ |
| Jul 2009 | 13 | 26.9 ± 0.5 | 21.3 ± 0.4 | 32.5 ± 0.4 | 83.4 ± 1.7 | 60.1 ± 2.8 | 99.3 ± 0.4 | 532.1 ± 27.8 | 1.2 ± 0.0 | $1,783.8 \pm 52.0$ |
| Aug 2009 | 17.2 | 26.4 ± 0.5 | 21.2 ± 0.4 | 31.7 ± 0.5 | 88.3 ± 1.1 | 64.0 ± 2.2 | 100.0 ± 0.0 | 501.4 ± 23.0 | 1.2 ± 0.0 | $1,697.9 \pm 54.0$ |
| Sep 2009 | 28.0 | 28.2 ± 0.3 | 20.9 ± 0.4 | 31.0 ± 0.7 | 94.4 ± 1.2 | 78.5 ± 3.1 | 99.9 ± 0.1 | 334.8 ± 27.8 | 1.2 ± 0.0 | $1,415.5 \pm 76.4$ |

survival for the 12-wk summer drawdown was minimal, it does indicate the capacity of this species to survive adverse environmental conditions and regrow when conditions become favorable. A result that is particularly unexpected for a macrophyte species that does not produce any sort of seed, tuber, or turion.

The parrotfeather that survived drawdown events in these studies were short (approximately 4 to 6 cm) emergent shoots growing in the moist soil of the pot. These shoots may have been able to survive, albeit at a reduced growth rate, on the interstitial water in the soil. The emergent form of parrotfeather has a transpiration coefficient of 260 ml H_2O mg DW⁻¹, which is similar to C-4 terrestrial plants (Sytsma and Anderson 1993b). Furthermore, the leaves of emergent shoots have sunken anomocytic stomata (Sutton and Bingham 1973), a thick waxy cuticle, and short cylindrical leaflets. When water is removed the stomates should close thereby increasing water retention in the leaves. These traits are typical for reducing transpiration and are common in plants growing in more xerophytic environments (Sytsma and Anderson 1993b). If only small shoots of emergent parrotfeather are present, plants could survive extended periods of time at reduced growth rates without standing water. Furthermore, emergent shoots can store up to 8% of available starch (Wersal et al. 2011), and would be able to utilize this stored energy to maintain and initiate new growth when favorable conditions return.

Parrotfeather has proven to be resilient towards less than optimal environmental conditions, and once established it persists in spite of management or environmental conditions (Moreira et al. 1999, Wersal and Madsen 2010). Our results suggest that a drawdown conducted in winter, without freezing conditions, would not be effective in managing this species. Summer drawdowns lasting 4 to 12 wk would result in short term suppression of parrotfeather as indicated by survival data, thereby alleviating the problems associated with nuisance growth. We propose that a summer drawdown lasting 12 wk or more may offer longer term efficacy as plants would have to survive the drawdown and then the winter season at a reduced growth rate. Parrotfeather biomass is much higher beginning in late spring and early summer followed by a peak in starch storage beginning in late summer (Wersal et al. 2011). Therefore, a summer drawdown would target the time in parrotfeather's life cycle where biomass is greatest and prior to carbohydrate storage for winter; this should limit parrotfeather survival as seen in this study. Based on these results the effectiveness of a drawdown will often depend upon the life history strategies of the target plants, and the availability of a freeze. Overall, these data serve as an initial base to develop an integrated approach to parrotfeather management.

SOURCES OF MATERIALS

¹Osmocote, Scotts-Sierra Horticultural Products Company, 14111 Scottslawn Rd., Marysville, Ohio 43041.

²Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532.

³Decagon Devices, 2365 NE Hopkins Ct., Pullman, WA 99163.

Table 2. Results of the mixed model, tests of effect slices, and mean parrotfeather survival following simulated drawdown durations of 0, 2, 4, 6, 8, and 12 wk. A significant difference (P < 0.01) was observed between winter and summer.

| | Weeks | | | | | | | | |
|--|-------|----------------|-------------|------------|-------------|-------------|--|--|--|
| Time | 0 | 2 | 4 | 6 | 8 | 12 | | | |
| Winter Survival ¹ | 1.0 | 0.70 | 0.80 | 0.68 | 0.68 | 0.78 | | | |
| Summer Survival ² P-value ³ | 1.0 | $0.75 \\ 0.96$ | 0.38 < 0.01 | 0.0 < 0.01 | 0.28 < 0.01 | 0.18 < 0.01 | | | |

¹No difference between times for winter (P = 0.89).

²A significant difference (P < 0.01) was observed between times during summer.

³P-value for comparing winter and summer within weeks.

ACKNOWLEDGEMENTS

Funding for this research was provided by the Aquatic Plant Management Society and Aquatic Ecosystem Restoration Foundation through a graduate research grant, the United States Geological Survey Invasive Species Program under Award Number 08HQAG013908121105, and additional support through graduate student scholarships from the MidSouth Aquatic Plant Management Society and the Midwest Aquatic Plant Management Society. We thank Jimmy Peeples, Matt Gower, Alan Pryor, and Thomas Hendrix for assistance setting up and harvesting the study. We also thank David Shaw, Eric Dibble, John Byrd, and Linda Nelson for providing comments on earlier versions of this manuscript. This manuscript has been approved for publication as Journal Article No. J-11781 of the Mississippi Agricultural and Forestry Experiment Station, Mississippi State University.

LITERATURE CITED

- Decagon Devices. 2006. Frequently Asked Questions About the ECH₂O Soil Moisture Probes and Accessories. Application Note. http://www.decagon. com/appnotes/soil_moisture/viewer.phpq=FrequentlyAskedQuestions AboutECH2O.pdf. Accessed 8 December 2009.
- Ferreira MT, Moreira I. 1994. The seasonal evolution of river plants. EWRS 9th Symposium on Aquatic Weeds. Abstracts.
- Fonseca PC. 1984. Estudo ecologico de valas da Leziria Grande de Vila France de Xira. Rel. Estagio Fac. Ciencias Lisboa. 93 pp. (Cited in Moreira et al. 1999).
- Maltchik L, Rolon AS, Schott P. 2007. Effects of hydrological variation on the aquatic plant community in a floodplain palustrine wetland of southern Brazil. Limnology 8:23–28.
- Moreira I, Monteira A, Ferreira T. 1999. Biology and control of parrotfeather (*Myriophyllum aquaticum*) in Portugal. Ecology, Environ. Conserv. 5:171-179.

- Orchard AE. 1979. *Myriophyllum* (Haloragaceae) in Australia I. New Zealand: A revision of the genus and a synopsis of the family. Brunonia 2:247– 287.
- Orchard AE. 1981. A revision of South American *Myriophyllum* (Haloragaceae), and its repercussions on some Australian and North American species. Brunonia 4:27–65.
- Orr BK, Resh VH. 1989. Experimental test of the influence of aquatic macrophyte cover on the survival of *Anopheles* larvae. J. Am. Mosquito Contr. Ass. 5:579–585.
- Sculthorpe CD. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold Publishing, London. 610 pp.
- Sutton DL. 1985. Biology and ecology of Myriophyllum aquaticum. pp. 59–71 In: Proceedings of the 1st International Symposium on Watermilfoil (Myriophyllum spicatum) and Related Haloragaceae Species. 23–24 July 1985. Vancouver, B.C.
- Sutton DL, Bingham SW. 1973. Anatomy of emersed parrotfeather. Hyacinth Contr. J. 11:49–54.
- Sytsma MD, Anderson LWJ. 1993a. Biomass, nitrogen, and phosphorus allocation in parrotfeather (*Myriophyllum aquaticum*). J. Aquat. Plant Manage. 31:244-248.
- Sytsma MD, Anderson LWJ. 1993b. Transpiration by an emergent macrophyte: Source of water and implications for nutrient supply. Hydrobiologia 271:97-108.
- Wersal RM, Madsen JD. 2010. Comparison of subsurface and foliar herbicide applications for control parrotfeather (*Myriophyllum aquaticum*). Invasiv. Plant Sci. Manage. 3:262–267.
- Wersal RM, Madsen JD. 2011a. Influences of water column nutrient loading on growth characteristics of the invasive aquatic macrophyte Myriophyllum aquaticum (Vell.) Verdc. Hydrobiologia 665:93–105.
- Wersal RM, Madsen JD. 2011b. Comparative effects of water level variations on growth characteristics of *Myriophyllum aquaticum*. Weed Res. 51:386– 393.
- Wersal RM, McMillan BR, Madsen JD. 2005. Food habits of dabbling ducks during fall migration in a prairie pothole system, Heron Lake, Minnesota. Can. Field Natural. 119:546–550.
- Wersal RM, Cheshier JC, Madsen JD, Gerard PD. 2011. Phenology, starch allocation, and environmental effects on *Myriophyllum aquaticum*. Aquat. Bot. 95:194–199.