J. Aquat. Plant Manage. 64(2): 23–28

Utilizing degree-day modeling on submersed *Myriophyllum aquaticum* to estimate potential invasive range in the United States

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ABSTRACT

Parrotfeather is an invasive, heterophyllous aquatic plant from South America. Since its introduction in the late 1800s, parrotfeather has become established on the East and West coasts of the United States as well as the southeastern United States, though establishment has not occurred within the Midwest. The current study developed an accumulated degree-day (ADD) model to estimate the invasive range of parrotfeather in the Midwest. Submersed parrotfeather was harvested from three populations in 2006 and 2007 in Mississippi. The submersed leaf form was used, as it is the growth form that would have to invade, survive, and overwinter under the ice in midwestern lakes. Submersed biomass peaked in February during both years. The resulting model estimated that 1,416 ADDs and 176 calendar days were needed to reach peak submersed biomass. A base threshold water temperature of 5 C was estimated, indicating that water temperatures below this would result in limited growth. The model suggests water temperature is not the limiting factor for parrotfeather invasion into the Midwest. The lack of light from ice and snow cover is likely inhibiting the photosynthetic potential of parrotfeather. Any submersed plants without light for an extended period become reliant on stored energy for survival. Parrotfeather lacks storage structures, and during winter months this would negatively impact its survivability in areas with prolonged snow and ice cover. Models can inform managers of the likelihood of invasion into certain areas, and as such these data can be integrated into preventative management programs.

Key words: parrotfeather, temperature, macrophyte, environmental, light

INTRODUCTION

Parrotfeather [*Myriophyllum aquaticum* (Vellozo) Verdecourt] is a heterophyllous perennial invasive plant that inhibits recreation, decreases native plant diversity, and promotes mosquito breeding with the dense mats it can form at the water's surface (Orr and Resh 1992, Stiers et al. 2011). Parrotfeather is dioecious; however, within North America, only pistillate plants are present (Sutton 1985). Due to the presence of only pistillate flowers, sexual reproduction is not able to occur, and parrotfeather exclusively reproduces asexually via fragmentation of stolons and emergent and submersed shoots (Aiken 1981). It is native to South America in the Amazon River Basin and established itself in the United States in 1890, in Haddonfield, NJ (Sutton 1985, Couch and Nelson 1991, Wersal and Madsen 2007, Becker and Wong 2023). Parrotfeather is currently found in the southeastern United States, the East Coast, and the West Coast up into British Columbia, Canada (U.S. Geological Survey 2024a). However, parrotfeather has yet to widely establish in the midwestern United States (hereafter the Midwest). The current northern distribution of parrotfeather is in regions where air temperatures are above freezing for most of the year (Lafontaine et al. 2013). Populations in regions such as southern Ohio will typically experience snow and/or ice cover; however, the exposure period is much shorter than states such as Minnesota or Wisconsin where populations are not currently present (U.S. National Ice Center 2024). The submersed parrotfeather form dominates during the winter months, when temperatures reach freezing (0 to 4 C), while the emergent form can begin growth again when water temperature surpasses 7 C (Monteiro et al. 1999). Because of the inability to produce specialized structures for overwintering, parrotfeather stores starch in its stolons (Wersal et al. 2011). Being a heterophyllous plant, parrotfeather can adapt and grow in a variety of environmental conditions; however, if parrotfeather is to establish itself in the Midwest, it is the submersed form that would need to survive cold temperatures and ice cover during winter months. To colonize, establish, and overwinter, the submersed form of parrotfeather would have to survive at 4 C, which is the temperature at which water is densest, thus representative of the temperature conditions under the ice in northern Midwest lakes (Johnson et al. 2017). With no established populations in the Midwest, water temperature may be the limiting factor as to why parrotfeather is unable to grow in this region (Wersal et al. 2011).

The spread of parrotfeather may increase as air temperature has increased by nearly 2 C since 1895; of that, 0.7 C of that increase has occurred from 1981 to 2016 (Kriticos and Brunel 2016, Vose et al. 2017). Increases in air temperature will translate to increases in water temperature and less intense winter conditions. Over the next 30 to 50 yr, there

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DOI: 10.57257/JAPM-D-25-00020

is a 2 to 3 C predicted change in air temperature (IPCC 2007). As temperatures increase, plant range expansion could increase because of increased photosynthetic rates (Riis et al. 2012). Accumulated degree-day (ADD) models can be used to estimate range expansions based on temperature. ADD models are good estimates for plant growth in aquatic and terrestrial plants throughout a year-long cycle (Spencer et al. 2000, Squires et al. 2024a,b). The models use heat units to predict when developmental stages (e.g. life stage events like flowering, peak biomass occurrence, and senescence) within the plant will occur (Snyder 1985, Snyder et al. 1999, Spencer et al. 2000). Accumulated heat, or physiological time, is measured in degree-days (Zalom et al. 1983). A degree-day represents one degree above the lower developmental threshold of a plant over 24 hr (Squires et al. 2024a). The lower threshold is the temperature at which metabolic activity and plant growth stops (Zalom et al. 1983).

Data regarding parrotfeather's ecophysiology in different environmental conditions are limited. Wersal et al. (2011) assessed the phenology and starch allocation of parrotfeather across two calendar years while considering environmental predictors such as water temperature and water depth, as well as reporting the biomass of the submersed and emergent shoots. Stolons accounted for 40 to 95% of total biomass followed by emergent shoot, submersed shoot, and root biomass (Wersal et al. 2011). Starch allocation was greatest in stolons where up to 16.3% of total starch was stored. Submersed shoots stored 0.6 to 11.0% of total starch followed by emergent shoots (0.4 to 7%) (Wersal et al. 2011). The sediment roots of parrotfeather stored less than 3.8% of total starch. Reduced biomass and starch storage occurred from October to March (Wersal et al. 2011). Percent starch in plant tissues was positively related to water temperature (Wersal et al. 2011). Other environmental studies of parrotfeather assessed water level, light intensity, and nutrient loading effects on growth characteristics within parrotfeather (Hussner et al. 2009, Wersal and Madsen 2011, Wersal and Madsen 2013, Wersal et al. 2013); however, no study identified in what temperature submersed parrotfeather is able to become metabolically active, or if it can physiologically survive at freezing temperatures. No studies have utilized degree-day modeling on parrotfeather. Degree-day modeling is very limited within aquatic plants. Recent studies have utilized modeling on Cuban bulrush (*Oxycaryum cubense*) (Squires et al. 2024a,b), and a study has focused on vegetative propagules in various aquatic plants (Spencer et al. 2000).

Parrotfeather has been documented nearing the borders of the Midwest; however, clear patterns of distribution have not been defined; thus, ADD models may help resource managers and researchers better understand potential geographic distribution of the plant in this region of the United States. With no information as to the base-threshold temperature of submersed parrotfeather, nor knowing if parrotfeather can survive water temperatures within the Midwest during the winter, this study looks to identify those gaps. The objective of this study was to develop a submersed parrotfeather ADD model that would identify the base-threshold water temperature for submersed parrotfeather.

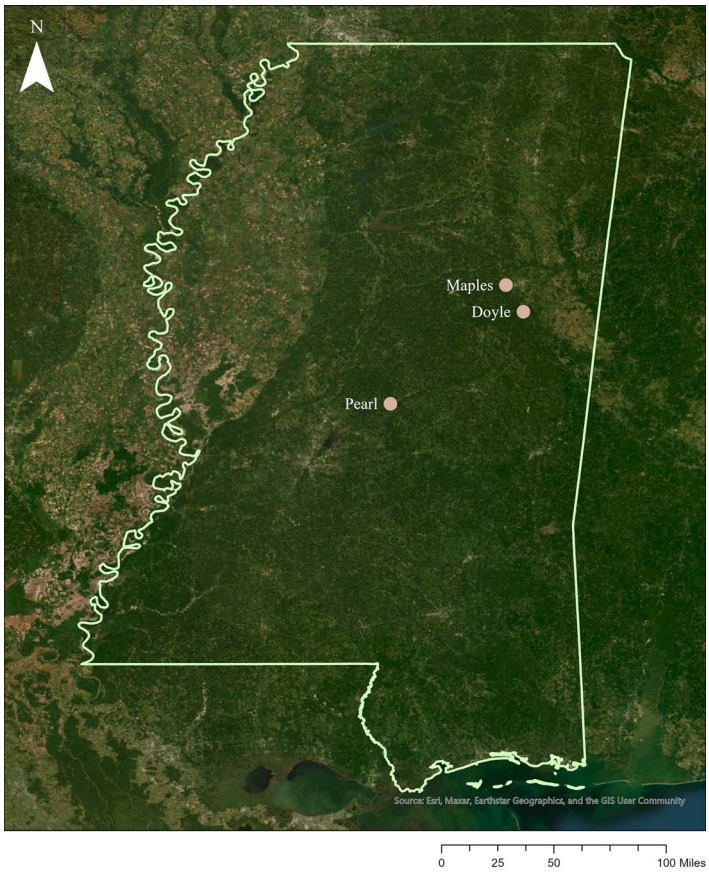

Figure 1. Sample site locations in Mississippi where biomass and temperature data were acquired in 2006 and 2007. The names in the map are site names and not cities.

Ultimately, this model will determine if temperature could be a limiting factor as to why parrotfeather is absent within the Midwest. Modeling data will inform aquatic plant managers of the potential range that parrotfeather may expand to and may be integrated into preventative management programs.

METHODOLOGY

Data on parrotfeather were collected monthly from three field locations in 2006 and 2007 in Mississippi (Figure 1). Thirty biomass samples were collected at each site, each month using a 0.018 m^2 PVC coring device as described in Madsen et al. (2007). Samples were transported to Mississippi State University and divided into emergent shoots, submersed shoots, stolons, and sediment roots. Plant parts were then dried for 72 hr at 70 C. Water depth was recorded for each sample at all locations prior to collecting a core; pH, conductivity, and turbidity were also collected for each site. The full methodology for field sampling, sample processing, and phenological data can be referenced in Wersal et al. (2011). Water temperature was recorded in 1-hr intervals across both years using HOBO pendent loggers that were deployed at each site (Wersal et al. 2011). With degree-day modeling becoming more prevalent for aquatic plants, previously collected data from 2006 and 2007 were used to create

an ADD model to assess the capability of parrotfeather to invade the upper Midwest. As indicated previously, there are few comprehensive studies on environmental drivers of parrotfeather, as well as no ecophysiology data on parrotfeather to put any ADD model data into context at the time of the original data collection (2006 to 2007). Anderson et al. (2026) offers a comprehensive comparison of photosynthetic responses of parrotfeather across a range of temperatures and light intensities, as well as directly comparing parrotfeather to other milfoils. Therefore, the current ADD model is more applicable and is strengthened by the inclusion of the new physiology data from Anderson et al. (2026).

Accumulated degree-day modeling

Peak submersed biomass was the life stage evaluated and was determined when at least 50% of samples attained maximum growth within a month at each sampling site (Snyder et al. 1999, Squires et al. 2024a). Binary values were used to signify if samples did 1) or did not 2) reach peak biomass. The model utilized data from three sampling sites that were pooled into one model as they were all located within Mississippi. Therefore, at least two of the three sites, or two-thirds, needed to reach peak biomass levels within the same month to exceed the 50% threshold (Snyder et al. 1999, Squires et al. 2024a,b). A one-way ANOVA was utilized to test for differences in the monthly submersed parrotfeather biomass. If a difference was determined, a Fisher Protected LSD was used to separate monthly biomass means to identify which month peak biomass occurred. All analyses were conducted at an $\alpha \leq 0.05$ significance level.

The model year was determined when submersed growth first began during a 365-day period. Submersed growth initiated in November; therefore, 1 November was chosen to be the beginning of the model year. ADD calculations were completed following the methodology outlined in Snyder et al. (1999) and Squires et al. (2024a), which estimated the ADDs needed to complete peak submersed biomass and the base threshold temperature. To determine the most accurate model, 40 potential models were evaluated. The root-mean-square error (*RMSE*) of the predicted number of days for submersed peak biomass to occur (*dpi*) was compared against the observed days for the submersed peak biomass to occur (*di*) over a range of potential base threshold temperatures (*n*) for each potential model. The following formula was utilized: $RMSE = \sqrt{\frac{(dpi-di)^2}{n}}$. The combination of ADD and base threshold temperature yielding the lowest *RMSE* was determined to be the best model. The R packages "ImerTest" (Kuznetsova et al. 2020), "emmeans" (Lenth 2022), "mosaic" (Pruim et al. 2021), "tidyverse" (Wickham 2022), "broom" (Robinson et al. 2022), "devtools" (Wickham et al. 2022), "drc" (Ritz and Strebig 2016), "nlme"(Pinheiro and Bates 2022), "rcompanion" (Mangiafico 2022), "FSA" (Ogle et al. 2022),"psych" (Revelle 2022), and "pollen" (Nowosad 2021) were used to calculate ADDs and statistically analyze models (R Core Team 2022).

Table 1. Results of submersed parrotfeather model fit analyses from RStudio relating the peak submersed biomass and accumulated degree-days (ADDs) for three lakes in Mississippi.

Model	Statistic	Test statistic	*P* value
Submersed Parrotfeather	Logistic regression (r^2)	0.66	<0.01
	Hosmer-Lemeshow (RMSE)	0.4	0.596
	Spearman (Rho)	0.55	<0.01
	Kendall (Tau)	0.46	<0.01

Model fit determination

Model fit was determined using RStudio and the "glm" function, which fits generalized linear models utilizing a binomial error distribution to evaluate the relationship between ADD and peak submersed biomass in plots for each month (Squires et al. 2024a). The goodness of fit for the linear regression model was evaluated using Hosmer and Lemeshow tests (Hosmer et al. 2013). The strength of the relationship between peak submersed biomass occurrence and ADD was evaluated using Spearman Rho (r_s) and Kendall tau (T) correlations (Spencer et al. 2000). Correlation strength was labeled as follows: 0 to 0.1 = no correlation, 0.1 to 0.4 = weak correlation, 0.4 to 0.6 = moderate correlation, 0.6 to 0.9 = strong correlation, and 0.9 to 1.0 = perfect correlation (Dancey and Reidy 2004). All statistical tests were conducted in R using the following packages: "rcompanion" (Mangiafico 2022), "car" (Fox et al. 2022), and "modEvA" (Barbosa et al. 2022, RCore Team 2022). All analyses were conducted in R statistical software at the $\alpha \leq 0.05$ significance level (R Core Team 2022).

RESULTS AND DISCUSSION

Model fit

Logistic regression analysis resulted in a positive (r^2= 0.66) relationship between ADD and submersed biomass in the Mississippi populations (Table 1). The Hosmer and Lemeshow tests indicated that there was no difference between the Mississippi model prediction and what was observed in the field ($P = 0.596$; Table 1). A moderately positive correlation was seen between ADD and submersed biomass ($r_s = 0.55$; $T = 0.46$; Table 1).

Accumulated degree-days

Submersed biomass peaked in February in both 2006 and 2007 (Table 2). Dry biomass in February averaged above 11 gm^{-2} during both sampling years. Submersed biomass senesced between June and August and began growing again in November (Wersal et al. 2011). The model estimated that 1,416 ADDs and 176 calendar days were needed for submersed parrotfeather to reach peak biomass. An estimated growing base water temperature threshold of 5 C was determined. Overall, there were 56 calendar days between the observed peak in submersed biomass and the model's predicted peak biomass date (Table 2).

The current model estimates 1,416 ADDs with a base threshold of 5 C for the submersed form of parrotfeather to reach its peak biomass. The submersed form of parrotfeather

Table 2. Accumulated degree-days (ADDs) calculated for a base temperature of 5 C (RMSE = 0.73) for each month from November to October utilizing averaged 2006 and 2007 data for three parrotfeather populations in Mississippi.

Month	Mean biomass (gm^{-2})	ADDs (base = 5 C)[1]
November	3.89	364.74
December	3.51	685.96
January	7.05	1,029.55
February	11.74	1,316.41
March	6.12	1,792.79
April	6.19	2,420.08
May	6.54	3,130.42
June	2.93	3,919.65
July	3.28	4,763.11
August	0.49	5,625.07
September	0.5	6,325.36
October	0.9	6,885.51

[1]The ADD model predicts 1,416 ADD (176 calendar days) to be needed for submersed parrotfeather to reach peak biomass.

is the form that would be needed to survive the winter months; thus, a submersed biomass model is much more informative of potential spread than an emergent model. Submersed shoots are the only part of parrotfeather that peaks in the winter months; emergent shoots, stolons, and root biomass peak in late spring or during the summer (Wersal et al. 2011). With a predicted base threshold of 5 C, this degree-day model suggests that parrotfeather is able to spread throughout the entire United States. The rate of plant growth and development is highly dependent on the temperature that the plant is subjected to, and each species has a specific range at which growth can occur (Hatfield and Prueger 2015).

Squires et al. (2024a,b) found the base threshold for growth in Cuban bulrush to be between −2 to −6 C depending on the state evaluated. Cuban bulrush models indicated varying base threshold air temperatures. Models based on air temperature rather than water temperature are subject to more potential variability within the model's base temperature threshold. The southernmost model, Florida, has the highest base temperature at −2 C but also the longest growing season (11 mo) while the northernmost model, Mississippi, had the lowest base temperature at −6 C but also the shortest growing season at approximately 8 mo (Squires et al. 2024a). This suggests that as data are collected closer to the limit of a plant's potential distribution, the model's predictive capability improves. However, the models produced by Squires et al. (2024a,b) were based on air temperature data, while those presented in this work were based on water temperature, which can be less variable and therefore a better predictor of plant growth.

Hydrilla has an estimated lower (8 to 16 C) and upper (12 to 21 C) water temperature threshold for sprouting depending on if the monoecious or dioecious form is present (Steward and Van 1987). Hydrilla follows a similar invasion pattern to parrotfeather as it also predominates the southeastern United States and along the East and West coasts (U.S. Geological Survey 2024b). However, since its introduction, hydrilla has begun spreading northward. Considering hydrilla does not sprout until a minimum water temperature of 8 C, its ability to survive and spread in the Midwest is due to its turions, which store almost 60% starch and 70% TNC (Madsen and Owens 1998). Likewise, sago pondweed (*Stuckenia pectinata*) germinates at water temperatures between 3 and 15 C and longleaf pondweed (*Potomogetum nodosus*) at 10 to 20 C (Spencer and Ksander 1992, Flint and Madsen 1995). Longleaf pondweed is spread throughout the United States and has an estimated germination temperature twice as high as submersed parrotfeather's base temperature for metabolic growth. Despite having a higher base threshold temperature, the pondweeds are able to survive the winter by producing winter buds and seeds that are able to stay dormant during unfavorable, freezing conditions (Frank 1966). Parrotfeather lacks seed production and similar storage structures and would be able to rely only upon its stolons for energy storage. Parrotfeather stolons store only 2 to 5% starch during the colder months of December through February (Wersal et al. 2011).

Even though parrotfeather does not have seeds or carbohydrate storage structures, it has the ability to photosynthesize at water temperatures below 5 C (Anderson et al. 2026). At 4 C, submersed parrotfeather had a net photosynthetic rate of 0.000775 μmol $g^{-1}s^{-1}$, which was statistically similar to both Eurasian watermilfoil and a hybrid watermilfoil strain (*Myriophyllum spicatum* × *Myriophyllum sibiricum*) (Anderson et al. 2026). All three submersed watermilfoils had appreciable photosynthetic rates at 4 C, but there were differences in light compensation points and light saturation points. Submersed parrotfeather had lower light compensation points and light saturation points than Eurasian watermilfoil and hybrid-5 watermilfoil across all temperatures tested, suggesting it may perform better under light-limiting conditions such as those experienced by lakes in winter (Anderson et al. 2026). However, in the almost 150 yr parrotfeather has been in the United States, there has never been a surviving population of parrotfeather within the central Midwest. Populations have not survived farther north than Missouri or southern Ohio in the central United States (USDA 2024).

The lack of parrotfeather within the Midwest is most likely not due to water temperature but a lack of light penetrating through the water column during winter months in the Midwest to drive photosynthesis and energy production. For survival, submersed, aquatic plants should receive at least 115 μmol $m^{-2}s^{-1}$ of photosynthetically active radiation (PAR) or 20% of ambient light reaching bottom sediments to support macrophyte growth (Chambers 1987, NIWA 2023). Winters in the Midwest result in high amounts of ice and snow coverage on the surface of waterbodies. Ice limits the amount of light that can penetrate to the bottom of the lake; for example, when ice thickness reaches 20 cm the mean daily, PAR value was just over 25 μmol $m^{-2}s^{-1}$ (Cavaliere et al. 2021). The light compensation point for submersed parrotfeather was approximately 50 μmol $m^{-2}s^{-1}$ photosynthetic photon flux density (PPFD) at 4 C, which was 73 and 83% lower than those of Eurasian- and hybrid-5 watermilfoils, respectively (Anderson et al. 2026). Adding snow on top of the ice results in little to no light being able to reach bottom sediments (Cavaliere et al. 2021). Despite submersed parrotfeather being able to photosynthesize at 4 C, there may be insufficient light from snow and ice cover, which limits plant

growth and energy storage. Though not established in the Midwest, parrotfeather has the ability to colonize waterbodies in cooler climates, specifically on the East and West coasts. The colonization of these areas is likely due to the high specific and latent heat characteristics that are inherent properties of water, and therefore the oceans would have a mediating effect on temperature in coastal areas with long-term ice cover being rare (Wright and Colling, 2007).

Additionally, parrotfeather is limited by its lack of sexual reproduction and energy storage structures or overwintering propagules. Parrotfeather only has stolons that store 2 to 5% starch to help survive over the winter months (Wersal et al. 2011), while other milfoils, like Eurasian watermilfoil, produce seed and have specialized structures like root crowns that store 20% starch, sugar, and TNC (Madsen 1997). Thus, lack of energy storage and localized climate factors, like ice and snow cover, may be limiting the spread of parrotfeather into the Midwest more so than water temperature. The submersed parrotfeather model considered populations only within the state of Mississippi; data from other models suggest that the base threshold may decrease if populations in northern locations were evaluated. However, to colonize and survive winters in the Midwest, parrotfeather will need to survive under ice in water temperatures of 4 C.

SOURCE OF MATERIALS

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ACKNOWLDGEMENTS

The authors would like to thank the Aquatic Plant Management Society and affiliated chapters for funding this research. We thank Allison Squires for her help with technical assistance in the construction of this model.

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