

Modeling accumulated degree-days for the invasive aquatic plants *Oxycaryum cubense* and *Eichhornia crassipes* in Mississippi

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ABSTRACT

Cuban bulrush [*Oxycaryum cubense* (Poepp. & Kunth) Lye] and water hyacinth [*Eichhornia crassipes* (Mart.) Solms] cause major ecological and economical impacts in the southeastern United States. These species are commonly associated with each other because of the epiphytic nature of Cuban bulrush, as it utilizes water hyacinth (and other floating plants or objects) as a colonization substrate. Increasing global temperatures may allow for the northward expansion of both species in North America. The purpose of this study was to model plant growth (i.e., biomass) as a function of accumulated degree-days (ADD) to predict peak biomass of both species growing in Lake Columbus, Mississippi. Models suggested water hyacinth and Cuban bulrush life cycles were asynchronous, thus ADD calculations did not occur over the same set of dates. Water hyacinth biomass peaked in September (estimated 5,399 ADD), and Cuban bulrush biomass peaked in February (6,549 ADD). Estimated base temperature threshold at which water hyacinth growth occurs is -1°C , while Cuban bulrush base threshold was estimated at -4°C . There was a difference of 10 and 100 ADD between the predicted and observed peak biomass occurrence of water hyacinth and Cuban bulrush, respectively. Models suggest Cuban bulrush can survive lower temperatures than water hyacinth and can potentially invade states farther north than its current distribution in the United States. It is likely that annual winter ice formation on water bodies will be the major barrier to northern expansion Cuban bulrush.

Key words: Cuban bulrush, environmental variables, epiphyte, floating plants, temperature, water hyacinth.

INTRODUCTION

Invasive plant species alter ecosystem structure and function through resource competition for light, water, and space (Gérard and Triest 2018, Spencer and Ksander 2006). Significant human resources are required to manage infestations of aquatic weeds that are left unchecked (Bryson et al. 2008,

Robles et al. 2011, Watson and Madsen 2014, Gettys et al. 2020). Approximately 50,000 invasive aquatic species cause nearly \$125 billion of major environmental damage and economic losses every year (Allendorf and Lundquist 2003). Any range expansion without proper prevention or management of invasive aquatic species will only exacerbate further economic and ecological losses (Allendorf and Lundquist 2003). However, with increasing global temperatures, range expansions of some species may be inevitable (Allendorf and Lundquist 2003, Kriticos and Brunel 2016).

Temperatures in the United States increased 1.8°C from 1895 to 2016, with 38% of that increase (0.7°C) occurring in the last 35 yr of that time range (Kriticos and Brunel 2016, Vose et al. 2017). The increase in temperatures is expected to cause warmer air and water temperatures worldwide (Rahel and Olden 2008). Climate-driven alterations to stream flow may also increase the dispersal of non-native species in many systems due to an increased rate of flooding (Rahel and Olden 2008). Therefore, due to temperature increases many invasive species may spread farther north in the United States (Rahel and Olden 2008, Kriticos and Brunel 2016, Vose et al. 2017). Furthermore, increases in temperature typically result in increased plant productivity due to increased rates of physiological processes (Riis et al. 2012). For example, an invasion of threadleaf water-crowfoot (*Ranunculus trichophyllus* Chaix) into several high-elevation lakes in the Himalayas has been associated with a decrease in the length of ice cover due to increased temperatures at higher altitudes (Rahel and Olden 2008). Several invasive species of the Pooideae subfamily on the sub-Antarctic Marion Island showed marked increases in photosynthesis with increases in temperature (Ripley et al. 2019). In addition, rising temperatures have shifted, and are expected to shift, plant hardiness zones northwards within the United States (Bradley et al. 2011). Accumulated degree-days (ADD) can be used to predict plant life cycle events as a function of temperature and therefore potentially predict potential range expansions as temperatures change (Snyder 1985, Snyder et al. 1999, Spencer et al. 2000).

Accumulated degree-days are heat units that measure the accumulation of energy over time such that higher temperatures yield increased ADD accumulation over time (i.e., calendar days). The use of ADD to predict the occurrence of specific life stages in plants (sprouting, peak biomass, flowering, senescence) is well documented and sometimes referred to as physiological time (Zalom et al. 1983, Snyder 1985, Snyder et al. 1999, Spencer et al. 2000). Physiological time can be measured in degree days, where one degree day is equal to one degree above the lower developmental threshold

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of a species over a 24-hr period (Zalom et al. 1983). The lower developmental threshold, or the base threshold, is the temperature below which plant development stops (Zalom et al. 1983, UC IPM 2016). Since ADD is based on temperature accumulation (rather than time), the ability of ADD to predict plant life stages is somewhat immune to changes in geographic location within a region when upper and lower threshold temperatures are incorporated (Snyder 1985, Snyder et al. 1999, Spencer et al. 2000). The Single Sine Method of ADD calculation utilizes the minimum and maximum temperatures recorded each day to produce a sine curve that estimates ADD by calculating the area above the base threshold and below the maximum threshold curves. This method assumes the temperature curve is uniform around the maximum temperature and works for any single threshold temperature or set of upper and lower threshold temperatures (Snyder 1985, Snyder et al. 1999, Spencer et al. 2000).

Water hyacinth [*Eichornia crassipes* (Mart.) Solms] and Cuban bulrush [*Oxycaium cubense* (Poepp. & Kunth) Lye] are two invasive floating aquatic plants in the southern United States that have phenological data available for use in ADD modeling (Clarke et al. 2023). Water hyacinth is a free-floating vascular plant that causes major ecological and socioeconomic issues as far north as Canada by forming dense, interlocking mats, which is done by its complex stolon and root structure and ability to rapidly reproduce (Villamagna and Murphy 2010). Water hyacinth reproduces sexually and asexually via clonal growth of stolons or via high levels of seed production (approximately 3,400 seeds m⁻²) and germination (Ueki and Oki 1979, Albano Pérez et al. 2011).

Cuban bulrush is an aquatic invasive plant, also from South America, and commonly associated with water hyacinth (Robles et al. 2011, Watson and Madsen 2014). Cuban bulrush has now spread to parts of Africa and Mexico and as far north as northern Alabama in the southeastern United States (Bryson et al. 2008, Carter 2005). Considered a perennial invasive plant, Cuban bulrush is known to exist as an epiphytic species that forms large floating islands, or tussocks, through roots and rhizomes that intertwine with other aquatic plants, which allow Cuban bulrush to use host species as a raft (Robles et al. 2011, Turnage 2018, Watson and Madsen 2014). For example, the leaf axils of water hyacinth's floating rosettes provide habitat for Cuban bulrush seeds to settle and germinate (Bryson et al. 2008). Once the rhizome network of Cuban bulrush assimilates enough sediment to form a tussock, the species is then capable of surviving independently and can begin reproducing via buoyant seeds and vegetative fragments that break off from the tussock (Watson and Madsen 2014, Turnage 2018). Multiple populations of Cuban bulrush are currently invading many multi-use lakes, reservoirs, and flowing waters that provide drinking water, hydroelectric power, outdoor recreational activities, and navigation for commercial and military vessels (Watson and Madsen 2014). Dense Cuban bulrush growth has also shaded out desirable submersed or emergent vegetation, including threatened and endangered species, which can cause cascading effects through the aquatic food web that negatively impact economically important fish species (Robles et al. 2007, 2011; Watson and Madsen 2014).

Cuban bulrush is known to tolerate tropical or subtropical climates (Grippio et al. 2014) but has been observed spreading

northward in the United States over the last two decades (Bryson et al. 2008, Rahel and Olden 2008, Fernandez 2013, Grippio et al. 2014, Vose et al. 2017). Water hyacinth reproduction and growth are strongly influenced by air and water temperature, where an increase in temperature correlates to more growth (Wilson et al. 2005). Similarly, a positive correlation exists between temperature and water hyacinth root length (Shu et al. 2014). The optimal temperature for maximum water hyacinth growth is 28–30 °C (Kriticos and Brunel 2016). Conversely, water hyacinth is not tolerant to winter frost for sustained periods, which has likely suppressed its growth in the northern United States and southern Canada (Owens and Madsen 1995, Kriticos and Brunel 2016, Miskella and Madsen 2019). As global temperatures increase water hyacinth is expected to expand its range poleward (Kriticos and Brunel 2016).

With increasing global temperatures, northern expansion of water hyacinth and Cuban bulrush is likely (Kriticos and Brunel 2016, Vose et al. 2017, IPCC 2022). Therefore, the objective of this study was to model and predict peak biomass development via ADD calculated in Mississippi plant populations to better understand the potential range expansion of both species into other states. This information will be valuable for water resource managers and other stakeholders trying to control or prevent the spread of aquatic invasive species.

MATERIALS AND METHODS

Site description

Lake Columbus is an impounded reservoir located in Lowndes and Clay counties (33°32'31"N; 88°29'27"W) in northeastern Mississippi (Figure 1). Covering approximately 32 km² (approximately 8,000 acres), Lake Columbus is the largest reservoir along the 370 km Tennessee-Tombigbee Waterway, which facilitates commercial transportation between the Gulf of Mexico and the Tennessee River (Auerbach et al. 1985, Green 1985). The waterway is also used for recreation (e.g., fishing) and provides wildlife habitat (Green 1985). The first record of Cuban bulrush within the waterway was in 2004 (Bryson et al. 2008) and shortly thereafter in Lake Columbus in 2005–2006 (Robles et al. 2011). Table 1 displays common co-occurring plant species with Cuban bulrush in Lake Columbus.

Plant sampling

The study was conducted on naturalized populations of water hyacinth and Cuban bulrush infesting Lake Columbus on the Tennessee-Tombigbee Waterway in northeast Mississippi from May 2019 to April 2021. Five sampling plots were established in Lake Columbus by using metal posts anchored into the lakebed at plot corners with each post geotagged in case of damage from water currents or floating debris. Mean depth of plots was 0.7 m (2.5 ft). Research plots were selected based on input from resource managers, ease of access for data collection efforts, and plant maturity within plots. Each month, Cuban bulrush and water hyacinth biomass was harvested from 12 random points in each plot by laying a 0.1 m² PVC frame on the water surface and collecting all biomass within the frame (Clarke et al. 2023), for a total of 60 samples

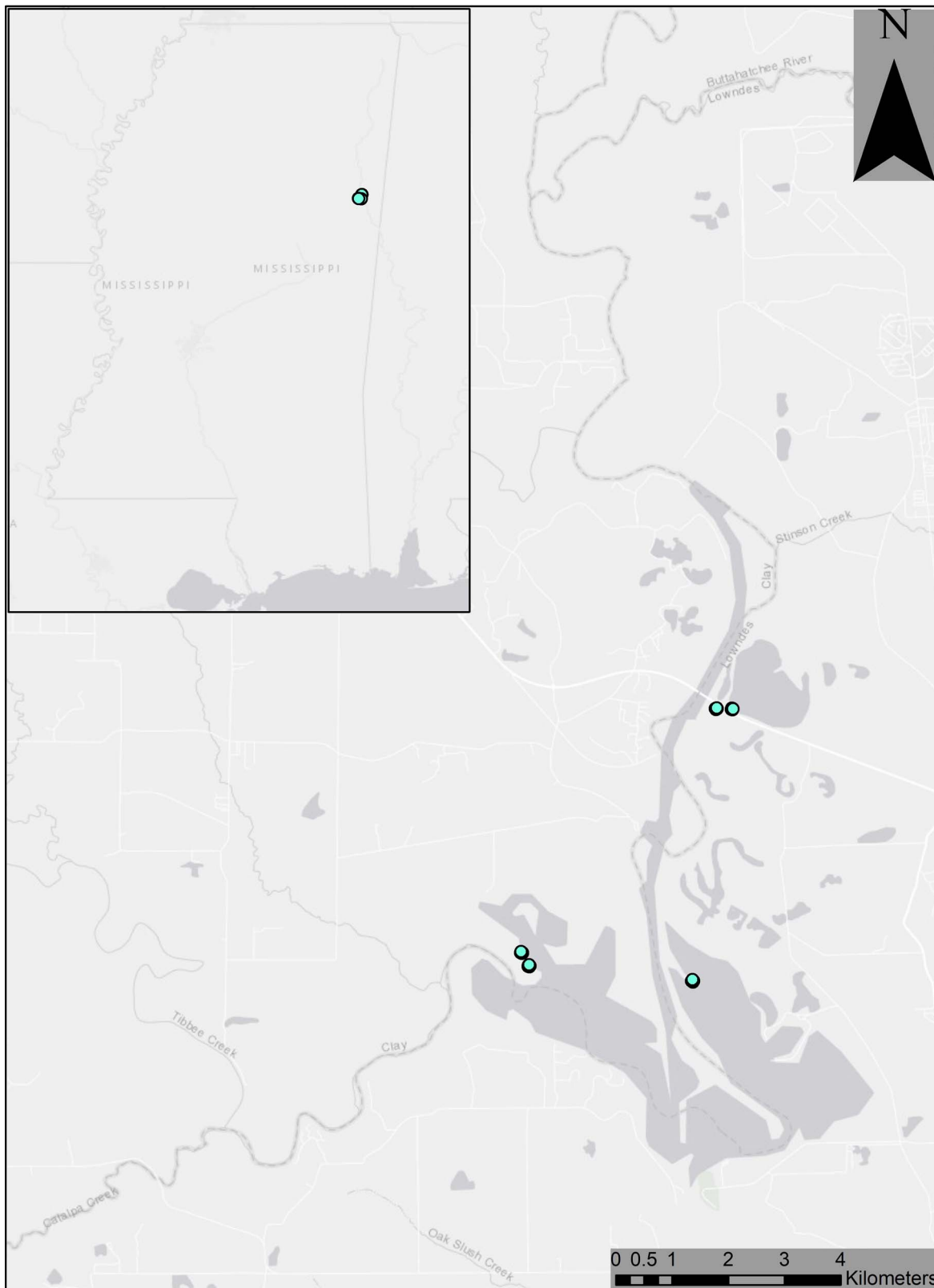


Figure 1. Plot locations in Lake Columbus, MS; sampling locations for monthly biomass harvesting of Cuban bulrush and water hyacinth are the teal dots.

TABLE 1. SPECIES LIST OF COMMON CO-OCCURRING PLANTS GROWING WITH CUBAN BULRUSH IN THE SAMPLING PLOTS DURING 2019 AND 2020. VISUAL OBSERVATION WAS USED TO IDENTIFY AND RECORD ALL PLANTS SPECIES WITHIN 3 M OF SAMPLING PLOTS. PLANT SPECIES IN BOLD FONT ARE CONSIDERED NON-NATIVE AND PROBLEMATIC SPECIES IN MISSISSIPPI OR OTHER PARTS OF THE UNITED STATES.

Scientific name	Common name
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	Alligatorweed
<i>Azolla caroliniana</i> Willd.	Carolina mosquitofern
<i>Bacopa caroliniana</i> (Walter) B.L. Rob.	Blue water hyssop
<i>Bidens cernua</i> L.	Nodding beggartick
<i>Cyperus esculentus</i> L.	Yellow nutsedge
<i>Eichhornia crassipes</i> (Mart.) Solms	Water hyacinth
<i>Eleocharis obtusa</i> (Willd.) Schult.	Blunt spikerush
<i>Hydrilla verticillata</i> (L.f.) Royle	Hydrilla
<i>Hydrocotyle ranunculoides</i> L.f.	Floating marshpennywort
<i>Hydrocotyle umbellata</i> L.	Many flower marshpennywort
<i>Hydrolea quadrivalvis</i> Walter	Waterpod
<i>Justicia americana</i> (L.) Vahl	American water-willow
<i>Landoltia punctata</i> (G. Mey.) D.H. Les & D.J. Crawford	Spotted duckweed
<i>Lemna minor</i> L.	Common duckweed
<i>Limnobium spongia</i> (Bosc) Rich. Ex Steud.	American frogbit
<i>Ludwigia grandiflora</i> (Michx.) Greuter & Burdet	Large flower primrose
<i>Ludwigia leptocarpa</i> (Nutt.) H. Hara	Anglestem primrose
<i>Ludwigia peploides</i> (Kunth) P.H. Raven	Creeping water primrose
<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	Parrotsfeather
<i>Oxycaryum cubense</i> (Poepp. & Kunth) Lye	Cuban bulrush
<i>Paspalum distichum</i> L.	Knotgrass
<i>Peltandra virginica</i> (L.) Schott	Green arrow-arum
<i>Sacciolepis striata</i> (L.) Nash	American cupscale
<i>Sagittaria latifolia</i> Willd.	Broadleaf arrowhead
<i>Salvinia molesta</i> Mitchell	Giant salvinia
<i>Schoenoplectus tabernaemontani</i> (C.C. Gmel.) Palla	Softstem bulrush
<i>Sesbania herbacea</i> (Mill.) McVaugh	Hemp sesbania
<i>Taxodium distichum</i> (L.) Rich.	Bald cypress
<i>Triadenum walteri</i> (J.G. Gmel.) Gleason	Greater marsh St. Johnswort

per month. Harvested Cuban bulrush biomass was separated from water hyacinth biomass and placed in labeled plastic bags, stored in a cooler, and transported on ice to Mississippi State University (Starkville, MS) where plants were separated into emergent (shoots and leaves), submergent (stolons and roots), and inflorescence biomass (Clarke et al. 2023). Water hyacinth biomass was not separated by tissue type, but all other processes were completed in the same manner as Cuban bulrush samples. All biomass samples were dried at 70 C for 5 days in a forced air oven. Once dried, samples were weighed and weights recorded. Biomass samples for both plants were not harvested in February 2020 because of heavy flooding.

Environmental data collection

Onset HOBO pendant loggers¹ were positioned on a post at the corner of each plot approximately 1 m above the water surface. Loggers from each site collected minimum and maximum air temperature every hour for the duration of the study. Temperature data that were unattainable because of weather events, equipment failure, or dates prior to the study start date were supplemented with comparable temperature data from a nearby weather station (27 km [17 miles] west of the study sites) at the Mississippi State University RR Foil

TABLE 2. WATER HYACINTH MEAN BIOMASS (±1 SE), AND ACCUMULATED DEGREE-DAYS (ADD) AT BASE 0 C AND -1 C FOR EACH MONTH OF 2019 AND 2020 COMBINED.

Month	Biomass (g DW/quadrat)	ADD (base = 0 C)	ADD (base = -1 C)
Jan.	51.8 (15.7) ^B	263	292
Feb.	24.6 (2.3) ^B	564	621.5
Mar.	41.8 (14.1) ^B	1,015	1,102
Apr.	42.0 (12.6) ^B	1,510	1,628
May	115.5 (23.8) ^B	2,193	2,341
June	201.47 (62.4) ^{AB}	2,953	3,132
July	242.0 (68.0) ^{AB}	3,798	4,008
Aug.	296.0 (68.7) ^{AB}	4,634	4,875
Sept.	534.82 (99.8) ^A	5,399	5,670
Oct.	322.7 (57.9) ^{AB}	5,979	6,281
Nov.	337.1 (80.0) ^{AB}	6,326	6,658
Dec.	337 (72.5) ^{AB}	6,605	6,966

An estimated 5,429 ADD were needed to attain peak water hyacinth biomass (20 September; 263 calendar days); hyacinth development was negligible below a base temperature threshold of -1 C (root mean squared error [RMSE] = 0.00); observed peak biomass was 30 September at 5,399 ADD; biomass values sharing a letter are not different at $\alpha = 0.05$ according to Dunn's All-Pairwise Comparisons test ($n = 11$).

Plant Science Research Station (33.470041°N; 88.78003°W). Air temperature was measured as it could have a greater influence on growth because water hyacinth and Cuban bulrush are emergent floating plants, but we acknowledge that water temperature will impact growth of both species. Air temperature was also chosen because it is often more readily available to resource managers.

Accumulated degree-days modeling

A Wilcoxon Rank Sum test was performed on temperature data to determine if differences existed between 2019 and 2020 because these years had two complete sampling seasons. Temperature data from 2021 were not analyzed because only 3 mo of data were available given that sampling ended in April 2021. Mean annual temperatures for 2019 and 2020 were 24.4 ± 1.2 and 21.4 ± 1.0 C, respectively, and were not different ($P = 0.10$). Biomass data were then pooled across years for each month, and a Kruskal-Wallis one-way analysis of variance test was performed on monthly biomass data to detect differences in biomass among months. Pooling data across years resulted in a model with $n = 10$ (plots sampled in each year) rather than two separate models with $n = 5$ plots. Biomass within the 12 subsamples in each plot was the dependent variable, and month was the independent variable. If differences were detected, a Dunn's All-Pairwise Comparisons test was used to further separate monthly biomass means. Peak biomass was defined as 50% of plots achieving peak biomass.

Water hyacinth and Cuban bulrush exhibited asynchronous life cycles (Tables 2 and 3) with the Cuban bulrush lifecycle occurring across calendar years rather than within a calendar year; thus ADD calculations for each species occurred over different periods of time. Snyder et al. (1999) provided an iterative process to simultaneously calculate ADD and estimate base temperature thresholds by assessing the root-mean-squared error (RMSE) between the predicted days for a life stage to occur (d_{pi}) versus the observed days for the stage to occur (d_i) over a range of dates (n) using the formula

TABLE 3. CUBAN BULRUSH EMERGENT BIOMASS (± 1 SE), AND ACCUMULATED DEGREE-DAYS (ADD) AT BASE 0 C AND -4 C FOR EACH MONTH OF 2019 AND 2021 COMBINED.

Month	Biomass (g DW/ quadrat)	ADD (base = 0 C)	ADD (base = -4 C)
Mar,	10.2 (4.7) ^{BC}	454	578
Apr.	8.5 (3.8) ^C	950	1,194
May	19.1 (7.4) ^{ABC}	1,633	2,001
June	20.8 (7.2) ^{ABC}	2,395	2,883
July	25.9 (10.4) ^{ABC}	3,240	3,852
Aug.	32.9 (10.6) ^{ABC}	4,077	4,813
Sept.	55.2 (19.3) ^{ABC}	4,842	5,698
Oct.	83.8 (23.8) ^{AB}	5,423	6,403
Nov.	79.7 (22.8) ^{ABC}	5,771	6,871
Dec.	126.7 (33.7) ^{AB}	6,051	7,270
Jan.	29.6 (8.1) ^{ABC}	6,296	7,639
Feb.	128.84 (16.9) ^A	6,549	8,001

An estimated 6,449 ADD were needed to attain peak emergent biomass (4 November; 249 calendar days); plant development was negligible below a base temperature threshold of -4 C (root mean squared error [RMSE] = 0.71); observed peak biomass was 28 February at 6,549 ADD; biomass values sharing a letter are not different at $\alpha = 0.05$ according to Dunn's All-Pairwise Comparisons test ($n = 11$).

$$\text{RMSE} = \sqrt{\left(\frac{(\text{dpi} - \text{di})^2}{n}\right)}.$$

The target life stage here was the occurrence of peak emergent biomass, and the combination of date, ADD, and base temperature yielding the lowest RMSE was assumed to define the strongest model for predicting peak biomass occurrence in water hyacinth and Cuban bulrush (Snyder et al. 1999). ADD calculations were conducted in R (R Core Team 2022).

Models were assessed in R using the 'glm' function with a binomial error distribution to assess the relationships between ADD and biomass for both species during each month. A Hosmer-Lemeshow test was used to evaluate the goodness of fit for each logistic regression model (Hosmer et al. 2013). Further assessment was done to evaluate the predictive ability of the model by conducting Spearman and Kendall correlations between ADD and the proportion of plots that had reached peak biomass. Correlation strength was defined as 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 (Dancy and Reidy 2004). All statistical tests were conducted using an $\alpha \leq 0.05$ in R statistical software.²

RESULTS AND DISCUSSION

Water hyacinth biomass peaked in the fall of each year; thus, water hyacinth ADD were calculated over a normal calendar year (1 January to 31 December). However, Cuban bulrush biomass peaked in the winter months of each year, therefore degree day accumulation began after the coldest minimum temperature was recorded each year and ended 365 days later. Cuban bulrush ADD was accumulated from 1 March to 28 February (365 days) each year.

Observed seasonal biomass and air temperature

Water hyacinth biomass peaked ($534.82 \text{ g DW m}^{-2}$) in September when average air temperature was 25 C ($P < 0.0001$;

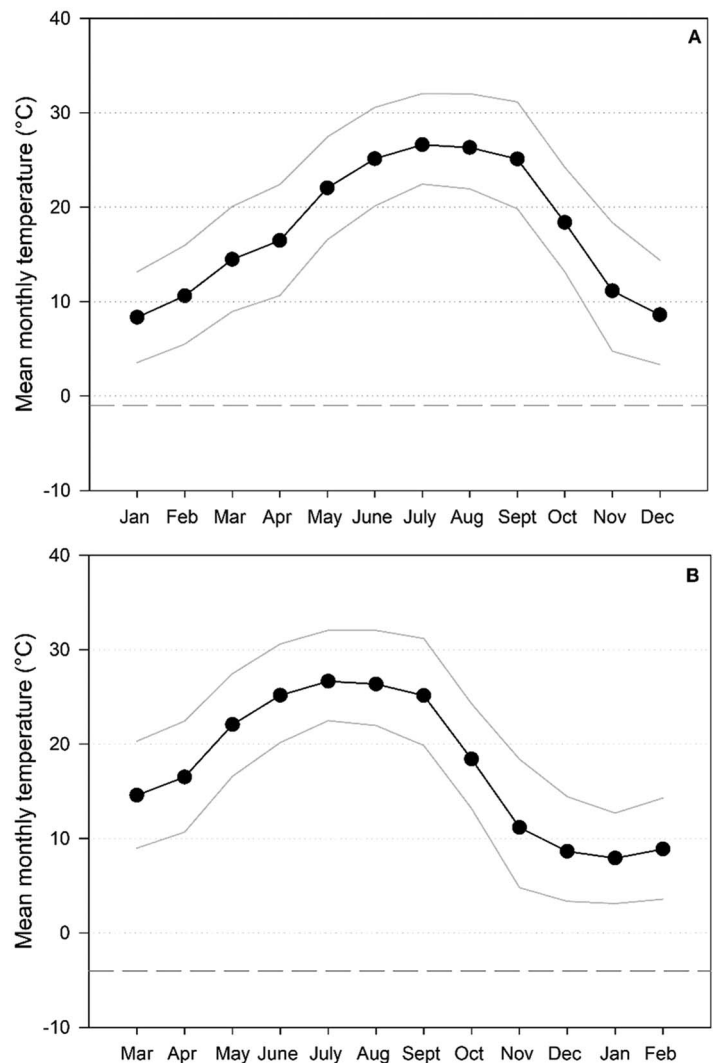


Figure 2. Mean monthly temperature (C) for water hyacinth (A) and Cuban bulrush (B) from combined years used to estimate accumulated degree-days needed to attain peak biomass; the dashed line is the estimated minimum temperatures threshold at which water hyacinth growth is negligible (-1 C) and Cuban bulrush growth is negligible (-4 C); gray lines are maximum and minimum temperatures observed each month.

Table 2; Figure 2). The calculated date of water hyacinth peak biomass was 20 September (263 calendar days; $\text{RMSE} = 0.000$), and the observed date of peak biomass was 30 September (273 calendar days). Cuban bulrush peak biomass (128.84 DW m^{-2}) was closely associated with minimum temperatures and occurred in February, which had average air temperatures of 10 C ($P < 0.0001$; Table 3; Figure 2). The calculated date of Cuban bulrush peak biomass was 4 November (249 calendar days from previous minimum temperature; $\text{RMSE} = 0.71$) and the observed date of peak biomass was 28 February (365 calendar days). Cuban bulrush growth began earlier (April) than water hyacinth (June) and continued longer each year likely due to a lower calculated base threshold for growth (-4 C ; Table 3) than that of water hyacinth (-1 C ; Table 2).

Previous studies assessing the relationship of water hyacinth phenology and air temperature found a strong positive linear relationship between biomass and increasing air temperature

TABLE 4. STATISTICAL TESTS FOR WATER HYACINTH (2019–2020) AND CUBAN BULRUSH (2019–2021) RELATING ACCUMULATED DEGREE-DAYS (ADD) AND PEAK BIOMASS FROM EACH COMBINED MODEL.

Model	Statistic ¹	Test statistic	P value
Water hyacinth	Logistic regression (r^2)	0.49	< 0.01
	Hosmer-Lemeshow (RMSE)	0.8	0.44
	Spearman (ρ)	0.56	< 0.01
	Kendall (τ)	0.48	< 0.01
Cuban bulrush	Logistic regression (r^2)	0.84	< 0.01
	Hosmer-Lemeshow (RMSE)	0.6	0.49
	Spearman (ρ)	0.8	< 0.01
	Kendall (τ)	0.68	< 0.01

¹Logistic regressions (r^2) assessed the strength of the relationship between ADD and the proportion of water hyacinth plots that reached peak biomass over time (0–1.0 scale); a Hosmer-Lemeshow (root-mean-squared error [RMSE]) test was used to evaluate of the goodness of fit for each logistic regression ($P > 0.05$ is a good fit); Spearman (ρ) and Kendall (τ) correlations were used to further evaluate the relationship between the proportion of plots that reach peak biomass and degree day accumulation (0–1.0 scale).

40 C (Bock 1969, Wilson et al. 2005, Villamagna and Murphy 2010), which was confirmed here (Table 2; Figure 2). Water hyacinth biomass decreased after the first frost, whereas Cuban bulrush biomass persisted and increased into the coldest months (Tables 2 and 3), which was also reported by Clarke et al. (2023) when assessing the correlation between Cuban bulrush biomass, water temperature, and incident light. Cuban bulrush growth in subfreezing air temperatures suggests Cuban bulrush may have a broader temperature tolerance than previously thought. However, Cuban bulrush growth in subfreezing air temperatures may also be due to the ability of water to moderate atmospheric temperatures for a short time (Oke 1987). As other plant species senesced, Cuban bulrush may have been released from competitive pressures and had access to more resources, as seen in Wundrow et al. (2012) when alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.] increased in abundance after removal of water hyacinth and water lettuce (*Pistia stratiotes* L.).

Degree-days and predicted seasonal biomass

Accumulated degree days were a moderate predictor of water hyacinth peak biomass occurrence ($r^2 = 0.49$; $P < 0.0001$; Table 4). Model predictions were not different from observed water hyacinth growth (RMSE = 0.8; $P = 0.44$; Table 4); there was only a difference of 10 calendar days and 30 ADD between predicted and observed peak biomass occurrence (Table 2). ADD was a strong predictor of Cuban bulrush peak biomass occurrence ($r^2 = 0.84$; $P < 0.0001$; Table 4). Model predictions were not different from observed Cuban bulrush growth (RMSE = 0.6; $P > 0.05$; Table 4) but were not as accurate as water hyacinth models as there was a difference of 116 days and 100 ADD between predicted and observed peak biomass occurrence. Peak emergent biomass occurrence had a strong positive correlation to ADD for Cuban bulrush ($\rho = 0.8$; $\tau = 0.68$; $P < 0.01$ for both) and water hyacinth ($\rho = 0.56$; $\tau = 0.48$; $P < 0.01$ for both) peak biomass occurrence (Table 4).

The current model predicted a base temperature threshold for water hyacinth growth of -1 C. Previous studies have confirmed that temperatures below 0 C killed emergent water hyacinth foliage (Center and Spencer 1981, Owens and Madsen 1995, Miskella and Madsen 2019). Owens and Madsen (1995)

reported 2–3 wk of exposure below freezing is necessary to kill the stem base of water hyacinth, and that short-term freeze events (approximately 48 hr) did not affect the stem base survival, even with ice formation. Unlike water hyacinth, Cuban bulrush growth continued until temperatures fell to -4 C, which suggests the species is metabolically capable of expanding its invaded range into states farther north (e.g., Nebraska; NOAA 2022) with average winter temperatures near the base threshold temperature calculated in this study. Pryor et al. (2013), predicted an increase of 2.7 C in the middle of the century (2046 to 2065) and 4.7 C by the end of the century (2081 to 2100) compared to temperatures recorded between 1979 and 2000. However, the major limiting factor to northern expansion of Cuban bulrush in North America will be prolonged ice cover in water bodies.

Future research should model water hyacinth and Cuban bulrush populations with water temperature, as the latent heat of water and the moderation of temperatures around an aquatic plant may elicit a more accurate model (Oke 1987, Owens and Madsen 1995). Experiments should also assess geographic variation in Cuban bulrush populations to validate the use of ADD as a predictive metric of plant growth across the invaded range. Additional environmental variables (such as photoperiod and water temperature) and plant variables (such as starch allocation) should also be assessed to further refine ADD models used to predict water hyacinth and Cuban bulrush growth across their invaded ranges. To our knowledge, this is one of the only studies examining the relationship between ADD and free-floating or epiphytic floating aquatic plants (Spencer et al. 2000, Spencer and Ksander 2006). The models developed here for water hyacinth and Cuban bulrush growth had similar levels of accuracy (correlation, goodness of fit) as previous studies examining ADD as a predictor of aquatic plant growth for other species (Spencer et al. 2000, Spencer and Ksander 2006), which suggests this method can be used to predict the growth of other floating aquatic plants.

SOURCES OF MATERIALS

¹Onset HOBO pendant logger, Onset Computer Corporation, Bourne, MA 02532.

²R Core Team, R Foundation for Statistical Computing, Vienna, Austria.

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