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ORIGINAL RESEARCH ARTICLE

Negative Impacts of an Invasive Pasture Grass on a Native Wetland Herb Increase with Hydroperiod

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Abstract
Many wetland ecosystems face the compounding challenges of invasive species and changing precipitation regimes. However, these effects and their interactions are not experienced uniformly by native plants across a given wetland due to temporal and spatial heterogeneity in both environmental and plant demographic factors. While hydroperiod is known as a key factor influencing plant community composition in wetlands, less is known about how native species' demographic traits may vary across a hydroperiod gradient and how this variation could impact interactions with non-native species. To fill these gaps, we conducted a plant demographic study in a wet meadow in south-central Idaho, United States, to understand: (1) how the demographic traits (survival, growth, flowering) of a native perennial geophyte *Camassia quamash* vary across a hydroperiod gradient, and (2) how the impacts of an invasive, rhizomatous pasture grass, *Alopecurus arundinaceus*, on this native species may vary across this same gradient. We found that *C. quamash* exhibits higher survival, but reduced flowering in drier upslope areas of the wet meadow, while *A. arundinaceus* had a greater per-unit negative impact on *C. quamash* in longer hydroperiod areas. This study is one of very few to assess how plant demographic traits vary with hydroperiod in wetlands and we suggest that variation in native plant demographic traits across environmental gradients should be considered in the study of species interactions in wetlands and beyond.

Keywords Plant demography · Hydroperiod · Interactive effects · Global change · Culturally-significant plants · Wet meadow

Introduction

Plant biodiversity is threatened by a range of interacting abiotic, biotic, and anthropogenic stressors that may alter plant demographic processes, potentially threatening population persistence (Tylianakis et al. 2008; Morris et al. 2020). The simultaneous and potentially nonadditive nature of these stressors significantly complicates our ability to prepare for and protect biodiversity under global change (Brook et al. 2008; Ehrlén et al. 2016). Chief among these stressors are climate change and invasive species (Ward and Masters 2007; Finch et al. 2021). Climate change is an overarching driver of change that is expected to impact all ecosystems, and will likely interact with key biotic drivers, including invasive species (Ward and Masters 2007; Franklin et al. 2016). For example, invasive species often have broad climatic tolerances, meaning their relative competitiveness could increase with changing climate, further limiting opportunity for native plant persistence (Hellmann et al. 2008). The future success of plant conservation rests, in part, on basic understanding of how these two key drivers of change will impact plant population dynamics. However, we have limited understanding of how multiple simultaneous drivers of global change and their interactions impact plant populations (Brook et al. 2008; Tylianakis et al. 2008; Ehrlén et al. 2016; Bernardo et al. 2019; Morris et al. 2020).

Wetlands are highly threatened, dynamic ecosystems ideally suited for studying the interactions of invasive species with climate because they are both prone to invasion (Zedler and Kercher 2004) and sensitive to changes in precipitation

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with climate change (Didiano et al. 2018; Cao et al. 2020). Wetlands are vulnerable to plant invasions, in part, because wetlands: (1) are landscape sinks that accumulate nutrients and debris that invasive plants may more efficiently capitalize on compared to native species, (2) may facilitate the transport of invasive plant seeds through water, and (3) the sediment and debris that flow into wetlands from surrounding land disturbances can flatten terrain and/or create canopy gaps for invasives to colonize (Zedler and Kercher 2004). Wetlands are also sensitive to climate change, and, in particular, changes to precipitation that may influence hydroperiod, or the percentage of time a wetland area is inundated. Hydroperiod largely drives plant species composition in wetlands, though other factors such as species interactions, soils, and disturbance history are also important (Boettcher and Johnson 1995; De Steven and Toner 2004; Foti et al. 2012). Wetland plants experience both periodic flooding as well as periodic drought (Li et al. 2013). Given the need for wetland plants to tolerate changing water and other environmental conditions, hydroperiod is an important driver not only of plant community composition, but also of plant vital rates (survival, growth, and reproduction) in wetlands, which in turn will impact species interactions. However, previous demographic studies of wetland plant species are very limited (Knox 1997; Hart-Fredeluces et al. 2025; Littlefield et al. 2025) and do not provide insights on how demographic traits may be impacted by the interactive effects of hydroperiod and invasive species.

Hydroperiod varies across a given wetland (Stewart and Kantrud 1971; Cowardin et al. 1979; Tiner 1984). In some wetlands, for example, vegetation zones may occur in more-or-less concentric rings around a central basin, with water persisting longest in the deepest central parts of the wetland, while only temporarily flooding the outermost wetland zone (Stewart and Kantrud 1971). Across these wetland zones, plant species composition will vary, and some studies have found longer hydroperiod areas to have greater plant biomass, but lower species richness compared to areas with a shorter durations of inundation (Boettcher and Johnson 1995; Jones et al. 2011). While previous work has explored the demography of plant species in core versus peripheral populations or in ecologically marginal conditions (Lesica and Allendorf 1995; Nantel and Gagnon 1999; Angert 2006) very few studies have explored variation in demography of a wetland species across a hydroperiod gradient, or even between longer and shorter hydroperiods over time (Littlefield et al. 2025).

Hydroperiod is also known to influence competitive interactions between non-native invasive and native plant species. Some invasive species in wetlands have been shown to be more tolerant to water level fluctuations and therefore may gain a competitive advantage and become more common with climate change, such as *Typha* x *glauca*, which is more tolerant of prolonged flooding than native species (Galatowitsch et al. 1999), or *Myriophyllum spicatum*, which was more tolerant of low water after a storm than surrounding native vegetation (ibid.), a concept known as the broader tolerance hypothesis (Zedler and Kercher 2004). The underlying mechanisms possibly supporting greater invasive competitiveness with increased water depth or duration of flooding include increases in root to shoot ratios, overall greater biomass, and production of plant tissues that help plants tolerate anoxia such as adventitious roots and aerenchyma (Coops 1996; Smith and Brock 1996; Miller and Zedler 2003).

In this study, we explore how the impacts of the non-native pasture grass *Alopecurus arundinaceus* on native *Camassia quamash* vary over a hydroperiod gradient at a wet meadow in south-central Idaho, USA. This study supports a basic understanding of interactive effects of invasive species and climate change on native plants, while also providing practical insights into the conditions that may allow for the persistence of native vegetation at this site. The introduction of Eurasian grasses to prairies and wet meadows in the USA has dramatically changed the structure and functioning of many wetlands (Galatowitsch et al. 1999), and our study site is at a critical stage of invasion where *A. arundinaceus* is quickly invading and expanding its range, but does not yet dominate the entire site. Our study site is also part of the traditional homelands of the Shoshone-Bannock Tribes, whose citizens continue to care for and harvest plants such as *C. quamash* from this place. Identifying conditions under which *A. arundinaceus* is less invasive or where *C. quamash* may be able to coexist with *A. arundinaceus* is critical to identifying management approaches that may limit the dominance of *A. arundinaceus* at this site and allow for the persistence of native vegetation.

To enhance our understanding of plant responses to multiple stressors, and to contribute knowledge relevant to state managers and cultural practitioners for the protection of *C. quamash* and this wetland, we ask the following:

1. How do *C. quamash* vital rates (survival, growth, and flowering) vary across a hydroperiod gradient (between upslope, midslope, and marsh bottom areas) at the Camas Prairie Centennial Marsh?
2. How is invasive *A. arundinaceus* impacting *C. quamash* vital rates across this gradient?

We expect that the survival rate of *C. quamash* plants will be highest in short hydroperiod areas because under resource-limitations, like drought, plants are known to allocate resources preferentially to survival rather than growth or flowering (Baden et al. 2021). Conversely, we expect growth and flowering to be higher in longer hydroperiod

areas because plants with longer hydroperiods would be larger plants and would be less resource-limited (Warwick and Brock 2003; Littlefield et al. 2025).

We further expect that *A. arundinaceus* will reduce *C. quamash* survival, growth, and reproduction through direct competition for light, space, and nutrients, and that this suppression will be strongest in longer hydroperiod areas because *A. arundinaceus* will take better advantage of the increased water availability by increasing its overall biomass (Miller and Zedler 2003).

Methods

Study Site

The Great Camas Prairie is a mountain valley in south-central Idaho that is approximately 1,420 square kilometers and is part of the traditional homelands of the Shoshone-Bannock Tribes. This area was reserved by the Shoshone-Bannock in the Fort Bridger Treaty of 1868. Our study site, the Camas Prairie Centennial Marsh (CPCM), which is approximately 25 km^2, is the largest remaining remnant camas meadow within the Great Camas Prairie. While Tribal citizens continue to harvest camas (*Camassia quamash*) and care for CPCM today, the treaty guarantee to reserve these lands for the Shoshone-Bannock has never been fulfilled by the U.S. government (Evans, 2017; Fellows et al. 2023; G. Smoak, 2004; G. Smoak, 2008).

Today, the Camas Prairie Centennial Marsh (CPCM) Wildlife Management Area is managed by the Idaho Department of Fish and Game, as well as through a co-tenancy agreement with the Shoshone-Bannock Tribes. CPCM is located on a large floodplain at 1,550 m that receives approximately 400 mm precipitation per year (Gregory 2014). This wetland is surrounded by farmland and sagebrush steppe and is seasonally flooded by snowmelt. The wetland is typically inundated from mid-April to mid-July, with 70% of the marsh covered by less than 30 cm of water (Gregory 2014). *Camassia quamash* is abundant in some parts of CPCM and is a culturally-significant food plant to the Shoshone-Bannock Tribes (Fellows et al. 2023). Mass purple blooms of camas also attract thousands of "lily lookers" each year to the CPCM, providing economic benefit to some members of the local rural community (Gregory 2014). The majority of the marsh is categorized as a palustrine, emergent, persistent wetland with a seasonally flooded water regime (Cowardin et al. 1979; Gregory 2014). Surrounding this vegetation type, and defining the transition between wetland and upland, is a scrub-shrub, broad-leaved evergreen, seasonally flooded wetland (Cowardin et al. 1979) with a predominant overstory cover of silver sagebrush (*Artemisia cana*) (Table 1).

Table 1 Total number of plant species recorded in each plot type ($n=6$ plots per zone, each 1 × 1 m in size) in 2020 or 2021 and average percent cover of common species in our plots across each hydroperiod zone. These percentages from our experimental plots are not necessarily representative of the marsh as whole, in part because plots for this study were only accepted plots if they had at least 5% *Alopecurus arundinaceus* and 15% *Camassia quamash* percent cover

Wetland zone	Upslope	Midslope	Marsh bottom
Total # species in study plots	16	18	24
Artemisia cana	14%	0%	0%
Poa spp.	17%	0%	0%
Eleocharis palustris	0%	10%	23%
Juncus nevadensis	0%	12%	16%
Senecio hydrophilus	1%	5%	10%
Camassia quamash	30%	26%	17%
Alopecurus arundinaceus	14%	26%	21%

Study Species

Common or blue camas, (*Camassia quamash*, Asparagaceae) is a native geophytic herb that occurs in seasonally wet habitats across the Pacific Northwest (Turner and Kuhnlein 1983; Beckwith 2004). *Camassia quamash*'s edible bulbs are a key component of the foodways of Indigenous Peoples across the Pacific Northwest (Turner and Kuhnlein 1983; Thoms 1989; Beckwith 2004; Carney et al. 2021), and *C. quamash* also provides food and habitat for animals from insects to elk (Thoms 1988; Beckwith 2004; Parachnowitsch and Elle 2005). *Camassia quamash* reproduces both sexually and asexually, though asexual reproduction may be rare, and the drivers of asexual reproduction are poorly understood (Thoms 1989; Stucki 2018). *Camassia quamash* at CPCM typically flowers in the last 10 days of May and senesces in June and July (T. Gregory pers. comm. 2020, GHF pers. observ. 2019–2025). Flowers on camas' racemose inflorescence take about 10 days to fully open, and flowering occurs earlier in drier portions of the marsh (GHF, pers. observ, A. V. Thoms 1989, p141).

Creeping meadow foxtail (*Alopecurus arundinaceus* Poaceae) is a long-lived, strongly rhizomatous, cool-season pasture grass that was introduced to North America from Eurasia by the early 20th century and is now naturalized in the Intermountain West, Great Plains, Pacific Northwest, and Great Basin (Boe and Delaney 1996). It is adapted to areas of high moisture and cold temperatures (Boe and Delaney 1996) and may display vigorous growth of rhizomes of up to 120 cm crown diameter per year (Tilley 2004). The Garrison cultivar, Garrison creeping meadow foxtail, that is present at CPCM, was first collected and named in North Dakota in 1963 (Tilley 2004). From here forward, the use of the scientific name *Alopecurus arundinaceus* in this article refers to this cultivar, Garrison creeping meadow foxtail. *Alopecurus arundinaceus* has been planted in the CPCM and surrounding areas for forage, hay

production, and erosion control (T. Gregory pers. comm. 2020, unpublished data, GHF, 2025). Spring growth and initiation of flowering in *A. arundinacueus* occur along a similar timeframe as *C. quamash* at the marsh, but *A. arundinacueus* may flower earlier and senesces later in the season (GHF, pers observ.).

While *A. arundinaceus* has not officially been identified as an invasive plant or noxious weed in Idaho, its rapid spread at the study site, the CPCM Wildlife Management Area, has been noted by the former CPCM manager, T. Gregory, who served in that role for over 30 years. He estimates that *A. arundinaceus* first became established in the CPCM in the early 2000s, that its abundance doubles approximately every 5 years, and that as of 2023 it occupied roughly 25–30% of the ~6,000-acre marsh (GHF, pers. comm. 2023). At this site, *Alopecurus arundinaceus* forms monotypic stands that exclude all other plants (GHF, pers. observ.).

Study Design

To understand impacts of invasive *A. arundinaceus* across hydroperiod zones on *C. quamash* populations, as well as to understand variation in *C. quamash* demography across these zones, we established plots across three hydroperiod zones at CPCM. Our first step was to calculate the topographic wetness index (TWI) for the entire wetland. Topographic wetness index is calculated from flow accumulation and slope as a measure of the potential for an area to accumulate moisture (Sørensen et al. 2006). We calculated TWI for CPCM using the 'dynatopmodel' package in R (Metcalfe et al. 2018). Calculated TWI then served as the basis for determining potential plot locations a priori. Sixty plot locations were randomly assigned across the wetland into areas with low TWI (7–14) (upslope zone, shortest hydroperiod), medium TWI (14.2–22) (midslope zone, medium hydroperiod) and high TWI (22.1–28.3) (marsh bottom, longest hydroperiod), with each potential plot location separated by at least 20 m. To further validate the accuracy of our TWI designations, we also measured soil moisture with a HydroSense II Handheld Soil Moisture Sensor (Campbell Scientific, Logan, UT) at each randomly selected plot location during the first week of June 2020. Low TWI plots (upslope areas) had soil moisture between 8 and 19% integrated across the top 20 cm of soil, medium TWI sites (midslope) had soil moisture between 16 and 30%, and high TWI (marsh bottom) areas had between 40 and 47% soil moisture.

Randomly assigned plot locations based on TWI were accepted if they contained at least 15% camas cover and at least 5% *A. arundinaceus* cover. If randomly selected plot locations did not meet the cover criteria, but *C. quamash* was present at that location, we selected two random numbers and walked that random number of paces in the E/W and N/S direction (E vs. W and N vs. S direction determined by coin flip) to establish a new plot. We repeated this random number process until arriving at a plot that met these criteria. If the area surrounding the plot did not have *C. quamash*, we selected a new random location. When establishing the plots, we first selected a medium TWI plot location, and then selected the closest high and low TWI plot locations among our randomized points that met the vegetation criteria described above. These three plots then represented a block. We established three blocks in this way in 2020. Due to low camas densities in the higher TWI region (marsh bottom) and our need to have similar sample sizes of individual *C. quamash* plants across TWI levels for modeling, in one of the blocks named 'Southeast', we established two rather than one plot, resulting in 10 rather than 9 total plots. Plots were 1 m^2 except for plots in the marsh bottom (high TWI) Southeast block where plots were 4 m^2 in order to provide sufficient sample size of *C. quamash* for analyses. Plot sizes often vary in plant demographic studies as models and measures are individually-based rather than spatially-based (Menges et al. 2006).

The following year, in 2021, we established a second set of paired plots within 50 m of each original plot, using the same criteria as described above, bringing the total number of plots in the experiment to 20. However, some plots were excluded from our analysis for particular transitions in this study because those plots were part of a separate experiment, or because time constraints prevented those plots from being monitored in particular years. Table A1 details the plots that were included in our analysis for each of the three transitions (Appendix A).

Plots varied from 5 to 30% *A. arundinaceus* cover and 15–50% *C. quamash* cover. Species diversity in our plots varied across our designated wetland zones, with highest species richness in the marsh bottom, highest *A. arundinaceus* cover in the midslope zone, and highest *C. quamash* cover in the upslope zone (Table 1).

As is common practice in plant demographic studies, data were not combined across annual transitions to build our vital rate models. Instead, each transition was analyzed separately (i.e., transition 1: 2020–2021, transition 2: 2021–2022, transition 3: 2022–2023). Given that plots within a block used across each of the three transition periods were not always the same, we are unable to disentangle effects of variation across years from effects of variation across plots. Therefore, each transition is best interpreted as an individual experiment, rather than a measurement over time, a topic we return to in the Discussion.

Measurements

Demographic Measurements

In all plots, we permanently marked all *C. quamash* individuals with metal tags staked to the ground. Seven hundred and fifty-five *C. quamash* individuals were tagged in the first year of this study in 2020, and an additional 910 plants were tagged in new plots used in this study in 2021. Small, single-leaf plants, including seedlings, were marked as a group with a single metal tag, as well as individually with plastic toothpicks to allow individualized tracking of plants and to limit the interference of metal tags in their growth. We measured all marked individuals in each plot when the plants were flowering (in late May or early June) in 2020, 2021, 2022, and 2023, with the exception of one of three blocks (Southeast) which was not measured in 2023 due to time restrictions and access challenges due to high water levels that year. We also tagged and measured new individuals that emerged within each plot each year that were not previously tagged. For each individual, we recorded survival, size, and flowering status. The ln(basal rosette diameter) measured with digital calipers was used as our size measure for *C. quamash* based on it having the strongest correlation with other estimates of total biomass (>0.83 correlation to bulb size, leaf width, leaf length and number of leaves, https://doi.org/10.7923/ebbf-ec66). Our four-year study period (2020–2023) allowed us to observe plants over three transition periods, 2020–2021, 2021–2022, and 2022–2023.

Soil Moisture

Soil moisture was measured at the individual *C. quamash* level in late June or early July each year with a Hydrosense II soil moisture meter with 20 cm probes (Campbell Scientific, Logan, UT). The soil moisture meter measures the average percent moisture (volumetric water content) integrated across the top 20 cm of the soil. In a separate allometry study including plants measured across three sites, *C. quamash* bulbs were found to be located at an average depth of 10 cm, with a range from 3.1 to 18.5 cm (allometry data available here: https://doi.org/10.7923/ebbf-ec66). Depth in this allometric data set was measured from the soil surface to the top of the bulb. Therefore, the 20 cm depth of the probes likely captures the most important soil moisture depths for *C. quamash*, though some *C. quamash* roots may extend deeper. In the case of clustered individual plants within a plot, the same soil moisture measurement was applied to all individuals within an 8 cm radius of the inserted probes.

Percent Cover

We estimated the density of co-occurring intraspecific and interspecific species visually as the percent cover within a 30 cm radius of each individual *C. quamash* plant using a metal hoop with two perpendicular crosshairs (Hart-Fredeluces et al. 2025). Within this 30 cm radius of each plant, we measured: (1) the percent cover of *C. quamash* plants excluding the focal plant, and (2) the percent cover of live *A. arundinaceus*. These measurements were taken in mid-June in 2020, 2021, and 2022.

Herbivory

We recorded herbivory on *C. quamash* on an ordinal scale from 0 to 3 with 0 indicating no herbivory, 1 indicating < 10% of leaves consumed, 2 indicating 10–50% of leaves consumed, 3 indicating > 50% of leaves consumed. Given that the vast majority of herbivory was level 1, and that the ordinal variable would increase parameter space in our models, we elected to include herbivory as a binary variable indicating either absence or presence of herbivory (0 or 1). Herbivory seemed primarily caused by meadow voles and located on leaves, with very limited cases of flowerstalk herbivory (GHF, unpublished data 2020–2022).

Wet and Dry Years

To support interpretations of our plant demographic models, we located annual mean water discharge statistics using the U.S. Geological Survey National Water Information System. We chose a water gage (Camas Creek NR Blaine ID – USGS 13141500) downstream of the Camas Prairie Centennial Marsh on Camas Creek, which is the creek that runs through the center of CPCM and is the source of flooding at the study site. To provide a broader context for water discharge observed in our study years, we also calculated the mean of all of the mean annual discharge values for all years available for this gage (2000–2025).

Data Analysis

We calculated descriptive statistics including: the proportion of plants surviving, the mean change in size, and the proportion of plants flowering across wetland zones. Next, for our modeling efforts, demographic, percent cover, soil moisture, and herbivory data were used to build vital rate regression models to identify the impacts of *A. arundinaceus* on *C. quamash* survival, growth, and reproduction across wetland zones. The models were built using individual-level demographic data (survival, growth, flowering),

as well as individual-level data on: herbivory, *A. arundinaceus* abundance, *C. quamash* size, intraspecific competition (*C. quamash* abundance), and soil moisture. Mixed-effects vital rate models were built in lme4 (Bates et al. 2015), or nlme (Pinheiro et al. 2024) when variance inflation factors were needed. For 2020–2021 (transition 1) and 2021–2022 (transition 2), the spatial structure of our experiment was included as a random effect in all models by nesting plot ($n=9$) nested within block ($n=3$) (Pinheiro and Bates 2000). For 2022–2023 (transition 3), only 2 blocks were included due to time restrictions on data collection, so for transition 3, plot ($n=6$) was included as a random effect and block ($n=2$) was included as a fixed effect.

Prior to modeling, predictors were mean-centered to reduce the collinearity of interaction terms (Aiken et al. 1991). Original models were tested for collinearity with the car package (Fox and Weisberg 2019), and predictors were removed if variance inflation factors were above 4. This included removing soil moisture from the 2020–2021 growth model because wetland zone and soil moisture were collinear. The *C. quamash* growth models were fit with a normal distribution, while the survival and flowering models were fit with a binomial distribution. Original models were tested against assumptions and adjusted with variance covariates when necessary (i.e., the constant power covariance structure was added to the growth 2020–2021 model).

Our initial models included *C. quamash* plant size, *A. arundinaceus* abundance, wetland zone (upslope, midslope, or marsh bottom), herbivory, *C. quamash* percent cover (intraspecific competition), and soil moisture as fixed effects. Given our interest in interactions between wetland zone and invasive *A. arundinaceus* abundance as well as the importance of plant size on invasive species impacts (Baden et al. 2021), we also included the interactions of *A. arundinaceus* with wetland zone and with plant size in our models. Due to low sampling size (e.g., low number of plants that flowered, very low level of herbivory) or collinearity in some years and wetland zones, some fixed effects or interaction terms were not included in each model in each year (see Table A2 for details on all factors included in each model). For example, in 2022, only 8 of 851 plants experienced herbivory, so herbivory was not included in the 2022–2023 transition models. In 2021, 75 of 76 plants in marsh bottom plot (TG_3) did not survive, and so this plot was removed from the growth and flowering models for that transition.

To arrive at our final models, a backward stepwise removal of the least significant paths from the models was conducted based on AIC values (Zuur et al. 2009). Model assumptions were checked by visually inspecting residual plots for homogeneity and quantile-quantile plots for normality. To visualize results for best-fit models containing interactions, we built an interaction plot using the package sjPlot (Lüdecke 2024). All analyses were conducted in R version 4.4.2 (R Core Team 2024).

Results

Wet and Dry Years

Annual mean water discharge was much higher in 2023 (4.29 $m^3\ s^{-1}$) compared to other study years, while 2021 (0.47 $m^3\ s^{-1}$) had the lowest mean annual water discharge (Table 2). The mean of all of the mean annual discharge values for all years available for this gage (2000–2025) was 2.77 cubic meters per second with a median value of 2.08 over that 25-year time period. This mean and median imply that our first transition, 2020–2021, experienced very dry conditions, plants in our second transition from 2021 to 2022 experienced dry conditions, and plants in our 2022–2023 transition experienced wet conditions. These designations correspond with our observations in the field with notably high inundation in 2023 and much less in 2020–2022.

Variation in *Camassia quamash* Demography with Hydroperiod

Survival

Survival was higher in shorter hydroperiod, upslope areas *Camassia quamash* survival was consistently highest in the upslope zone and survival tended to decrease with increasing hydroperiod (Fig. 1). For transition 1 (2020–2021), *C. quamash* mean survival (±std dev across plots) was 94±24% ($n=284$) in upslope areas, 64±49% ($n=156$) in marsh bottom areas, and 43±50% ($n=249$) in midslope areas. For transition 2 (2021–2022), *C. quamash* survival was again highest in the upslope areas (97±18%, $n=426$), followed closely by the midslope (90±30%, $n=443$)

Table 2 Mean annual water discharge on Camas Creek >Source: USGS water resources annual statistics for the nation, national water information system. Water years are designated by the calendar year in which they end. Bolded are the water years in which we collected plant demographic data for this study

Water year (Oct. 1st –Sept. 30th)	Annual mean water discharge (cubic meters per second)
2019	5.98
2020	**0.77**
2021	**0.47**
2022	**0.83**
2023	**4.29**
2024	2.40

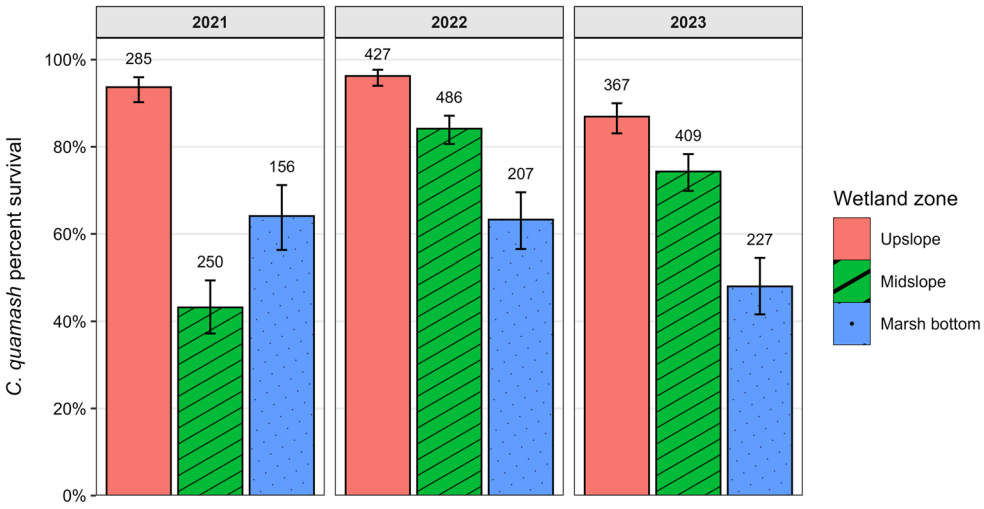


Fig. 1 Percent survival of *C. quamash* plants across years and wetland zones. Error bars represent 95% Wilson confidence intervals. Sample sizes are shown above each bar

and then by the marsh bottom (78±41%, $n=152$) areas. For transition 3 (2022–2023), *C. quamash* survival was 90±30% ($n=350$) in upslope areas, and lower and more variable in the midslope (83±37%, $n=330$) and marsh bottom (67±47%, $n=153$) areas.

Survival generally increased with size, though this varied by year and by hydroperiod *Camassia quamash* survival also tended to increase with size, but effects of size varied across wetland zones only for transition 3. *Camassia quamash* size was not included in the best-fit model for transition 1 (Table A2). In the best-fit model for transition 2 (2021–2022), survival was higher in upslope areas, increased with plant size, and decreased with intraspecific competition (*C. quamash* localized abundance) (Table A2). In the best-fit model for transition 3 (2022–2023), survival increased with plant size in the midslope and marsh bottom areas, but decreased with plant size in the upslope areas (Fig. 2).

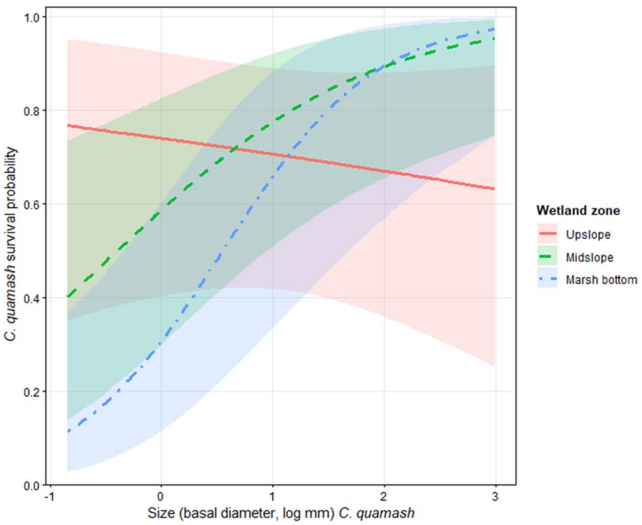


Fig. 2 *Camassia quamash* survival probability during transition 3 (2022–2023) increased with size in midslope and marsh bottom areas, but decreased with size in upslope areas. Lines show model-predicted values; shaded ribbons represent 95% confidence intervals

Growth

The impacts of hydroperiod on *C. quamash* growth were inconsistent across years Mean growth of *C. quamash* (change in mm basal diameter from one year to the next) was variable across years and included negative growth (shrinkage) in some years. Differences in growth across wetland zones were significant only for transition 1 and transition 3. For transition 1 (2020–2021), *C. quamash* growth (mean change in mm basal diameter from one year to the next) was significantly lower in the upslope (-0.05±0.37, $n=226$), than in the midslope (0.14±0.38, $n=106$), or marsh bottom (-0.01±0.37, $n=100$) areas. While for transition 3 (2022–2023), *C. quamash* growth (mm basal diameter) was significantly lower in midslope (-0.18 +/- 0.44, $n=275$) areas, compared with upslope (0.15 +/- 0.39, $n=314$), as well as marsh bottom (0.14 +/- 0.34, $n=22$) areas. For transition 3, the percent cover of *C. quamash* surrounding a focal plant (intraspecific competition) also reduced growth, though this affect was not detected in other years (Table A2).

Flowering

Flowering rates and inflorescence abortion were higher, and phenology earlier, in upslope, shorter hydroperiod areas. Flowering rates varied across years (Fig. 3). Best-fit models indicated that flowering was significantly higher in the drier upslope areas for transitions 1 (2020–2021) and 3 (2022–2023) (Table A2). Inflorescence abortion was not modeled, but showed a tendency to be greater in 2020 and 2021, as well as to be higher in the upslope zone in

those years (Fig. 3). In addition, for transition 1, flowering decreased significantly with herbivory, and for transition 3, it decreased significantly with *C. quamash* percent cover. Flowering phenology was also earlier in the shorter hydroperiod plots and areas of the study site.

Flowering probability increased with size and the size of flowering plants increased with hydroperiod In our best-fit models, flowering probability increased significantly with plant size for transitions 1 and 3, while for transition 2, plant size interacted with wetland zone to determine flowering probability (Fig. 4). For this transition (2021–2022), the probability of flowering increased with size more quickly in drier, shorter hydroperiod areas, before reaching a plateau at 10 mm basal diameter (Fig. 4). Calculations of mean size of flowering plants across wetland zones mostly corroborated this finding from our models of smaller mean flowering size in drier, upslope areas. Specially, in 2021, flowering plants in upslope areas were smaller (mean of 5.2 mm basal diameter), on average, than those in the midslope (mean of 9.0 mm basal diameter) and marsh bottom (mean of 9.8 mm basal diameter) areas. This was also true in 2022, where flowering plants in upslope areas were again smaller (mean of 4.4 mm basal diameter), on average, than those in the midslope (mean of 7.6 mm basal diameter) and marsh bottom (mean of 5.9 mm basal diameter) areas. However, in 2023, flowering plants were larger than in previous years, and size trends over landform position were reversed, with upslope areas having the largest flowering plants. Those in upslope areas were larger (mean of 10 mm basal diameter), on average, than those in the midslope (mean of 7.8 mm basal diameter) and marsh bottom (mean of 5.7 mm basal diameter) areas. However, few plants flowered in 2023 compared to previous years (Fig. 3).

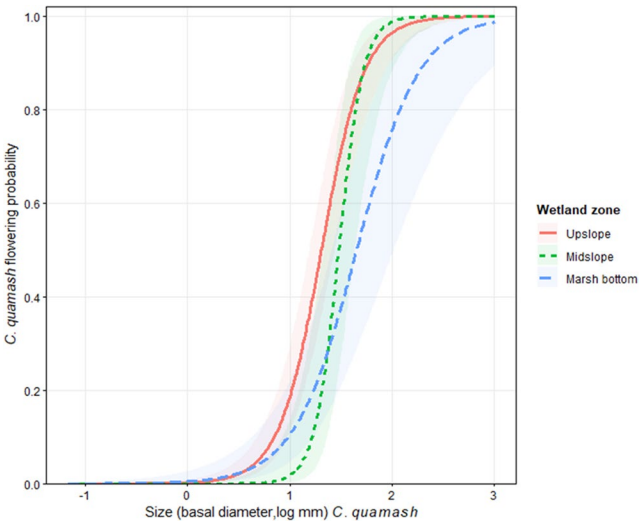


Fig. 4 *Camassia quamash* flowering probability in 2022 increased with size before reaching a plateau around 10 mm basal diameter where flowering was nearly guaranteed. Plants in drier areas tended to flower at a smaller size. Lines show model-predicted values; shaded ribbons represent 95% confidence intervals

Variation in Effect of *A. arundinaceus* on *C. quamash* Demography with Hydroperiod

Negative effects of *A. arundinaceus* on *C. quamash* survival increase with hydroperiod In the best-fit model for transition 1 (2020–2021), survival probability decreased with *Alopecurus arundinaceus* percent cover, and this decrease was more pronounced in longer hydroperiod areas (Fig. 5a). Survival probability also decreased with *A. arundinaceus* abundance for transition 3 (2022–2023) in marsh bottom areas, though had little impact in upslope and midslope areas (Fig. 5b). No effect of *A. arundinaceus* on *C.*

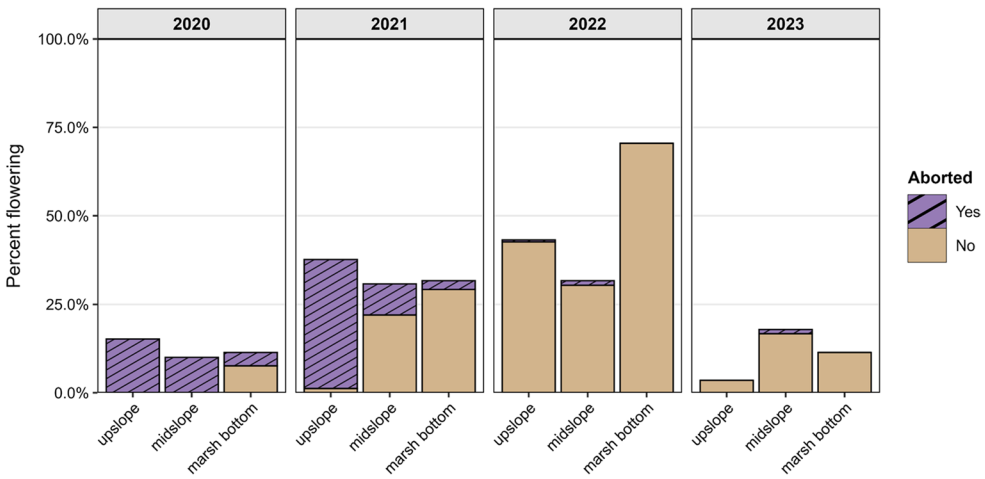


Fig. 3 *Camassia quamash* percent flowering and percent inflorescence abortion by year and wetland zone. Rates shown are for plants above 2 mm basal diameter because plants below this size rarely flowered. Samples sizes for upslope, midslope, and marsh bottom areas, respectively are: 2020 (n = 145, 121, and 132), 2021 (n = 137,52, 82), 2022 (n = 190, 82, 61), and 2023 (n = 198, 106, 35)

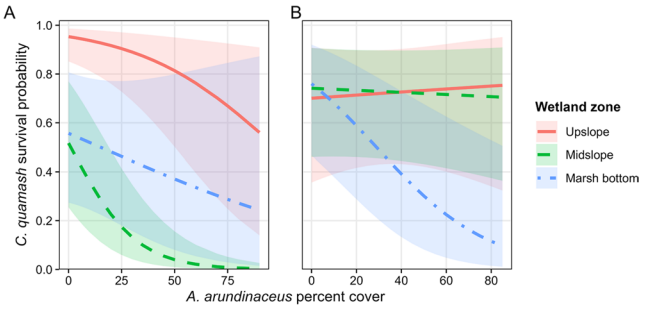


Fig. 5 *Camassia quamash* survival probability decreased with increasing *A. arundinaceus* abundance across wetland zones during transition 1 (2020–2021, **A**). *Camassia quamash* survival decreased with *Alopecurus arundinaceus* abundance in the marsh bottom, but had little relationship to survival in midslope and upslope areas during transition 3 (2022–2023, **B**). Lines show model-predicted values; shaded ribbons represent 95% confidence intervals

quamash was included in the best-fit model of survival probability for transition 2 (2021–2022).

Arundinaceus arundinaceus percent cover decreased *C. quamash* growth only for transition 3 (2022–2023), but this effect did not vary with hydroperiod. We did not detect any impact of *A. arundinaceus* abundance on flowering probability in any of our models.

Discussion

Variation in *Camassia quamash* Demography with Hydroperiod

In our study, *C. quamash* plants in upslope areas, which have a shorter hydroperiod, had distinct demographic and morphological characteristics compared to plants in longer hydroperiod areas, such as higher survival rates, higher flowering rates, higher inflorescence abortion rates, smaller average size, earlier flowering, and flowering at a smaller size.

Increased allocation to survival in shorter hydroperiod areas Across plant species broadly, high survival rates are expected to be favored, at the expense of fecundity and growth, in resource-poor environments (Baden et al. 2021). This may be particularly true for perennial plants such as *C. quamash* where survival tends to be more important than growth or reproduction for long-term population persistence (Franco and Silvertown 2004; Jacquemyn et al. 2010; Pino and de Roa 2007; but see Jacquemyn et al. 2010). A shorter hydroperiod reduces water resources, which would reduce the window of time for photosynthesis, thereby reducing annual carbohydrate production and potentially forcing trade-offs in allocation between survival/growth and reproduction. As reflected in their higher survival rates in this study, *C. quamash* plants in drier areas may have preferentially allocated resources to bulb reserves to support survival, limiting the production of aboveground biomass.

The higher survival rates in the upslope areas, could also be the result of reduced competition there from other plant species compared to midslope or marsh bottom areas. *Camassia quamash* is thought to be relatively intolerant of shading (Hebda 1992), such that the increased density and height of co-occurring plant species in wetter areas may have reduced survival of *C. quamash* in those areas. In our study plots, there was greater plant species diversity in wetter areas (Table 1) as well as less bare ground, and greater production of plant litter in wetter areas, such as from common spikerush (*Eleocharis palustris*) (pers. observation GHF). Shading, intraspecific competition, as well as soil anoxia, therefore may also help explain lower survival rates in the marsh bottom and midslope areas (Mony et al. 2010).

Higher rates of flowering and earlier flowering in shorter hydroperiod areas While flowering rates were higher in upslope areas than midslope and marsh bottom in some years, it is notable that inflorescence abortion rates were also higher in upslope areas. We observed that *C. quamash* plants in upslope areas often began to form flower stalks, but then inflorescences withered before flowering. This greater inflorescence abortion rate in upslope areas could also be explained by reduced water availability (Song et al. 2011), as limited resources are known to cause floral abortion (Stephenson 1981; Turc and Tardieu 2018; Guo et al. 2023; Saini et al. 2025). So, while the probability of emergence of flowering stalks was higher in some transitions in the upslope zone, the inflorescence abortion rate was much higher in the upslope areas in those same transitions, leading to a lower level of flower production in upslope areas.

The earlier flowering of *C. quamash* plants in drier areas in our study (pers. observ. GHF) was also observed for *C. quamash* by Thoms (1989) at other camas prairies and may be explained by earlier warming of soil or differences in the winter chilling period across a hydroperiod gradient (Eppich et al. 2009; Davis and Davis 2021). Earlier flowering in *C. quamash* in shorter hydroperiod areas could be an adaptation to reduced water availability where plants complete their life cycle more quickly in drier areas to avoid the negative effects of drought. Acceleration of the life cycle is a common drought response in plant species referred to as 'drought escape' (Kazan and Lyons 2016; Buchmann and Papaj 2024). The earlier sesnescence of plants in drier areas that we observed may be driven by this same accelerated phenology, and/or the earlier drying out of the soil, and/or earlier expenditure of carbohydrate reserves (Eppich et al. 2009; Davis and Davis 2021). Photoperiod, temperature, and moisture are the primarily physical environmental cues that influence seasonal onset of flowering (Rathcke and

Lacey 1985). A study of meteorological factors influencing flowering phenology in 200 mostly geophytes in Hungary found that average daily temperature, followed by number of frost days, were the strongest predictors of seasonal onset of flowering (Eppich et al. 2009). The same study found that withering of flowers was most strongly predicted by the number of days with precipitation. Our observations are consistent with another study that found less rainfall predicted earlier flowering in species of the bulb-forming genus *Crinum* found in Namibia (Kwembeya and Pazvakawambwa 2019).

Interactive effects of size and hydroperiod on survival Plant vital rates are known to be size-dependent, with a general trend of vital rates increasing with plant size (Obeso 2002; Vaupel et al. 2004; Crone et al. 2011; Baden et al. 2021). However, plant size may also interact with environmental factors to determine vital rates (Ehrlén et al. 2016; Baden et al. 2021). For example, for the understory herb beargrass, *Xerophyllum tenax*, the effects of plant size on vegetative reproduction depended on fire severity with higher rates of vegetative reproduction after low severity fire in larger, but not smaller plants (Hart-Fredeluces and Ticktin 2019). In our study, the effects of wetland zone (hydroperiod) on *C. quamash* survival depended on plant size in one of the three transitions studied (2022–2023). In this transition, plant size increased survival in wetter zones, but decreased survival in the upslope areas. While we do not know why this occurred, given 2023 was a particularly wet year (Table 2), perhaps plant size was especially important that year to having sufficient carbohydrate and/or oxygen reserves for surviving soil anoxic conditions in wetter areas. However, in upslope areas, larger *C. quamash* plants may have been more susceptible to rot or decay compared to smaller plants in this zone (Abubakar et al. 2019). Alternatively, transition 3 results may have been different from other years because they did not include plots in the Southeast block due to time restrictions on data collection for that year. If plot omissions help explain our transition 3 survival results, spatial variation in factors like soil type, aspect, or management history are likely impacting *C. quamash* demography, topics that would need to be explored in future studies.

Flowering at a smaller size in short hydroperiod areas The onset of plant reproduction is a key life history trait that has significant impacts on plant fitness (Rathcke and Lacey 1985). Plasticity in reproductive timing has been documented in several herbaceous species, and life history theory suggests that plants in unfavorable environments will flower earlier (ontogenetically) because this maximizes fitness given their expected shorter lifespan (Sultan 2000). Earlier flowering is advantageous in poor environments because plants that delay flowering may die before flowering or never reach the minimum size for flowering (Brys et al. 2011). Our finding that *C. quamash* in shorter hydroperiod areas flowered at a smaller size concurs with established life history theory and with other studies. A study of the facultative biennial houndstongue (*Cynoglossum officinale*) found that plants in drier, open habitats flowered a smaller size (Wesselingh et al. 1997), while a study of the biennial field mustard (*Brassica rapa*) found that drought selected for plants that flowered at a smaller size and earlier ontogenetic stage (Franks and Weis 2008). It is interesting to consider how our result that *C. quamash* flowers at a smaller size in dry areas could also provide evidence for the importance of plant age in controlling flowering for this species. Transition from vegetative to flowering stages in plant species is generally understood to be influenced by plant size, plant age, and environmental conditions (Jong et al. 1998; Van Dijk 2009; Alahuhta et al. 2021). *Camassia quamash* plants in drier areas in our study may have flowered at a smaller size, in part, because they reached flowering age at a smaller size. While we are not aware of any demographic studies of *Camassia* that include plant age, previous researchers have reported that *C. quamash* first flowers between 4 and 7 years of age (Bailey 1910, p. 224; A. V. Thoms 1989). The relative importance of size, age, and environmental factors in determining onset of maturity in *Camassia quamash* would need to be explored with future study.

Impacts of wetland zone and *A. arundinaceus* on plant growth Plants in upslope areas grew less than plants in midslope or marsh bottom areas in the very dry year of our study, 2020–2021, suggesting plants in upslope areas may have been significantly stressed by drought in low water years. No differences in growth by wetland zone were noted in the somewhat wetter water year of 2021–2022. The 2022–2023 transition was very wet. In this year, midslope plants shrunk, while upslope and marsh bottom plants saw positive growth. We are unsure why this occurred in this year, but the finding further supports the need for long-term demographic studies that can disentangle environmental and demographic stochasticity. Finally, we also detected negative effects of *A. arundinaceus* and *C. quamash* density on growth only for this this transition. This may be because the wetter conditions increased plant sizes overall (Luo et al. 2025), increasing intra and interspecific competition in 2023.

Impacts of Non-native *Alopecurus arundinaceus* Across Wetland Zones

Negative impacts of *A. arundinaceus* on *C. quamash* survival were more pronounced in wetter (longer hydroperiod) areas of the marsh in certain years, representing an

interaction between invasive species and hydrological conditions. Previous research suggests that hydroperiod and water depth have a strong influence on competitive interactions in wetlands by increasing the competitive advantage of invasives in acquiring resources, by leading to greater increases in the size of invasive plants relative to native plants, and by triggering morphological adaptations in invasive species, such as stem elongation or aerenchyma, to better survive particular hydrological conditions such as anoxia (Coops 1996; Smith and Brock 1996; Insausti et al. 1999; Miller and Zedler 2003; Davis et al. 2009). Our results seem to support these theories. We observed that *A. arundinaceus* grows taller in wetter areas, suggesting it is blocking more light and producing more thatch and litter that may have suppressed *C. quamash* more significantly in wetter areas. While we did not assess *A. arundinaceus* morphology in this study, it is possible that this species exhibits other morphological adaptations to wetter conditions such as increasing its shoot length to biomass ratio, or producing aerenchyma in response to longer hydroperiod or in when growing near the plants common in wetter parts of the marsh (Miller and Zedler 2003; Hockaday et al. 2024). Another possibility is that *C. quamash* faced greater competitive pressure in wetter areas from a number of co-occurring plants compared to drier places. We observed higher native species diversity in wetter areas, greater overall percent cover of co-occurring native plant species, and more native plant litter, such as from *E. palustris*. Under these more competitive conditions, *C. quamash* may have been more sensitive to the added stressor of *A. arundinaceus* presence and abundance. Importantly, however, it may be that differences in competitive interactions between native and non-native species are driven not only by changes in non-native species morphology or chemistry, but also by changes in the native plant's demography or morphology. *Camassia quamash* may have been more susceptible to *A. arundinaceus* in wetter areas because, as we demonstrated above, it invests more in above ground growth and reproduction under wetter conditions, meaning it has more to lose if out-competed by *A. arundinaceus* for resources.

It was surprising to find that we did not detect any impacts of *A. arundinaceus* on *C. quamash* flowering in this study and that effects of *A. arundinaceus* on growth were only detected in the wettest year. In a previous prescribed fire experiment that our team conducted at the same site, we found that *A. arundinaceus* suppressed both growth and flowering of *C. quamash*, while effects of *A. arundinaceus* on *C. quamash* survival depended on fire history (Hart-Fredeluces et al. 2025). This difference between studies could be explained by differences in stage of invasion and subsequent density of *A. arundinaceus* in each study. While the previous fire experiment was conducted in dense patches of *A. arundinaceus* where it formed a near monoculture including an average of 37.5 (+/- 17.3 SD) % cover of live *A. arundinaceus*, in addition to 56.5 (+/- 21.9 SD) % cover of necromass (thatch and litter), this study we report on here was conducted in plots with more limited *A. arundinaceus* biomass (8.8 (+/- 18 SD) mean % biomass, and 6.5 (+/- 5.4 SD) % necromass), representing an earlier stage of invasion. The difference in impact of *A. arundinaceus* with increases in its cover suggests that as *A. arundinaceus* first invades, direct competition for light and other resources mostly impacts *C. quamash* survival and growth, but those plants that survive continue to flower. Those *C. quamash* plants that persist past the earlier stages of invasion may be larger bulbs that are able extend their shoots up above the accumulating thatch to access light. For these surviving bulbs, they are likely experiencing an extirpation debt, meaning that without a shift back to favorable conditions, they will eventually die.

The invasion of non-native species has been categorized into stages of invasion, including transport, colonization, establishment, and landscape spread (Theoharides and Dukes 2007), and factors like time-since-invasion are known to alter the impacts of invasive species (Diez et al. 2010; Iacarella et al. 2015). At the scale of the marsh overall, *A. arundinaceus* is in the final stage of landscape spread. At the scale of each experiment plot, time-since-invasion appears to influence impacts of *A. arundinaceus* on *C. quamash*, particularly due to the accumulation of thatch and necromass over time. This accumulation of necromass is cumulative, as most of our study site has not been grazed, mowed, or burned since its establishment in 1987. While some studies have found that the effects of invasive grasses tend to decline with time since invasion (Iacarella et al. 2015), for example because negative soil feedbacks suppress invasive plant growth more significantly with increasing time since invasion (Diez et al. 2010), at our study site the opposite seems to occur as negative impacts on flowering may increase with time-since-invasion. Future work may explore if there is a critical threshold level of *A. arundinaceus* abundance, under different disturbance regimes, where *C. quamash* can no longer persist (O'Loughlin et al. 2021).

Impacts of Herbivory on *C. quamash* Vital Rates

Of the two transition periods (2020–2021 and 2021–2022) for which we could measure the impacts of herbivory on *C. quamash* vital rates, herbivory reduced flowering rate from 2020 to 2021 by approximately 4%, while having no detectable impacts on vital rates over the 2021–2022 transition period. On average, less than 10% of leaf tissue was removed by the observed herbivory that we suspect is from the abundance of meadow voles observed that year.

Herbivory has been shown to reduce flowering in other wetland perennial plants (Hill Bermingham 2010) and polycarpic perennials (Brys et al. 2011) as well as to reduce plant vital rates more broadly (Doak 1992). The loss of photosynthetic tissue can lead to reproductive trade-offs where plants allocate more resources to survival, growth, or vegetative reproduction instead of flowering, in the context of herbivory. In addition to direct effects of herbivory, it would be helpful for future studies to explore the indirect effects of *A. arundinaceus* in creating habitat for herbivores that, in turn, consume *C. quamash*.

Conclusions

Understanding how native wetland species respond and adapt to variation in hydroperiod and how these changes interact with the impacts of invasive species is critical for developing management plans to address the joint impacts of climate change and invasive species on wetlands. In terms of hydroperiod, rather than finding any "goldilocks effect" where *C. quamash* plants survived, grew, and flowered at the highest rates in an intermediate hydroperiod zone, we found trade-offs in vital rates between upslope compared to wetter areas (mid slope and marsh bottom), where upslope areas had higher survival rates, but lower fecundity. At the same time, invasive *A. arundinaceus* had a stronger per-unit negative effect on *C. quamash* in the wetter areas. A follow-up study, comparing population (rather than individual vital rates) growth rates across wetland zones, would allow better prediction of the *A. arundinaceus* cover conditions and hydrological conditions where *C. quamash* can persist.

The findings from this study provide a second, supporting source of evidence that *A. arundinaceus* is suppressing *C. quamash* populations at this site. Our first publication at this site demonstrated that *A. arundinaceus* suppressed *C. quamash* in places heavily dominated by *A. arundinaceus* (Hart-Fredeluces et al. 2025). This article expands on our understanding of these impacts of invasive *A. arundinaceus* by showing that suppression also occurs in areas at an earlier stage of invasion with lower *A. arundinaceus* density, and that the per unit impacts of *A. arundinaceus* on *C. quamash* are more severe in longer hydroperiod (wetter) areas of the marsh. In addition, our study suggests that the life history responses of *C. quamash* to hydroperiod may be increasing their susceptibility to *A. arundinaceus* in wetter areas. *Camassia quamash* plants in drier areas appear to be allocating a larger proportion of resources to survival, which may also buffer those plants from the impacts of invasive *A. arundinaceus*. In wetter areas, *C. quamash* plants are investing more heavily in sexual reproduction, which may increase vulnerability to the negative impacts of non-native plant species.

From a management perspective, different strategies across wetland zones may be needed to address invasion of *A. arundinaceus* and to protect *C. quamash*, and potentially other native plant species, rather than a uniform approach. While plants in upslope areas are negatively impacted by *A. arundinaceus*, they appear mostly limited by lack of water. Whereas, for plants in midslope and marsh bottom areas, where *C. quamash* plants are larger and more fecund, strategies to reduce the dominance of *A. arundinceus* seem most critical. Targeting longer hydroperiod areas for treatments to reduce *A. aundinaceus* abundance (e.g., burning in combination with targeted grazing, hand removal, etc.) where *C. quamash* is abundant or which have high native plant biodiversity may be most effective, while *C. quamash* plants in drier areas may be best supported by hydrological management that can increased the length of inundation in dry years.

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Data Availability The datasets generated during and analyzed during the current study are available in the VERSO repository at the University of Idaho Library, https://doi.org/10.60841/000000274.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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