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RESEARCH ARTICLE

The impact of drought duration on two *Potamogeton* species with different growth forms

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Abstract

When facing new climate extremes, aquatic plant communities may experience more frequent or increasing durations of water shortages. Aquatic macrophytes of permanently inundated habitats (true hydrophytes) may lack the physiological or morphological characteristics that protect terrestrial plants from drying out. Aquatic hydrophytes with floating or emergent leaves are expected to be more resilient to droughts than completely submerged plants, as they have morphological characteristics adapted to air-exposed conditions. Therefore, we expected the latter to survive longer periods of air exposure and perform better with increasing drought than a completely submerged growing species. Here, we conducted a microcosm experiment and exposed two *Potamogeton* species—the completely submerged growing *Potamogeton perfoliatus* and the areal leaf producing *Potamogeton nodosus*—to different drought conditions (1, 5, and 15 days). We aimed to detect how two species with different growth strategies cope with and respond to increasing air exposures with waterlogged sediment. Both species showed a resistance to 1–5 days of drought but showed high mortality after 15 days. They displayed significant differences in all measured morphological responses (shoot length, side shoot, and leaf counts), plant chemistry (carbon, nitrogen, and phosphate), and the produced biomass (shoot, root, leaves), and reacted significantly to increasing drought durations. Differences in their resistance were observed based on the mortality rate and morphological responses. To prevent long-term droughts and keep mortality low, we recommend to the water managers to identify areas of risk and increase water levels during dry periods.

Keywords Aquatic macrophytes · Climate change · Survival · Drought response · Plant morphology · Plant chemistry

Introduction

Climate change is expected to alter temperatures, weather extremes, and water regimes worldwide (Masson-Delmotte et al. 2021; Thompson et al. 2022). The new global climate models show that the warmer climate will increase evaporation causing wetter winters and drier summers in many regions of the northern hemisphere and will induce more frequent, longer, and more intense dry periods (European Commission. Joint Research Centre et al. 2020; Masson-Delmotte et al. 2021; Wang et al. 2016). Droughts, periods of low water availability, are natural and often seasonal occurrences in many ecosystems such as intertidal areas, wetlands, floodplains, and rain-fed rivers (Barnes et al. 2013). However, they are expected to be exacerbated and intensified by the more extreme weather and changing climate in combination with anthropogenic drivers, such as damming and water extraction for farming and drinking

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water production (Crausbay et al. 2017; Haile et al. 2020; Vicente-Serrano et al. 2020). An increasing number of water bodies are additionally influenced by unpredictable fluctuations in water levels caused by dam management (also called hydropeaking), which can increase the number of short drawdowns (Bejarano et al. 2018; Wang et al. 2016). Consequently, droughts may increase in frequency and/or in duration in many ecosystems. How and to what magnitude natural and anthropogenic systems will be impacted by longer and unpredictable periods of water scarcity depends on the system's resilience (the ability to adapt or recover after periods of drought) and on its resistance (the ability of the system to maintain in the initial state during disturbances (Haile et al. 2020; Holling 1973; Yao et al. 2022).

In ecosystems such as temporary wetlands or alluvial forests that naturally fall dry and experience drought, the biological community consists of species that have physiological, morphological, behavioral, or life-cycle adaptations that promote survival (Bornette and Puijalon 2009; Brock et al. 2003; Crausbay et al. 2017; Gupta et al. 2020; De Wilde et al. 2014; Wassens et al. 2017) or recovery after water deficits (Bornette and Puijalon 2009; Brock et al. 2003; Gupta et al. 2020; Johnson et al. 1996; Wassens et al. 2017). They may, for example, have smaller leaves that reduce water loss or increase water storage (Farooq et al. 2012; Wells and Pigliucci 2000). Alternatively, they might wait for drought to pass in dormant forms, such as subterrestrial tubers or in seedbanks (Brock et al. 2003; Spencer and Ksander 1992; Wassens et al. 2017). These ecosystems are therefore quite resilient to drought (Holling 1973).

However, species in permanently inundated ecosystems may lack those adaptations and may not be able to cope with moisture deficit and air exposure (Bejarano et al. 2018; Bornette and Puijalon 2009; Wang et al. 2016). Through die offs and slow recovery rates, species are replaced by more drought tolerant ones, causing changes in community composition (Crausbay et al. 2017; Garssen et al. 2014; Geest et al. 2005; Wassens et al. 2017). Drought might therefore lead shifts from aquatic to terrestrial communities (Bejarano et al. 2018; Garssen et al. 2014), and influence essential ecosystem services of aquatic habitats such as biomass production and carbon storage or attribution to good water quality (Carr et al. 1997; Garssen et al. 2014; QI et al. 2021; Reitsema et al. 2018; Vicente-Serrano et al. 2020). Furthermore, loss of species and altered ecosystem functioning may limit the resilience to future disturbances (Dalla Vecchia et al. 2020; Engelhardt and Kadlec 2001).

Due to their dependency on water, desiccation represents a critical challenge to the survival of submerged macrophytes (Barnes et al. 2013; Barrat-Segretain and Cellot 2007; Bornette and Puijalon 2009; Coughlan et al. 2018; Han et al. 2021). The effects of drying depend on the individual characteristics of the species, but also on the life stage of the plant and the duration and intensity of drought (Yao et al. 2022; Fleta-Soriano and Munné-Bosch 2016). The leaves of fully submerged aquatic plants (e.g., *Potamogeton crispus)* are thin, with no cuticle layer or strong cell walls to protect them when falling dry. Even short periods of drought pose a challenge to these plants, and when their leaves are exposed to air, they wither quickly (Barnes et al. 2013; Coughlan et al. 2018; De Wilde et al. 2014; Frost-Christensen and Sand-Jensen 1995; Iida et al. 2007; Wells and Pigliucci 2000). In contrast, the floating or aerial leaves of rooted submerged plants (e.g., *Potamogeton malaianus*) are more similar to leaves from terrestrial plants. They have cuticle layers, strong supportive cell walls, and stomata (Anderson 1982; Frost-Christensen and Sand-Jensen 1995; Iida et al. 2007; Wells and Pigliucci 2000). These promote efficient photosynthetic light harvesting, gas exchange, and reduced water loss, which makes such species more drought resilient and increase their chance of survival (Anderson 1982; Bejarano et al. 2018; Bornette and Puijalon 2009; Boyer 1982; Yao et al. 2022).

Drought events can last from a few hours to several weeks or months depending on the local geography, water requirements, and weather (European Commission. Joint Research Centre et al. 2020). Flowering plants respond along such drought gradient (e.g., different drought durations). Short periods of water deficits may not be fatal for aquatic plants but result in changes on a morphological, physiological, chemical, and metabolic level (Boyer 1982; Gupta et al. 2020; Filippou et al. 2011; Iqbal et al. 2020; Lambers et al. 2008; Sun et al. 2020). Prolonged drought increasingly disrupts the normal development and photosynthesis and eventually leads to death of the plant (Fleta-Soriano and Munné-Bosch 2016; Gupta et al. 2020).

The effect of drought on the development of terrestrial flowering plants and their genetic and physiological responses under water stress have been widely explored (Gupta et al. 2020; Farooq et al. 2012; Lambers et al. 2008; Sun et al. 2020). The scientific literature often focuses on ecosystem productivity (Ciais et al. 2005; Fleta-Soriano and Munné-Bosch 2016) and crop yields (Boyer 1982; Filippou et al. 2011; Gupta et al. 2020; Iqbal et al. 2020). Even more than for terrestrial plants, drought can have profound negative effects on submerged aquatic plants and prolonged exposure leads to wilting and eventually death (Bejarano et al. 2018; Han et al. 2021; Wang et al. 2016; De Wilde et al. 2014). Short-term drought effects (less than a day) on aquatic plants are mostly studied in relation to survival and germination of propagules (Barnes et al. 2013; Glisson et al. 2020; Spencer and Ksander 1992). This is often done in context with the dispersion of invasive species (Bruckerhoff et al. 2013; Coughlan et al. 2018; Glisson et al. 2020). Long-term (2 weeks or more) studies on whole aquatic plants focus on survival (Iida et al. 2007; Venter et al. 2017) and on changes in physiological variables such as stems, leaves, and dry weights (Iida et al. 2007; Venter et al. 2017; Wang et al. 2016; De Wilde et al. 2014). To our knowledge, short-term drought events in relation to the survival and physiological response of established aquatic plants (hydrophytes) have not been explored. An exception here is Venter et al. (2017), who followed the physiological changes of *Eichhornia crassipes* plants during prolonged drought from day 2 until day 36. All the mentioned drought studies above give no information about the influence of drought on the chemical composition of the plants. In the current study, we explore how two rooted aquatic plant species with different growth strategies cope with different drought durations. We focus on the survival and recovery of established plants in an indoor laboratory setting. Specifically, we question how the duration of drought affects survival and viability of these two plants and discuss potential differences found between the species in relation to their growth strategy. We add to the extremely limited knowledge on this topic and increase the understanding of the response and resilience of true aquatic plants to droughts.

We chose two species of the genus *Potamogeton* (Potamogetonaceae): *P. perfoliatus* L., which grows fully submerged (but blooms above water), and *P. nodosus* Poir., which can also form aerial (floating) leaves (Anderson 1982; Ganie et al. 2015). These two species were chosen as they cohabitate flowing and standing waters (Ganie et al. 2015), and both can be found for example in the catchment of the free-flowing gravel river Border Meuse, Limburg, the Netherlands (NDFF 2023). This rain-fed gravel river is strongly affected by summer drought and daily hydropeaking events, which present challenges for these two species.

We hypothesize that these two species with different growth forms will show differences in resistance and physiological response (produced biomass, morphological responses, chemical composition) to increasing drought based on their morphological properties. We expect that *P. perfoliatus* is highly sensitive to drought and will show lower survival rates and more dramatic physical responses with increasing drought than *P. nodosus*.

Material and methods

Plant collection and preparation

P. nodosus was collected on 26 August 2021 by hand or with a hand rake in the Meuse near Katwijk, Maashaven, the Netherlands (51.753389 N, 5.872915 E). The plants were stored in outdoor tanks at FLORON (Plant Conservation Netherlands), Nijmegen, the Netherlands (51.822972 N, 5.873555 E), until the start of the experiment on 14 September 2021. *P. perfoliatus* was supplied from stock in outdoor tanks, maintained by FLORON. Before the start of the experiment, plant material was rinsed under tap water to remove fauna and algae and transported to the Aquatic Ecology and Water Quality Management research group of Wageningen University and Research (WUR), the Netherlands.

Healthy looking (firm), rootless, apical shoots with no visible pests or damage on leaves and shoots were selected for use in the experiment. *P. nodosus* shoots were cut into sections with at least two surface leaves and two nodes, of which one was positioned in the lower 3 cm of the cutting. This was done to enable root formation after insertion into the sediment. *P. nodosus* showed a big variation in leaf size among shoots, resulting in initial fresh weight (FW) between 0.59 and 2.43 g. *P. perfoliatus* was trimmed by removing one node and leaf at a time starting from the base of the shoot until FWs between 1.25 and 1.42 g were reached. Apical parts of shoots of both species remained intact so plants can quickly resume growth.

Experimental setup

We exposed *P. nodosus* and *P. perfoliatus* to three drought conditions (1, 5, and 15 days) and a control group which did not experience any drought (0 days of drought), resulting in eight experimental treatments with four replicas (4 drought treatments × 2 species × 4 replicates = 32 aquaria). We harvested all plants after 43 days, which gave the plants 42, 38, and 28 days to recover after their drought treatment (for 1, 5, and 15 days of drought, respectively). The experimental units (32 Perspex cylinder aquariums: height 45 cm, diameter 14.5 cm, a volume of about 5.5 L) were randomly placed into a water bath to control water temperature around 19 ± standard deviation (SD) 1 °C. This temperature was chosen as it imitate the summer conditions based on local temperatures in the Netherlands. We used the RAND formula in Excel (Microsoft Corporation, 2021. *Microsoft Excel*, Available at: https://office.microsoft.com/excel) for randomizing the placement.

The aquaria had a base layer of 4 cm clean sand (grain size = 0.4–0.8 mm), topped with a layer of 4 cm of sand mixed with 3 g of artificial Slow-Release Fertilizer (SRF, Basacote Plus 6 M 16–8-12(+ 2 + TE), Combo Expert GmbH, Muenster, Germany; concentration 2 ± 0.1 g SRF/L sand) and on top a 2-cm layer of clean sand to reduce fertilizer leakage from the sediment into the overlying water layer (Fig. 1; following Verhofstad 2017). The aquaria were filled with 5.5 L of Smart and Barko (1985) medium resulting in a water layer of approximately 25 cm on top of the sediment layer. There was a constant air supply (aeration) with help of electronic air pumps.

The light conditions were 16 h of light and 8 h of darkness per day (after Verhofstad 2017). The light intensity was

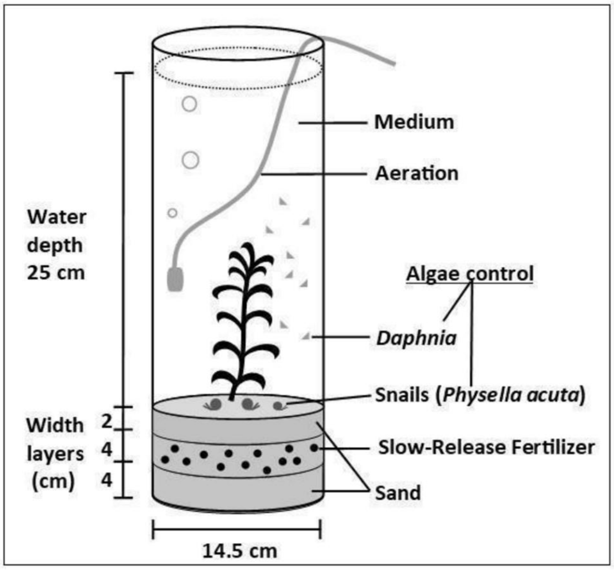

Fig. 1 Drawing of the experimental aquarium set-up used in this study

determined with a LI-190R Quantum Sensor and LI-1500 Light Sensor Data Logger from LI-COR at every aquarium. The average was set at 245 mol/m^2/day (SD = 18.2, $n = 32$) and represents the photosynthetically active radiation (PAR: 400–700 nm range) that is delivered per m^2 over a 24-h period. Other growth conditions (water chemistry, pH, temperature) were controlled for low variation. Surface and sediment pore water nutrient concentrations were measured at the beginning and end of the experiment to confirm fertilizer release until the end of the experiment and to exclude nutrient availability in the sediment as a limiting factor to the survival of the plants. Chlorophyll concentrations were measured to exclude large increases in algae as a contributing factor to plant death. The averages and standard errors of the environmental variables can be found in Table 1. More information on the measurements and control of the aquarium environment can be found in the Supplementary information (SM1 and SM2 in Online material 1; Figs. S1–S3 in Online material 2; Table S1 in Online material 3). All raw data can be accessed on Mendeley data (https://doi.org/10.17632/r825jfx9y5.1).

Tweezers were used place a single shoot into the sediment of each aquarium, ensuring it was inserted deeply enough to bury at least one node. An acclimatization period of 30 days was applied before the drought experiment started. Combined with the 43 days of the actual experiment, plants grew for 73 days in the aquaria. To control excess algal growth, we added ten *Daphnia* sp. and three snails (*Physella acuta*) per aquarium. To keep the snail population under control, snail eggs were removed manually.

To create drought conditions, tubes were used to siphon the water out of the aquaria until the water table was level with the sediment following the methods of De Wilde et al. (2014), waterlogged sediment. During the drought period, the sediment was kept saturated with water. After the drought period, the aquaria were refilled with Smart and Barko (1985) medium to initial water levels for the recovery period. The medium was kept with aeration in the water bath

Table 1 Environmental variables measured throughout the experiment. Shown here are the average ± standard error (SE) and n = number of observations

	Variables	Average ± SE	*n*
Aquarium environment[a]	Dissolved oxygen (mg/L)	9.793 ± 0.023	672
	Water temperature (°C)	19.09 ± 0.044	672
	Water conductivity (µS/cm)	283.9 ± 0.020	672
	pH	7.954 ± 0.008	672
	Alkalinity (meq/L)	0.560 ± 0.010	320
Surface water[b]	Total chlorophyll (µg/L)	27.801 ± 6.534 (start)	64
		21.543 ± 4.827 (end)	
	Ammonium (mg N/L)	1.748 ± 0.285 (start)	64
		0.334 ± 0.171 (end)	
	Phosphate (mg P/L)	0.015 ± 0.010 (start)	64
		0.009 ± 0.003 (end)	
Pore water[b]	Ammonium (mg N/L)	35.79 ± 9.449 (start)	64
		7.233 ± 3.571 (end)	
	Phosphate (mg P/L)	3.022 ± 0.798 (start)	64
		1.488 ± 0.563 (end)	
Light intensity[c]	Light (mol/m^2/day)	244.8 ± 3.210	32

[a] Measured twice a week

[b] Measured at the beginning and end

[c] Measured once for 24 h

to acclimatize before adding it to the experimental aquaria. The aquaria of the control treatment had a water level of ca. 25 cm throughout the experiment (Fig. 1).

Plant measurements

Twice a week, the plant shoot length (cm) was measured with a ruler and the number of leaves and side shoots were counted. The survival of the plants was recorded at the end of the experiment by visually checking whether the plant had leaves and shoots that looked green, firm, and undamaged. The shoots, leaves, and roots were collected separately and washed with tap water to remove algae. Fresh weights (FW, dried with paper tissues) and dry weights (DW, dried at 60 °C for 2 days) of the shoots, leaves, and roots were measured and summed up to determine total FW and total DW.

Total phosphate concentrations in the biomass was measured following the digestion methods of Novozamsky et al. (1983, 1984). Digests were analyzed using the segmented flow analyzer (SKALAR San++ auto-analyzer, Breda, the Netherlands) according to the protocols of the Dutch Normalization Institute (NNI 1983, 1990). Carbon and nitrogen concentrations of the plant material were analyzed by filling 1–5 g (accuracy of 0.001 g) of pulverized dry plant material into tin capsules. The capsules were closed tightly and burned in an organic elemental analyzer (FlashSmart Elemental Analyzer, Thermo Fisher Scientific (Bremen) GmbH, Bremen, Germany).

Statistical analysis

All the following statistical tests were performed in IBM SPSS Statistics (Version 27). To determine whether drought treatments and species identity influenced plant survival, we performed a generalized linear model (GLM) with a binomial distribution and "logit" as link function, following Hosmer et al. (1989). "Survival" was used as dependent variable, "identity" and "duration" (in days, continuous) as explanatory variables. We tested the full factorial model using the likelihood ratio functions of the Chi-square statistics. We excluded the intercept. To explore whether our variables improve the accuracy of our model, we consulted the Akaike Information Criterion (AIC) in the goodness-of-fit output of SPSS. Here, we compared the AIC of the null model without explanatory variables with the model including identity and duration. A smaller AIC value represents a better fit.

To test the influences of drought and plant species on the morphological and chemical response variables as well as the produced biomass (dry weights), we employed generalized linear models (GLMs). Plant response measurements were used as dependent variables and species identity and drought duration (in days, continuous) as independent variables. We performed full factorial models (main terms and interactions) and excluded the intercept. For count-data analysis, we selected a quasi-Poisson error distribution with a logarithmic link function to account for overdispersion. For length measurements and plant chemistry, we utilized a normal distribution with identity link function. The variables were tested individually.

Results

All original data for the measured plant response and environmental variables throughout the experiment are available at Mendeley Data (https://doi.org/10.17632/r825jfx9y5.1).

Survival

All plants survived in the control treatment and the 1-day drought treatment (Fig. 2). After 15 days of drought, both species showed a reduction in survival of 75%. A difference in survival rate could be seen between the species after 5 days of drought with all *P. nodosus* surviving and 50% of *P. perfoliatus* plants dying. The GLM confirmed that the plant species and duration of drought had a significant impact on survival ($p = 0.010$ and $p = 0.009$, respectively), but their interaction term did not ($p = 0.270$, Table 2). The full model had a lower AIC (16.257) than the null model (35.233), indicating that including the duration and species identity improved the fit of the model.

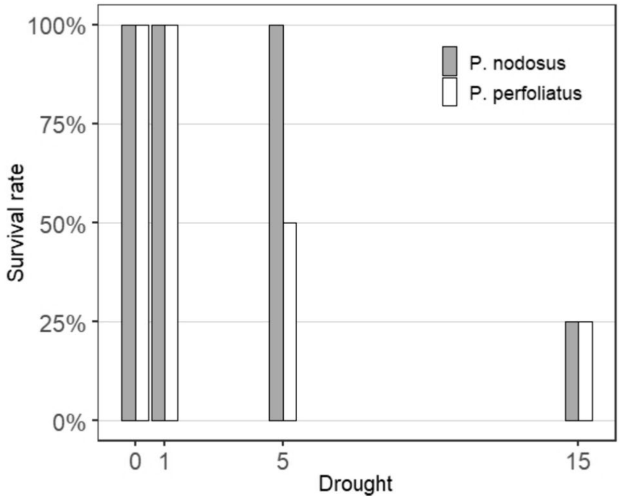

Fig. 2 The survival rate of *Potamogeton nodosus* and *Potamogeton perfoliatus* at the end of the experiment. Drought represents the duration of drought for the control (0 days), and the three drought treatments

Table 2 Outcomes of the generalized linear models of survival, produced dry biomass, and morphological response variables of the survived plants at the end of the experiment

Dependent variable	Source[a]	Likelihood two-ratio Chi-squared	*df*	Sig	*F*	*df*1	*df*2	Significance (*p*-value)[b]	
Survival	Identity	36.924	2	0	18.462	2	4	0.010	*
	Duration	23.22	1	0	23.220	1	4	0.009	**
	Identity × duration	1.635	1	0.201	1.635	1	4	0.270	

Dependent variable	Source	Wald Chi-square	*df*	Significance (*p*-value)	
Total DW (g)	Identity	36.832	2	0.000	***
	Duration	5.346	1	0.021	*
	Identity × duration	0.312	1	0.576	
Shoot DW (g)	Identity	10.409	2	0.005	**
	Duration	0.777	1	0.378	
	Identity × duration	0.119	1	0.730	
Leaf DW (g)	Identity	17.952	2	0.000	***
	Duration	1.000	1	0.317	
	Identity × duration	0.714	1	0.398	
Root DW (g)	Identity	6.737	2	0.034	*
	Duration	0.704	1	0.401	
	Identity × duration	1.016	1	0.313	
Plant length (cm)	Identity	52.581	2	0.000	***
	Duration	9.583	1	0.002	**
	Identity × duration	3.094	1	0.079	t
Internode distances (cm)	Identity	36.842	2	0.000	***
	Duration	4.195	1	0.041	*
	Identity × duration	5.891	1	0.015	*
Leaf count	Identity	1062.221	2	0.000	***
	Duration	10.787	1	0.001	**
	Identity × duration	0.004	1	0.951	
Node count	Identity	1118.265	2	0.000	***
	Duration	11.375	1	0.001	**
	Identity × duration	0.057	1	0.811	
Sideshoot count	Identity	192.813	2	0.000	***
	Duration	12.605	1	0.000	***
	Identity × duration	0.337	1	0.561	

[a] Identity represents the plant species: *Potamogeton nodosus* and *Potamogeton perfoliatus*, DW the respective dry weight, and duration the increasing duration of drought

[b] *p*-values: *t* for *p* 0.05–0.1, $*p<0.05$, $**p<0.01$, and $***p<0.001$

Physical plant responses to drought: produced biomass

P. nodosus produced, on average, 39%, 33%, and 72% more total, shoot, and leaf dry biomass, respectively, than *P. perfoliatus* (Fig. 3a–c, Table S2 in Online material 3). *P. perfoliatus* produced 78% more root biomass than *P. nodosus* (Fig. 3d). The generalized linear model supported significant differences between the species in all measured dry weights (Table 2). However, a significant effect of drought duration was only found for the total DW ($p=0.021$). The total DW decreased for both species with increasing drought duration (Fig. 3a). We could not detect significant differences between the species and their response to drought. The other dry weights did not change significantly with increasing drought.

Physical plant responses to drought: morphological responses

P. perfoliatus plants were, on average, 78.32 cm (± 20.02 cm) about 55% longer than *P. nodosus* (Fig. 4a, Table S2 in Online material 3). It also had about 80% more leaves, 75% more nodes, and 10% more sideshoots

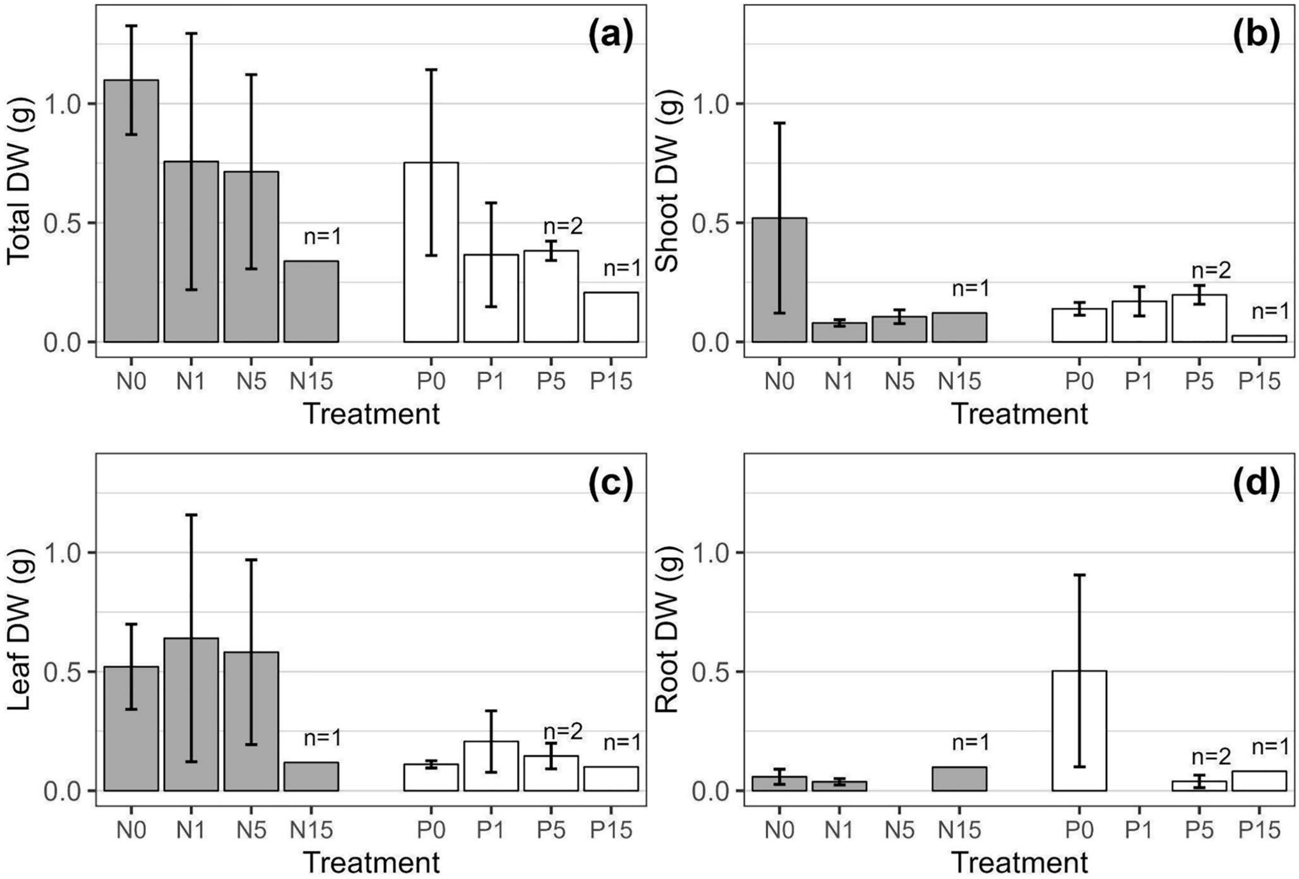

Fig. 3 Average dry weights (DW) and standard errors of the surviving *Potamogeton nodosus* (N) and *Potamogeton perfoliatus* (P) plants at the end of the experiment. **a** Total DW and the DWs of **b** shoots, **c** leaves, and **d** roots. Treatment represents the drought duration in days, with N0 and P0 as controls without drought. Replica counts deviating from four ($n = 4$), are given next to the error bar

than *P. nodosus* (Fig. 4b, c, e). Internode distances were, with an average of 1.31 cm (±0.36 cm), about 41% larger in *P. nodosus* than *P. perfoliatus* (Fig. 4d). All these morphological responses were found to be significantly different between the two species, and significantly influenced by drought (Table 2).

When comparing the different drought treatments, the number of leaves, nodes, and side shoots decreased significantly with increasing drought for both species (Fig. 4c–e). Though plant length and internode distances decreased steadily with drought for *P. nodosus*, they increased for *P. perfoliatus* with the 1-day treatment before decreasing with increasing drought (Fig. 4a, d). These differences were also found in the GLM as a significant interaction between identity and drought (Table 2). The species did not show a difference in their response in the other morphological response variables.

Physical plant responses to drought: chemical composition

Carbon concentrations were on average 75% higher in leaves and 21% in shoots of *P. nodosus* than in *P. perfoliatus* (Table 3, Table S2 in Online material 3, Fig. S4 in Online material 2). Nitrogen concentration were on average 70% higher in leaves and 30% in shoots of *P. nodosus* than in *P. perfoliatus* (Table 3, Table S2 in Online material 3, Fig. S5 in Online material 2). Carbon and nitrogen concentration were about 80% and 81% higher in the shoots of *P. perfoliatus*. Phosphate concentrations in shoots were on average 80% higher in *P. nodosus* (Table 3 and Table S2 in Online material 3, Fig. S6 in Online material 2). Phosphate concentrations in roots and leaves were higher in *P. perfoliatus*, at 65% and 50% respectively.

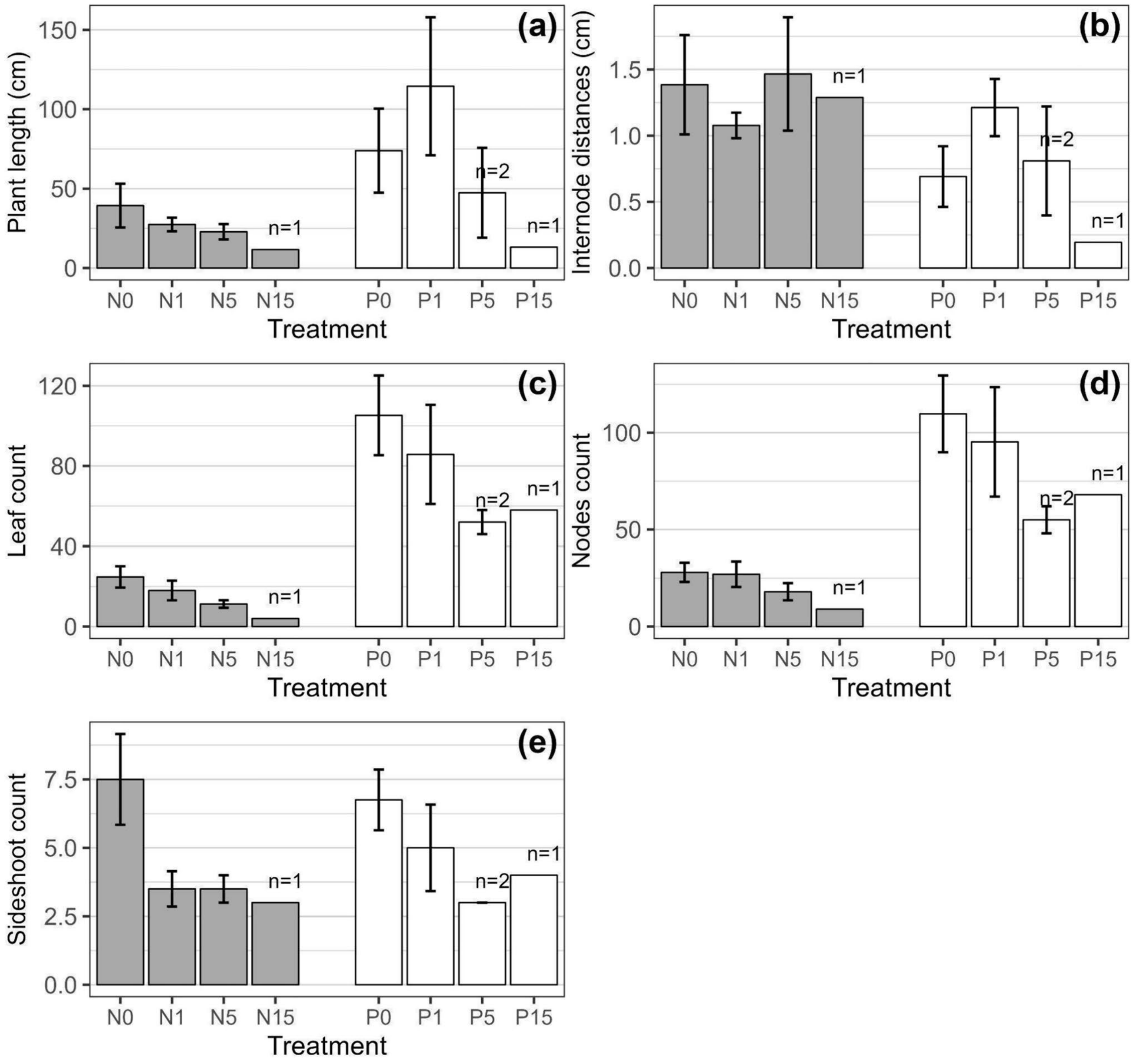

Fig. 4 Average morphological plant responses and their standard errors of the surviving *Potamogeton nodosus* (N) and *Potamogeton perfoliatus* (P) plants at the end of the experiment. **a** Plant length, **b** internode distances, **c** number of leaves, **d** nodes, and **e** sideshoots. Treatment represents the drought duration in days with N0 and P0 as controls without drought. Replica counts deviating from four ($n=4$), are given next to the error bar

All these differences between the species were found to be significant (Table S3 in Online material 3). No significant changes were found with increasing drought duration, and no interaction between drought and identity were found (Table S3 in Online material 3).

For completeness, we also presented here the nutrient concentrations of dead replicas, whenever it was possible to identify and measure the plant tissue.

Discussion

Survival and physiological differences between species along the drought gradient

Our results showed that established plants of *P. perfoliatus* could cope with short-term drought events of 1 day.

Table 3 The average and standard error of measured carbon (C), nitrogen (N), and phosphate (P) concentrations along a drought gradient in leaf, root, and shoots of surviving and dead plants at the end of the experiment

Potamogeton nodosus		Days of drought				
		0	1	5	15	
Survival[a]		Alive	Alive	Alive	Alive	Dead
		$n=4$	$n=4$	$n=4$	$n=1$	$n=3$
C (%)	Leaf	38.75 (±5.47)	35.27 (±3.06)$^{n=3}$	41.32 (±1.93)$^{n=3}$	32.41	34.80$^{n=1}$
	Root	33.77 (±11.45)$^{n=3}$	29.96 (±17.84)	31.65 (±7.43)$^{n=3}$	37.70	38.88$^{n=1}$
	Shoot	30.33 (±12.55)	38.25 (±2.13)$^{n=3}$	33.06 (±15.21)	39.29	35.41 (±9.25)$^{n=2}$
N (%)	Leaf	2.80 (±0.38)	2.75 (±0.41)$^{n=3}$	3.31 (±0.33)$^{n=3}$	2.62	3.37$^{n=1}$
	Root	2.41 (±0.57)$^{n=3}$	1.91 (±1.15)	2.36 (±0.35)$^{n=3}$	2.20	3.19$^{n=3}$
	Shoot	2.22 (±0.93)	2.42 (±0.14)$^{n=3}$	2.11 (±0.78)	2.38	2.28 (±0.72)$^{n=2}$
P (%)	Leaf	0.16 (±0.15)	0.58 (±0.26)$^{n=3}$	0.30 (±0.03)$^{n=2}$	0.12	1.27 (±1.57)$^{n=2}$
	Root	1.45 (±1.82)$^{n=2}$	0.35 (±0.16)$^{n=3}$	0.40$^{n=1}$	0.43	0.26 (±0.10)$^{n=2}$
	Shoot	0.16 (±0.08)	0.33 (±0.27)	0.3 (±0.07)$^{n=3}$	0.27	0.31(±0.09)$^{n=2}$

Potamogeton perfoliatus		Days of drought					
		0	1	5		15	
Survival[a]		Alive	Alive	Alive	Dead	Alive	Dead
		$n=4$	$n=4$	$n=2$	$n=2$	$n=1$	$n=3$
C (%)	Leaf	36.32 (±7.84)	31.20 (±13.99)	32.47 (±12.92)		31.45	
	Root	32.36 (±9.69)	27.86 (±15.23)$^{n=3}$	21.54 (±1.97)		20.03	
	Shoot	37.74 (±1.40)$^{n=3}$	32.58 (±7.97)	38.94$^{n=1}$	34.36$^{n=1}$	28.02	
N (%)	Leaf	4.40 (±0.09)	2.75 (±1.35)	2.60 (±0.57)		3.84	
	Root	2.78 (±1.06)	1.42 (±0.56)$^{n=3}$	1.50 (±0.15)		1.67	
	Shoot	3.07 (±1.11)$^{n=3}$	1.74 (±0.41)	1.60$^{n=1}$	1.65$^{n=1}$	2.02	
P (%)	Leaf	0.17 (±0.21)	0.22 (±0.01)$^{n=3}$	0.04 (±0.02)	0.15$^{n=1}$	0.13	0.25 (±0.02)$^{n=2}$
	Root	0.10 (±0.11)$^{n=2}$	0.16 (±0.12)		0.17$^{n=1}$	0.10	0.18 (±0.05)$^{n=2}$
	Shoot	0.10 (±0.09)$^{n=3}$	0.18 (±0.14)$^{n=3}$	0.03 (±0.04)	0.15$^{n=1}$	0.07	0.14 (±0.06)$^{n=2}$

[a] Survival indicates how many replicas survived. If the numbers used for calculating the concentrations differed from the replicas above, the actual number is indicated with as superscript

During longer exposure events (15 days), *P. perfoliatus* and *P. nodosus* died off. However, under intermediate drought duration (5 days), all *P. nodosus* plants survived but 50% of *P. perfoliatus* died. As such, the species that can grow surface leaves did indeed perform better than the one that only grow submerged leaves under intermediate drought durations. We expected this result, as the species with floating leaves to survive better under increasing drought since they possess innate characteristics closer to terrestrial plants (e.g., thicker cuticle, stomata layer), that fully submerged plant are missing (Amano et al. 2012; Iida et al. 2007; Kaplan 2002).

Indeed, we observed clear differences between the two species in all measured dry weights and morphological and chemical responses (see 3.2–3.4). As such, our findings support previous findings on the innate differences in the morphology of submerged *Potamogeton* plants with and without floating leaves (Amano et al. 2012; Barnes et al. 2013; Coughlan et al. 2018; Frost-Christensen and Sand-Jensen 1995). These studied described the leaves of submerged plants as thin and translucent and those of species that reach the surface as denser, thicker, with thick waxy and stomata layer (Amano et al. 2012; Coughlan et al. 2018; Frost-Christensen and Sand-Jensen 1995; Ganie et al. 2015; Han et al. 2021; Iida et al. 2007).

Plants experiencing increasing stress are known to have different strategies to increase survival or decrease damage, which concern shifts in resource allocation (Farooq et al. 2012; Wang et al. 2016) and morphological changes (Bejarano et al. 2018; Farooq et al. 2012; Lambers et al. 2008). As our plants have different growth strategies and are different physiologically, we expected them to show differences in response to increasing drought. Especially, since the species of the genus *Potamogeton* are known to be highly responsive to environmental stressors (Amano et al. 2012; Kaplan 2002; Spencer and Ksander 1992;

Wiegleb and Brux 1991), and the two growth forms (with and without floating leaves) are known to react differently to environmental conditions (Iida et al. 2007; Kaplan 2002). Even the species we chose for our study showed different responses to increasing flow stress (Ganie et al. 2015; Kaplan 2002): *P. perfoliatus* adjusted by producing thinner, wider leaves and *P. nodosus* narrower and longer leaves.

In our study most biomass, chemical, and morphological responses of the two species such as a general reduction of biomass, number of leaves, and plant height, did not differ between the species and can be considered general plant response to drought stress (Bornette and Puijalon 2009). We did however observe different responses of *P. perfoliatus* compared with *P. nodosus* in plant length and internode distances to 1 day of drought (see 3.3). This indicates that under short-term drought there was a plastic response in growth related to stem elongation. The increase in stem growth is a contra-intuitive response to drought. Normally it is observed in hydrophytes that aim to increase light availability by fast stem elongation under flooded conditions (Bornette and Puijalon 2009; Iida et al. 2007). It is an interesting observation, though it cannot be explained by the factors in the current study. We did not detect any differences between the species with increasing drought for the other biomass or morphological responses (see 3.3–3.4).

We observed differences of how the two species respond to increasing drought in few response variables (Table 3). Such a lack of differences may have been caused be our experimental setup. The plants in our experiment had a steady supply of water and nutrients available to their roots, even when they could not absorb water through their stems and leaves. Consequently, the drought might not have been severe enough to trigger changes in plant morphology. Most of the plants were able to take up sufficient water to avoid tissue damage, functionality, and were able to recover after rewatering without adjusting their tissues. Observations in the literature do support a positive effect of saturated soils during drought events on plant performance and survival (Venter et al., 2017). Additionally, the drought duration of one or 5 days might have simply been too short to induce physiological changes in the variables we measured. Most studies investigating the responses of established aquatic plants to exposure do not look at short and intermediate droughts, but they concentrate on periods of 13 days or more (60 day of drought in De Wilde et al., 2014; 40 days in Iida et al. 2007; 13 and 20 days of drought in Venter et al., 2017). These previous experiments chose drought durations that were too long and ended in the death of all water plants that cannot grow terrestrial forms. They do not explore like us the changes of short-term drought events on the survival and physiological response of the aquatic macrophytes. Consequently, the responses to such short-term drought stresses on established macrophytes are unclear and need further exploration.

Response of *Potamogeton perfoliatus* to drought

Potamogeton perfoliatus is commonly described as an extremely heat and drought sensitive species (Amano et al. 2012; Iida et al. 2007). For example, in the experiment from Iida et al. (2007), all *P. perfoliatus* shoots died off in the first 5 days of the drought treatment. In our results, *P. perfoliatus* seemed to be more resistant to drought than previously thought. This probably relates to the fact that our plants grew in a fully saturated sediment while the drought treatment of Iida et al. (2007) was performed in containers with the water level lowered to −4 cm. Since humidity is an important factor for the survival of water plants (Coughlan et al. 2018), the higher humidity in our cylinders may have decreased the severity of drought conditions and hence more plants survived. For more insight on the survival during natural summer conditions, a transplant experiment in the field could provide more information.

Implication of drought duration

In this study, we gained new insights into the response of aquatic macrophytes to short-term and intermediate drought conditions. Our results suggest that as long as the sediment stays saturated, short drought events might not change the distribution of the two species. However, under natural conditions, there are complex additional effects that influence the performance of aquatic macrophytes (Bornette and Puijalon 2009). These include direct effects, such as tissue damage through increased temperatures or light intensities (Bornette and Puijalon 2009), and indirect effects, such as the decrease in water quality (Farooq et al. 2012) or intensification of drought through increased evaporation and loss of soil moisture (Crausbay et al. 2017). These complex effects might increase macrophyte mortality during short droughts in a natural setting. Nevertheless, longer periods of drought during dry hot periods are a greater threat to the survival of the two native species than short drought events, such as hydropeaking. This is problematic because most aquatic plants that cannot grow terrestrial shoots (e.g., *Ranunculus aquatilis*) will die during longer droughts (De Wilde et al., 2014; Iida et al., 2007; Venter et al., 2017). Therefore, preventing such long-term drought events is in the interest of water managers of rivers such as the Border Meuse.

It is necessary to protect the populations of those species in shallow areas of the water systems and increase their resilience against disturbances, especially as hot summer spells and erratic rain patterns will become more frequent (Barnes et al. 2013; Bornette and Puijalon 2009). Measures designed to keep the sediment water saturated during a drought and the exposure times as short as possible will increase the resilience and survivability of the submerged plants.

Conclusions

Our results showed that *P. perfoliatus* and *P. nodosus* indeed differed on biomass production and morphological characteristics. Both were resistant to 1–5 days of drought but showed high mortality after 15 days of drought with waterlogged sediment. *P. nodosus* survived better than *P. perfoliatus*, offering an edge in competition with other more drought-sensitive species during the changing and more unpredictable climate. Water managers might have to take this finding into account and could, for instance, increase water flow in risk areas to prevent droughts of more than a few days and the resulting die off of these native species. Future research with adjusted methodology and including other species and their responses to drought will help understanding how aquatic plant communities might change in a more unpredictable climate, as this will affect their aquatic ecosystems.

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Author contributions Order of authors (with contributor roles): M.M.D. (data curation; formal analysis; investigation; visualization; writing—original draft, corresponsing author) D.O. (conceptualization; data curation; methodology; writing—review and editing) M.J.J.M.V. (conceptualization; methodology; writing—review and editing) R.H.J.E. (supervision; writing—review and editing) E.T.H.M.P (conceptualization; formal analysis; supervision; visualization; writing–review and editing).

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Data availability statement All original data for the measured plant response and environmental variables throughout the experiment are available at Mendeley Data (https://doi.org/10.17632/r825jfx9y5.1).

Declarations

Conflict of interest I declare that the authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

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