

Heat wave effects on biomass and vegetative growth of macrophytes after long-term adaptation to different temperatures: a mesocosm study

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ABSTRACT: Elevated temperatures and extreme climatic events, such as heat waves, can negatively affect submerged macrophytes. Here, we investigated how submerged macrophytes adapted to 3 different temperatures (ambient, ca. +3°C and ca. +4.5°C) responded to a heat wave. After 10 yr of adaptation, the shoots of 2 species of submerged macrophytes, *Elodea canadensis* and *Potamogeton crispus*, were collected from each of the 3 temperature treatments and transferred to 2 heated treatments for 1 mo. The 2 heated treatments were then exposed to a 1 mo heat wave with an additional 5°C temperature increase. For *P. crispus*, total biomass did not differ among the plants adapted to the different temperatures or between the 2 heated treatments for the duration of the experiment. Plants adapted to the highest temperatures, however, produced a larger number of smaller turions before the heat wave and allocated less biomass to elongation before and after the heat wave. For *E. canadensis*, the plants adapted to higher temperatures had higher total biomass before and during the heat wave and allocated more biomass to roots and leaves during the heat wave. Most indicators (e.g. length and biomass) of macrophyte performance measured during the experiment did not differ between the 2 heated treatments. In summary, after the 10 yr adaptation to higher temperatures, the submerged macrophytes showed adaptive changes in growth and asexual reproduction and responded in a complex way to the heat wave depending on species, growth status and adaptation temperature.

KEY WORDS: *Potamogeton crispus* · *Elodea canadensis* · Heat waves · Extreme events

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1. INTRODUCTION

According to the Intergovernmental Panel on Climate Change (IPCC) 2007 report (IPCC 2007), global

mean surface air temperature will have increased by between 1.1 and 6.4°C by the end of this century relative to the decadal scale averages of 1980s and 1990s temperatures (an average increase of ca. 3°C

in the IPCC A2 model scenarios). The recent IPCC 2014 report suggests a similar increasing temperature trend in the high CO₂ emission scenarios and an increased occurrence of more extreme weather events such as flooding, droughts and heat stress in the future (IPCC 2014).

Warming is expected to significantly affect freshwater ecosystems via impacts on fish, invertebrates, zooplankton, phytoplankton, submerged macrophytes and their interactions (McKee et al. 2003, Moss et al. 2003, Kosten et al. 2009, 2011, Jeppesen et al. 2012, Cao et al. 2014). Several studies have focused on the effects of elevated temperatures on submerged macrophytes, a key structuring element in shallow lake ecosystems. Field studies indicate that warming results in an earlier start to the growing season, stimulates growth and increases the spatial extent of macrophyte communities in clear-water lakes (Rooney & Kalff 2000). Mesocosm studies have shown that an increase of 3°C extends the growing period (Patrick et al. 2012) and increases macrophyte biomass (McKee et al. 2002). Elevated temperatures may also promote the growth of submerged macrophytes through complex snail–periphyton–macrophyte interactions (McKee et al. 2003, Cao et al. 2014). Warming has also been shown to reinforce the symptoms of eutrophication in shallow nutrient-rich lakes, hampering macrophyte growth (Moss et al. 2011), while the impact of warming on lake eutrophication under low-nutrient conditions is more ambiguous (Kosten et al. 2011).

Heat waves are likely to happen more frequently in the future, as illustrated by the sudden temperature increase by an average of >4°C in most parts of Europe in summer 2003 (Beniston 2004) and >5°C in Russia in summer 2010 (Otto et al. 2012), lasting for several months. Previous studies have shown that heat waves can induce higher growth at high elevation and growth suppression at low elevation for terrestrial plants (Jolly et al. 2005); and thereby strongly affect primary productivity (Ciais et al. 2005), ecosystem biodiversity (Thomas et al. 2004) and nutrient cycling (Wang et al. 2008). Thus, the response of submerged macrophytes to heat waves is not well elucidated and requires further study.

In this study, we investigated the responses of 2 commonly found submerged macrophytes (*Elodea canadensis* and *Potamogeton crispus*) adapted to different temperatures in a warming or heat wave scenario under low-nutrient conditions. The experimental setup involved macrophytes adapted for 10 yr to 3 different temperatures, the exchange of macrophytes adapted to different temperatures between heated

mesocosms to investigate their responses and the simulation of a heat wave. As far as we know, our experiment is the first attempt to study the effects of extreme events, such as a heat wave, on submerged macrophytes. We hypothesised that (1) the 2 species of macrophytes would show different responses under the warm or heat wave scenario due to their species-specific features such as life history or growth status and (2) macrophytes adapted to higher temperatures would cope better with warming than plants adapted to ambient temperatures.

2. MATERIALS AND METHODS

2.1. Experimental setup

We conducted our experiment in a mesocosm system in Denmark (56° 14' N, 9° 31' E) which has been continuously running since its establishment in 2003. The setup consists of 12 fully mixed (by paddles) flow-through cylindrical stainless steel tanks with a diameter of 1.9 m and a total depth of 1.5 m. Three temperature treatments (4 replicates) were involved: ambient temperature, A2 scenario (ca. +3°C, depending on season; IPCC 2007 report) and A2 + 50 % scenario (hereafter referred to as T1, T2 and T3 treatment, respectively; samples adapted for 10 yr prior to changes to other treatments are referred to as preT1, preT2 and preT3, respectively). Nutrient levels were low (total phosphorus <20 µg l⁻¹ and total nitrogen <1 mg l⁻¹), the only source of nutrients being unenriched tap water. Levels of water temperature, total alkalinity, pH, nutrient concentrations and other related variables during the experiment are given in Table A1 in the Appendix. The retention time of the mesocosms was approximately 75 d. Each mesocosm held 1 male three-spined stickleback *Gasterosteus aculeatus*, corresponding to natural fish densities in Danish low-nutrient lakes. More details about the setup can be found in Liboriussen et al. (2005).

2.2. Plant exchange and heat wave

Elodea canadensis, which is a species native to North America, is a submerged hydrocharitacean that was introduced to Europe in the 1840s (Cook & Urmi-König 1985), and *Potamogeton crispus* is a Euro-Asiatic native species (Nichols & Shaw 1986). Both are perennial and present in the many natural aquatic ecosystems in Eurasia. The 2 species have remained in the mesocosms ever since their estab-

ishment; however, *E. canadensis* has recently disappeared from the T3 treatments.

The experiment was undertaken from May to September 2014. On May 23, 10 cm long new unbranched shoots of each species were collected from each treatment (termed preT1, preT2 and preT3) and were then planted in the 2 warmed treatments, T2 and T3, where they grew for 1 mo prior to the heat wave before harvesting. We placed 3 shoots from each preT in a square plastic pot (bottom length 6 cm, top length 9 cm, height 8 cm), and these pots were then inserted into frames (ca. length 50 cm × width 30 cm) in the mesocosms. Each frame had 12 cells and was fixed at 30 cm water depth. Thus, 48 individuals of *E. canadensis* (2 preTs × 2 heated treatments × 4 replicates × 3 individuals; only preT1 and preT2 because *E. canadensis* missing in T3) and 72 individuals of *P. crispus* (3 preTs × 2 heated treatments × 4 replicates × 3 individuals) were collected. The pots were filled with the insulation material Rockwool® and 1 nutrient capsule (Nutrition Capsules, Tropica Aquarium Plants). The nutrient release rates from the nutrient capsule were low, ca. 1.50 mg nitrogen and 0.18 mg phosphorus per day (determined after a 2 wk test experiment).

On July 1, we collected 96 individuals of *E. canadensis* and 144 individuals of *P. crispus* in total, twice the number of macrophytes collected in May. They were distributed in the heated treatments following the same procedure as above. After this, a 1 mo heat wave was simulated for the 2 heated experimental treatments with T2 + 5°C (ca. +8°C over ambient temperature) and T3 + 5°C (ca. +9.5°C over ambient temperature). After 1 mo of growth (on August 1), the heat wave simulation was stopped, and half of the macrophytes were harvested. Subsequently, the heated treatments returned to the standard experimental warming regime of T2 and T3, and the remaining macrophytes were left for 1 additional month and then harvested on September 1. After harvesting, the length of the macrophytes was measured. In the lab, macrophytes were washed in tap water and separated into leaf, stem, root or turion; dried at 80°C for 48 h; and weighed to determine biomass.

Turion abundance of *P. crispus* and branch numbers of *E. canadensis* were determined to characterise asexual reproduction. We also calculated average turion weight by dividing total turion biomass by turion numbers for each phase. Some *P. crispus* turions had germinated at the end of the post heat wave phase 'after the heat wave'. These germinated turions were counted, and their proportion was calculated.

The experiment included 3 phases: before, during and after the heat wave. For the first 2 phases, the values of plant variables quantified at the end of each phase were subtracted from those at the beginning of that phase. The results of the final post heat wave phase were obtained by subtracting the results after 2 mo of incubation from the final results after the heat wave (plant incubation of these 2 sets started on the same date). The changes in variables in the post heat wave phase were considered as indicators of the recovery potential for these 2 species, although seasonal effects may also be included. To obtain information about the growth status in the mesocosms, we measured the plant volume inhabited (PVI) of each species in 12 mesocosms during the experiment, and the results are presented in Fig. A1 in the Appendix. PVI was determined according to the formula plant coverage × average plant height per water depth.

2.3. Statistical analysis

The indicators of macrophytes (e.g. length and biomass) were log transformed [$\log(x+1)$], if needed, to homogenise variance and analysed using 2-way ANOVA, the main factors being the 3 (or 2) adaptation temperatures and the 2 heated treatments. Multiple comparisons were undertaken according to Tukey's test by the package multcomp in the software R (version 3.1.1) (R Core Team 2014). The function interaction.plot was used when interaction between 2 factors was found. Data are shown as average ± standard deviation.

3. RESULTS

3.1. Length

Prior to the heat wave, the increase in *Potamogeton crispus* length was significantly higher for plants from preT1 than from preT2 and preT3 in both T2 and T3 (Fig. 1), but no difference was found between plants from preT2 and preT3 in either T2 or T3. During the heat wave, there were no significant differences in growth among the plants from preT1 to preT3, while after the heat wave the length reduction was smaller for plants from preT2 than from preT3. Length changes did not differ between the 2 heated treatments in any of the 3 phases (Table 1).

For *Elodea canadensis*, the length increment was significantly lower for plants from preT1 than for

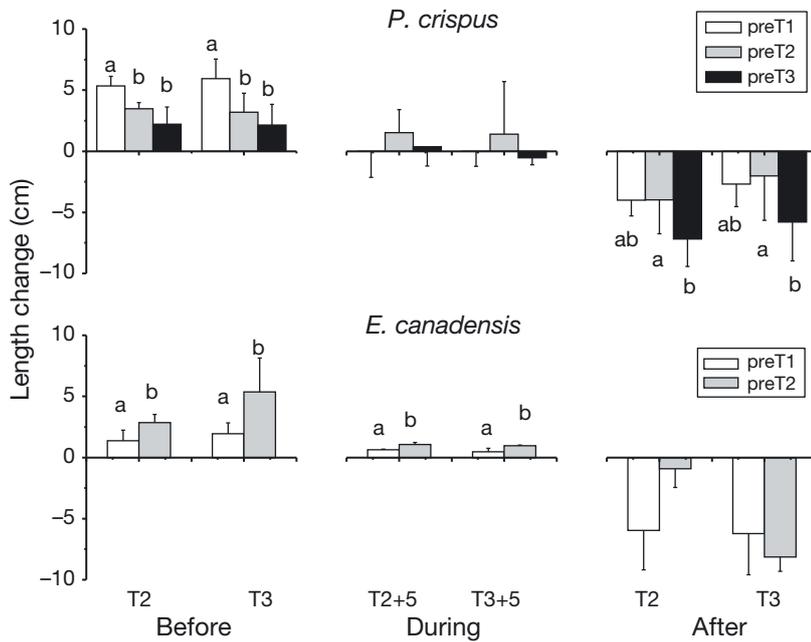


Fig. 1. Length change of the 2 macrophyte species (*Potamogeton crispus* and *Elodea canadensis*) measured at the end of the 3 phases (before, during and after the heat wave). PreT1, preT2 and preT3 in the legend refer to the 3 adaptation temperatures. The characters (a and b) indicate a significant difference ($p < 0.05$) between the adaptation temperatures

plants from preT2 before and during the heat wave, but no difference was observed between plants from preT1 and preT2 after the heat wave. There were no significant differences in length increment between the 2 heated treatments for the first 2 phases. After the heat wave, however, the length reduction was smaller for plants growing in the T2 heated treatment than in the T3 heated treatment, and the interaction between heated treatments and adaptation temperatures was significant (2-way ANOVA, $F = 7.583$, $p < 0.05$).

Table 1. Statistical significance tests on the change in macrophyte attributes between the 2 heated treatments measured at the end of each of the 3 phases (before, during and after the heat wave). Characters in the column below (e.g. T2 or T2 + 5) refer to the different heated treatments. (–) not detected, NS: not significant, * $p < 0.05$, ** $p < 0.01$

Attribute	<i>Potamogeton crispus</i>			<i>Elodea canadensis</i>		
	Before	During	After	Before	During	After
Length	NS	NS	NS	NS	NS	T2 < T3*
Leaf biomass	NS	NS	NS	NS	T2 + 5 > T3 + 5**	NS
Stem biomass	NS	NS	NS	T2 < T3*	NS	NS
Turion or root biomass	NS	NS	NS	NS	NS	NS
Total biomass	NS	NS	NS	NS	T2 + 5 > T3 + 5**	NS
Turion or branch number	NS	NS	NS	NS	NS	NS
Average turion weight	NS	NS	NS	–	–	–

3.2. Biomass

Changes in leaf, stem, turions and total biomass of *P. crispus* did not differ between the 3 preTs or the 2 heated treatments throughout the experiment (Fig. 2, Table 1).

For *E. canadensis*, the increases in leaf, stem, root and total biomass were lower for plants from preT1 than for plants from preT2 before and during the heat wave, except for changes in stem biomass, which did not differ between plants from preT1 and preT2 during the heat wave. The stem biomass increase was higher for plants growing in T3 than in T2 before the heat wave, and the increases in leaf and total biomass also differed significantly between T2 + 5 and T3 + 5 during the heat wave, being higher in T2 + 5. After the heat wave, there were no significant differences for any of these variables between T2 and T3, but the interaction between adaptation temperatures and temperature treatments was significant for stem biomass, root biomass and total biomass (2-way ANOVA, $F = 4.903$ to 8.366 , $p < 0.05$).

3.3. Asexual reproduction

Prior to the heat wave, the density of *P. crispus* turions was lower and average turion weight was higher for plants from preT1 than from preT2 and preT3 (Fig. 3), with average turion weight of the preT1 plants reaching 0.16 ± 0.10 g dry weight. During and after the heat wave, there were no significant effects of preTs or temperature treatments (Table 1) on turion numbers or average turion weight. As an aspect of the recovery potential, the germination proportion (Fig. 4) did not differ significantly among the 3 preTs (2-way ANOVA, $F = 0.4674$, $p > 0.05$), but it was lower for plants growing in T3 than in T2 (2-way ANOVA, $F = 4.601$, $p < 0.05$) at the end of the experiment.

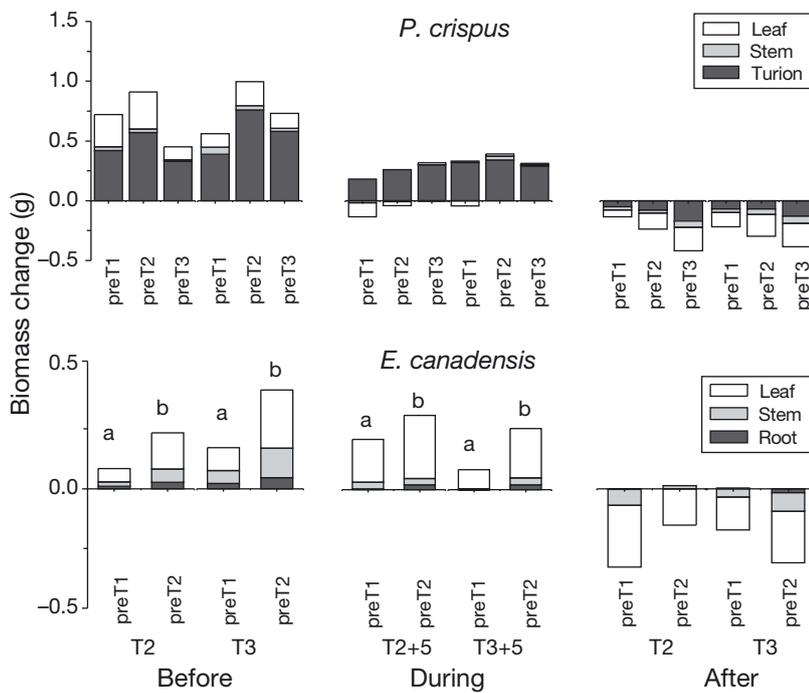


Fig. 2. Biomass change of the 2 macrophyte species (*Potamogeton crispus* and *Elodea canadensis*) measured at the end of the 3 phases (before, during and after the heat wave). PreT1, preT2 and preT3 in the legend refer to the 3 adaptation temperatures. The characters (a and b) indicate a significant difference ($p < 0.05$) between the adaptation temperatures for total biomass

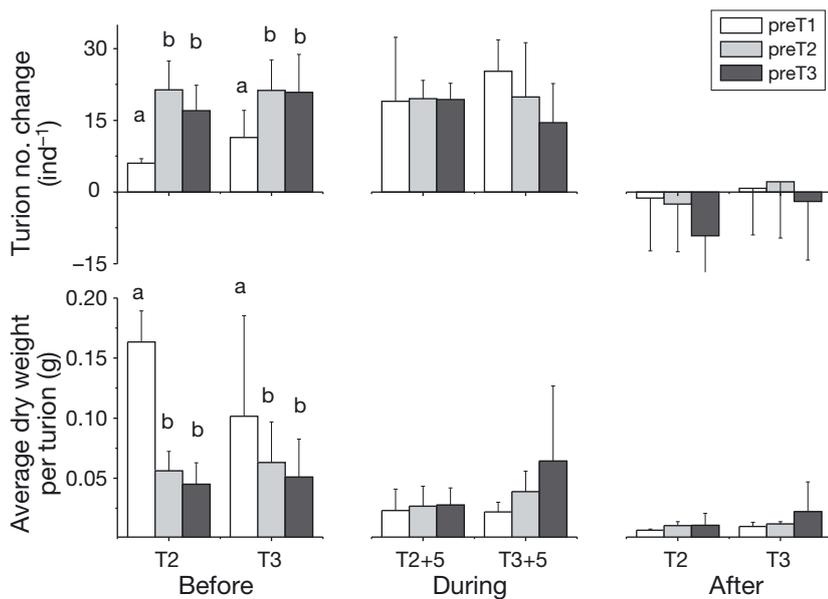


Fig. 3. Change in turion numbers and average weight of *Potamogeton crispus* measured at the end of the 3 phases (before, during and after the heat wave). PreT1, preT2 and preT3 in the legend refer to the 3 adaptation temperatures. The characters (a and b) indicate the presence of a significant difference ($p < 0.05$) between the adaptation temperatures

The branch number changes of *E. canadensis* did not differ between the 2 preTs or between the 2 heated treatments, perhaps due to large variations among the 4 replicates (Fig. 5, Table 1).

4. DISCUSSION

The 2 submerged macrophyte species (*Potamogeton crispus* and *Elodea canadensis*) responded differently to warming and to the heat wave. There were also significant differences as a result of the 10 yr adaptation to different temperatures. Prior to the heat wave, the change in *P. crispus* total biomass was not affected by the different adaptation temperatures. The plants adapted to the highest temperatures, however, were significantly shorter and had smaller but more abundant turions, indicating that they allocated fewer resources to elongation and more to asexual reproduction. Though the change in total turion biomass did not differ between the 3 adaptation temperatures, there appeared to be a trade-off strategy reducing the size of turions of *P. crispus* to maintain abundance to optimise asexual reproduction, a common reproduction strategy in plants (Jakobsson & Eriksson 2000). This is in accordance with Li (2014), who suggested that submerged macrophytes with a potential for both asexual and sexual reproduction rely on asexual reproduction to maintain the current population size. We cannot completely rule out, however, that the plants adapted to different temperatures were in a different state of development, as *P. crispus* was generally in decline during the experimental period, without showing any clear effects of adaptation temperature (Fig. A1). After 10 yr of adaptation, *P. crispus*, showing both sexual and asexual reproduction in the ponds, had apparently changed its asexual reproduction and adapted to the higher temperatures. *E. cana-*

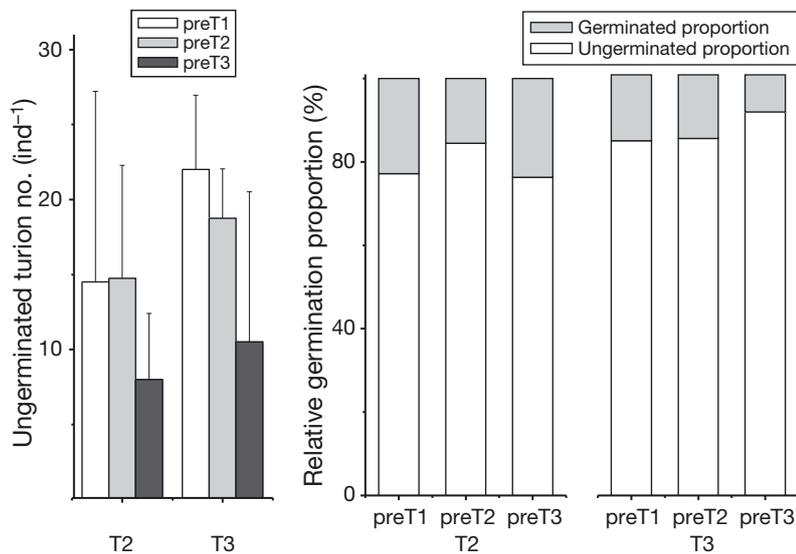


Fig. 4. Number of turions ungerminated and germination rate of *Potamogeton crispus* at the end of the experiment. PreT1, preT2 and preT3 in the legend refer to the 3 adaptation temperatures. Ungerminated proportion means the ungerminated turion number divided by total turion number

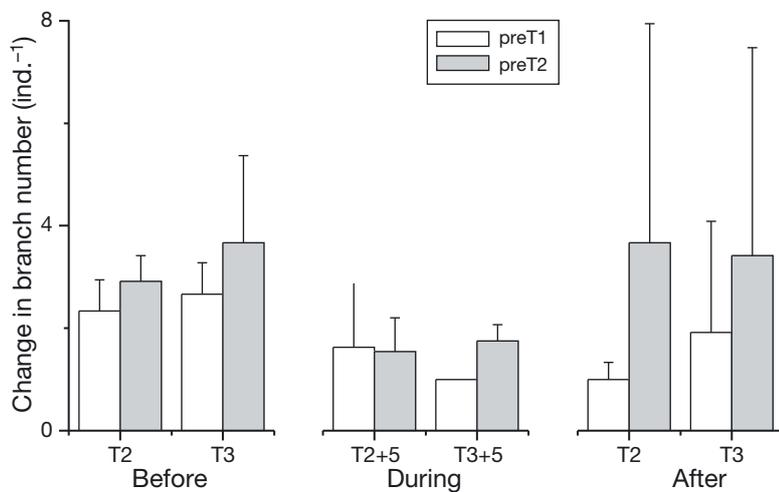


Fig. 5. Change in branch number of *Elodea canadensis* at the end of the 3 phases (before, during and after the heat wave). PreT1 and preT2 in the legend refer to the 2 adaptation temperatures

densis showed a different pattern from *P. crispus*, as the plants adapted to the highest temperatures had a higher length increment and a higher increase in leaf, stem, root and total biomass, but not in branch number, prior to the heatwave than at lower temperatures. *E. canadensis* reproduces vegetatively with broken pieces of shoots or stems and does not produce special asexual reproduction organs such as turions, while *P. crispus* does, making it more difficult to separate asexual reproduction and growth for *E. canadensis*.

Prior to the heat wave, total biomass changes of the native species *P. crispus* and the invasive species *E. canadensis* did not differ between the 2 heated treatments (ca. +3° and ca. +4.5°C) irrespective of adaptation temperature. In a mesocosm experiment conducted in the subtropical part of China, a temperature increase of ca. 3°C above ambient temperatures promoted the growth of the native species *Vallisneria spinulosa* (Cao et al. 2014); in an outdoor experiment in the UK, higher temperatures promoted growth of the invasive species *Lagarosiphon major* and *Myriophyllum spicatum*, while no effects of elevated temperature were traced for the native species *E. nuttallii*, *P. natans* and *M. sibiricum* (McKee et al. 2002, Patrick et al. 2012). These differences suggest species-specific responses to temperature elevation, potentially favouring the growth of invasive species. However, it is important to emphasise that the responses of submerged macrophytes to warming are not straightforward. Several complex, temperature-related interactions exist with, for instance, phytoplankton or epiphyton shading, nutrient release and inorganic carbon as well as the chemical and physiological features and growth status of the plants, which may affect the response of macrophytes to increased temperatures (Kosten et al. 2011, Cao et al. 2014, Maberly 2014).

During the heat wave, *E. canadensis* adapted to higher temperatures exhibited a greater increase in total biomass, with a larger allocation of biomass to roots and leaves than plants adapted to lower temperatures. This concurs with Bowmer et al. (1995), who found that *E. canadensis* under unfavourable conditions produces condensed shoots, which are able to root readily at the nodes. In addition, the optimal partitioning theory states that plants allocate energy to specific parts, optimising the uptake of resources that limit growth (McCarthy & Enquist 2007). Plants may need more nutrients and energy to resist the effects of heat waves, and nutrients may therefore become limiting. This leads to

enhanced development of root and leaf biomass to absorb more nutrients (Madsen & Cedergreen 2002). The stronger growth of leaves and roots of *E. canadensis* adapted to higher temperatures during the heat wave may therefore indicate a better capacity to withstand higher temperatures than plants adapted to lower temperatures.

After the heat wave, changes in *E. canadensis* biomass (total, root and stem) did not differ among plants adapted to different temperatures or between the 2 heated treatments, but the interaction between these 2 factors was significant. The latter results indicate that *E. canadensis* adapted to ambient temperatures and incubated at the 2 higher temperatures underwent a large reduction in biomass after the heat wave irrespective of temperature scenario, while the ca. +9.5°C heat wave apparently was more devastating than the ca. +8°C heat wave for the macrophytes adapted to higher temperatures. Changes in the total biomass of *P. crispus* did not differ significantly between the adaptation temperatures. In nature, *P. crispus* is an early-growing species exhibiting active growth mainly from spring to mid-summer, whereas *E. canadensis* is a relatively late-growing species with an active growth period extending to late October in our experimental mesocosm system (T. L. Lauridsen unpubl. data). Cao et al. (2014) reported that *P. crispus*, being a spring species in Wuhan (subtropical China), enters a senescent state from May and does not respond to elevated temperatures during the biomass decline, while *V. spinulosa*, an actively growing species, benefits from warmer conditions (ca. +3°C). In the present study, the total biomass of *P. crispus* adapted to the different temperatures did not show any variation in their response to the heat wave, possibly because they already were in a state of decline (Fig. A1).

During the heat wave, *E. canadensis* exhibited a higher leaf and total biomass increase in the ca. +8°C than in the ca. +9.5°C heated treatment, indicating reduced growth at the highest temperatures. After the heat wave, however, the length and total biomass of both submerged macrophyte species decreased and, at least for *E. canadensis*, this may imply heat stress, as the PVI of this species in the unheated mesocosms did not decrease, and the plants showed no sign of decay (Fig. A1). Also, after the heat wave, the *P. crispus* turion germination rate was higher in the ca. +3°C treatment than in the ca. +4.5°C treatment, indicative of reduced germination at higher temperatures, which is in agreement with the findings of Rogers & Breen (1980). A higher-temperature scenario, therefore, appears to have reduced the recovery potential

of *P. crispus* by inhibiting the germination of turions, but it might not have affected the recovery potential of *E. canadensis*, as we found no differences in branch number for this species. Contrary to studies of the response of terrestrial plants to heat waves (Jolly et al. 2005), our 2 study species did not show a coherent response, which may reflect that soil moisture is an overall dominant factor regulating the growth of terrestrial vegetation under a heat wave, thus synchronising the response (Fischer et al. 2007).

Biochemical and physiological processes including enzyme activity in plants are closely related to temperature (Olesen & Madsen 2000). Both of the macrophyte species used in our study are able to use CO₂ and bicarbonate as carbon source (Nichols & Shaw 1986), and the bicarbonate concentration was mostly sufficient for optimal growth at the level of 1 mmol l⁻¹ (Table A1 in the Appendix). So, the carbon supply in the water was probably not the reason for the different responses of the 2 species. A low carbon to nitrogen (C:N) ratio has been considered an indicator of low production for marine macrophytes (Niell 1976). A previous study conducted in the same mesocosms as used in our study by Ventura et al. (2008) likewise showed that the C:N ratio of *E. canadensis* decreased with increasing temperature; however, C:N ratio data are not available from our experiment.

In conclusion, after a 10 yr period of adaptation to different temperatures, submerged macrophytes adapted to increased temperatures showed some adaptive responses, including a trade-off between turion size and turion number and differential mass allocation among leaf, stem and root, potentially contributing to macrophyte resistance to heat stress. Furthermore, the heat wave seemed to have adverse effects on the submerged macrophytes and, at least for *E. canadensis*, the higher the temperature the more severe the effect. As we did not have a real control (collected individuals of macrophytes grown in the ambient temperatures) for the heat wave treatment, our results should be interpreted with caution, however. As in an earlier study (Cao et al. 2014), our results provide some, albeit not conclusive, evidence that the response of macrophytes to higher temperatures is sensitive to the growth status of the plants, indicating that the effects of the heat wave observed might differ depending on the timing of the heat wave and thus the growth phases of the plant species involved, a topic that requires further investigation. More studies of the biochemical and physiological response of macrophytes are also needed to fully understand the reaction of submerged macrophytes to extreme weather events.

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Appendix. Additional experimental information

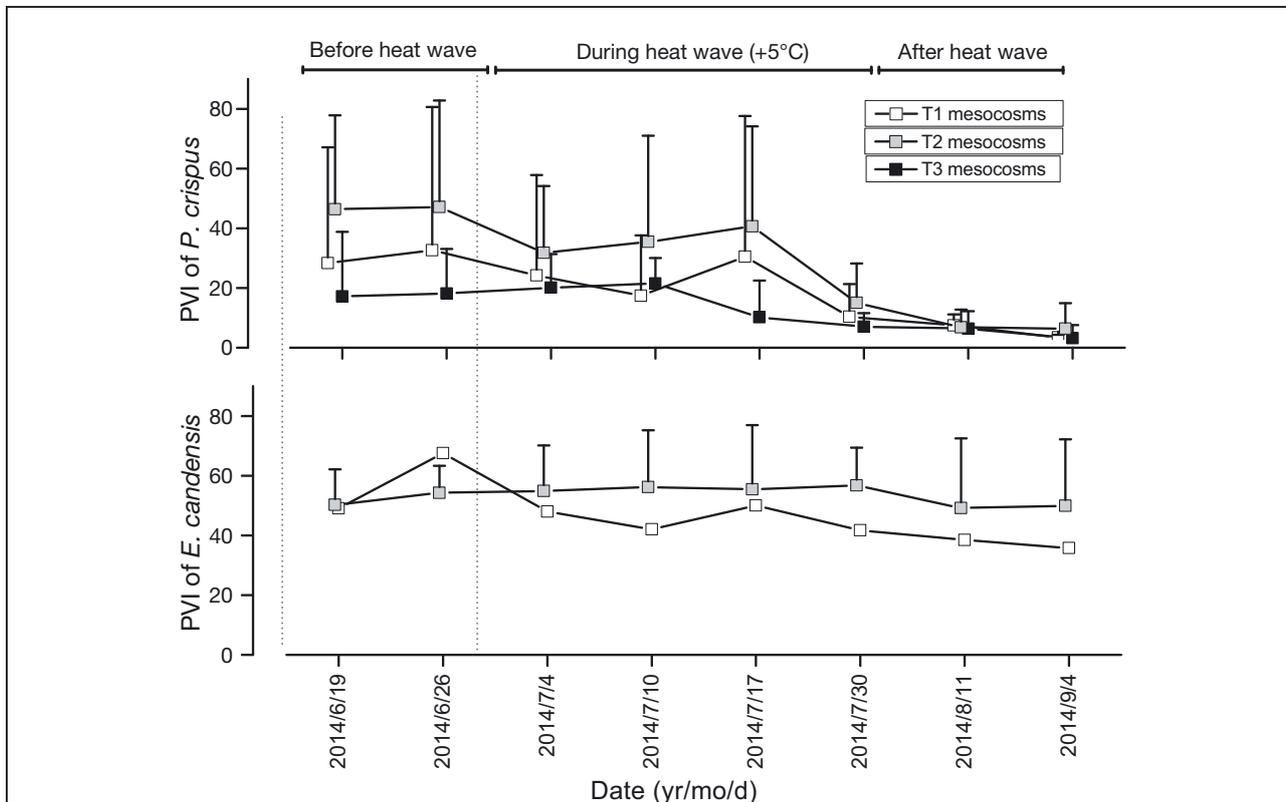


Fig. A1. Plant volume inhabited (PVI, %) of each species (*Potamogeton crispus* and *Elodea canadensis*) in the 12 mesocosms during the experiment (dotted line shows the 2 samplings undertaken before and during the heat wave). T1, T2 and T3 represent the 3 simulated temperature scenarios (see Section 2.1). Error bars indicate the standard deviation

Plant volume inhabited

The plant volume inhabited (PVI) of *Potamogeton crispus* started to decrease after July in both the T1 (unheated, without heat wave) and T2 and T3 (heated, with heat wave) mesocosms, while the PVI of *Elodea canadensis* remained relatively stable (Fig. A1).

Table A1. Main environmental variables: water temperature ($^{\circ}\text{C}$); pH; total alkalinity (TA, mmol l^{-1}); and concentrations of free CO_2 ($\mu\text{mol l}^{-1}$), bicarbonate (HCO_3^- , mmol l^{-1}), dissolved oxygen (DO, mg l^{-1}), total phosphorus (TP, $\mu\text{g l}^{-1}$), dissolved inorganic phosphorus (DIP, $\mu\text{g l}^{-1}$), total nitrogen (TN, mg l^{-1}) and dissolved inorganic nitrogen (NO₂₃-N, including only $\text{NO}_2\text{-N}$ and $\text{NO}_3\text{-N}$, mg l^{-1}) during each experimental phase (before, during and after the heat wave) in the 12 mesocosms. See Section 2.1 and 2.2 for description of temperature treatments

Background variable	Before heat wave (June 26)			During heat wave (July 28)			After heat wave (August 28)		
	T1	T2	T3	T1	T2 + 5	T3 + 5	T1	T2	T3
Temperature	17.09 ± 0.39	19.55 ± 0.34	20.80 ± 0.39	22.58 ± 0.52	29.95 ± 0.48	31.35 ± 0.48	15.44 ± 0.50	19.22 ± 0.45	21.07 ± 0.55
pH	8.59 ± 0.52	9.02 ± 0.15	8.45 ± 0.46	8.26 ± 0.40	8.26 ± 0.37	7.96 ± 0.30	8.37 ± 0.43	8.76 ± 0.56	8.34 ± 0.47
TA	1.28 ± 0.82	0.61 ± 0.12	1.34 ± 0.49	1.44 ± 0.54	1.16 ± 0.54	1.70 ± 0.30	1.60 ± 0.54	1.02 ± 0.53	1.47 ± 0.32
Free CO_2	14.0 ± 15.0	1.1 ± 0.6	12.3 ± 9.1	20.0 ± 15.6	17.6 ± 2.2	31.3 ± 31.5	22.4 ± 23.0	10.7 ± 18.9	15.5 ± 15.6
HCO_3^-	1.21 ± 0.84	0.52 ± 0.11	1.28 ± 0.50	1.40 ± 0.55	1.12 ± 0.55	1.64 ± 0.33	1.54 ± 0.56	0.93 ± 0.56	1.38 ± 0.37
DO	10.68 ± 0.84	11.11 ± 0.73	9.10 ± 1.01	8.89 ± 0.78	7.84 ± 1.10	7.09 ± 0.58	11.35 ± 0.96	11.19 ± 1.01	9.42 ± 0.98
TP	12 ± 7	8 ± 2	9 ± 3	14 ± 7	11 ± 1	21 ± 16	6 ± 3	4 ± 2	12 ± 15
DIP	4 ± 2	3 ± 1	2 ± 0	5 ± 4	2 ± 1	2 ± 1	3 ± 2	1 ± 0	1 ± 0
TN	0.21 ± 0.08	0.19 ± 0.09	0.14 ± 0.04	0.23 ± 0.19	0.25 ± 0.14	0.54 ± 0.37	0.45 ± 0.7	0.13 ± 0.07	0.38 ± 0.30
NO ₂₃ -N	0.03 ± 0.04	0.01 ± 0	0.01 ± 0	0.03 ± 0.04	0.08 ± 0.13	0.19 ± 0.21	0.39 ± 0.72	0.04 ± 0.05	0.13 ± 0.11

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