Article

Warming shows differential effects on late-season growth and competitive capacity of *Elodea canadensis* and *Potamogeton crispus* in shallow lakes

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Abstract

Submerged macrophytes are likely to be affected by climate changes through changes in water temperatures and length of growing season. We conducted a lab experiment to examine the influence of a late-season temperature increase on growth, biomass allocation, and acclimation of 2 submerged macrophyte species, *Elodea canadensis* and *Potamogeton crispus*. We also ran competitive interaction experiments between the 2 species with mono- and mixed-species cultures in pots placed in outdoor heated mesocosms (5 years at ambient temperature and a higher temperature following the IPCC A2 scenario downscaled to local conditions but enhanced by 50%). In the lab, macrophytes collected in the 2 types of mesocosms were grown at ambient temperatures (12 °C in September and 8 °C in October) and 4 °C higher. Warming had an overall stronger effect on *E. candensis* than *P. crispus*, particularly within the low temperature range studied. Hence, the relative growth rate (RGR) of *E. canadensis* acclimated to ambient mesocosm conditions increased 6-fold from low (8 °C) to high (16 °C) temperature, whereas the RGR of *P. crispus* increased <2-fold. In the competitive interaction experiment, warming increased the biomass and RGR of *E. canadensis* in the monoculture. In addition, warming increased shoot elongation of the plant in both the monoculture and mixed culture. *P. crispus* was generally unaffected by warming when grown in both monoculture and mixed culture, but competition decreased the elongation of shoots pre-adapted to ambient conditions and grown in the warmer mesocosms. The decomposition rate of *E. canadensis* accelerated with warming but was unaffected in *P. crispus*. We conclude that *E. canadensis* is a stronger competitor than *P. crispus* under warmer late-season conditions; however, it may have a higher demand for oxygen due to the increased decomposition rates at higher temperatures, particularly in the peripheral growing season, with potential profound effects on lake ecosystems. Although acclimatisation was evident, we suggested that temperature changes will affect the growth pattern of the 2 plant species and thereby perhaps induce a switch in macrophyte species dominance.

Key words: competitive interaction, decomposition, growth, submersed vegetation, warming

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Introduction

The global climate is expected to undergo significant changes in this century and this is considered one of today's most important threats to ecosystems (Parmesan and Yohe 2003, Thomas et al. 2004). Global warming impacts the length and timing of the seasons as well as the biological interactions in lakes (Schindler 1997, Netten et al. 2010, 2011). Notably, the current temperature increase is particularly pronounced during autumn and winter in northern temperate lakes (Jørgensen et al. 2001).

Submerged macrophytes, which play a key role for biodiversity and water transparency in shallow temperate lakes (Scheffer et al. 1993, Jeppesen et al. 1998), may be exposed to strong temperature fluctuations at both diel and seasonal scales. Most plants have an ability to acclimate to temperature variations through phenotypic modifications, which may be both physiological and morphological (Olesen and Madsen 2000, Pilon and Santamaría 2002, Odgaard 2009). In addition, macrophytes from different habitats have shown large differences in the response of photosynthesis to temperature, which may reflect genotypic variations in the photosynthetic apparatus, allowing the macrophytes to thrive under different temperature regimes (Palmer et al. 2012).

Changes in macrophyte morphology and biomass allocation as influenced by warming may lead to increased growth or competitive ability (Pilon and Santamaría 2002, Riis et al. 2012). Hence, *Potamogeton pectinatus* grown at a range of temperatures showed increased stem length up to 15 °C, and the number of nodes and branches reached a maximum at ~25 °C (Pilon and Santamaría 2002). Additionally, particularly the root:shoot ratio increases markedly with temperature (Santamaría and van Vierssen 1997). Temperature also affects the seasonal dynamics of some macrophytes. Thus, earlier seasonal growth has been observed for both *Potamogeton crispus* and *Elodea canadensis* at warm temperature regimes, but for *P. crispus* growth also peaks earlier in the growing season (Haag and Gorham 1977).

Competition has been acknowledged as an important factor determining species distribution in aquatic macrophyte communities, with implications for the structure and functioning of lake ecosystems (Moss et al. 2003, Doyle et al. 2007, Hussner et al. 2014). The competitive capacity of the different species may be affected by warming (Mulholland et al. 1997, Winder and Schindler 2004, Patrick et al. 2012), ultimately affecting the species composition in lakes (Carpenter et al. 1992, Mulholland et al. 1997).

With warming, interspecific differences in decomposition rates are also anticipated (Hill and Webster 1982, Chimney and Pietro 2006), depending on macrophyte quality for decomposers (Heal et al. 1997, Battle and Mihuc 2000, Chimney and Pietro 2006, Parton et al. 2007), and such differences may also alter the outcome of competitive interactions among the species involved (Mooney 1991, Pearson and Dawson 2003).

In this study we focused on the influence of autumn temperatures on growth, biomass allocation, interspecific competition, and decomposition of 2 submerged macrophyte species, *E. canadensis* and *P. crispus*. Both are perennial, tolerant species in natural aquatic ecosystems in Eurasia and common in eutrophic waters. Originally, *P. crispus* is a Euro-Asiatic species (Nichols and Shaw 1986) that tolerates low temperatures in winter and exhibits early spring blooming (Nichols and Shaw 1986). In contrast, *E. canadensis* originates from North America. It was observed for the first time in Europe Alsace, France, in 1875 (Rencke 1882) and has since developed into the most common alien aquatic species in Europe (Hussner 2012).

We used *E. canadensis* and *P. crispus*, grown for 5 years in experimental mesocosms placed in Central Jutland, Denmark, at naturally occurring ambient temperature and at a higher temperature corresponding to the A2 climate scenario reported by the Intergovernmental Panel on Climate Change (IPCC), downscaled to the local condition, but enhanced by 50% (A2+50%) (Liboriussen et al. 2005). We aimed to answer the following questions: (1) Will plant performance differ among specimens that have been exposed to short- and long-term increased temperature? We used transplantation experiments to test whether the growth response to elevated temperature (+4 °C) differs between plants acclimatised for 5 years to enhanced temperature versus non-acclimatised plants grown at ambient temperatures. (2) Will *E. canadensis* be a superior competitor to *P. crispus* in late autumn/winter when lakes get warmer, and do they perform better when growing alone than when the 2 species are mixed? We performed a transplantation experiment in the mesocosms using both monocultures and mixed cultures of the 2 species. (3) Will the 2 species show different decomposition rates? We ran decomposition experiments in the mesocosms.

Materials and methods

Experimental mesocosm facility

In spring 2003, a flow-through mesocosm experiment was initiated in Central Jutland, Denmark (56°14′N, 9°31′E). The mesocosms were filled with sediment, and natural aquatic freshwater communities were established and allowed to develop in the following month, leading to extensive growth of the submerged macrophytes *P. crispus*

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and *E. canadensis*. The plants used in the experiments originated from inoculums from the sediment from a pond as well as surface sediment added from 5 lakes with contrasting nutrient levels. The plants were cross-mixed before the start of the experiment to obtain similar starting conditions. Electrical-powered heating to A2+50% conditions was initiated in August 2003 (Liboriussen et al. 2005). Heating was continuously controlled relative to the ambient temperature mesocosms. The mesocosms consisted of cylindrical stainless steel tanks measuring 1.9 m in diameter and 1.5 m in total depth, equipped with a flow-through system. The water level was 1.0 m and the total volume ~2800 L per mesocosm (Liboriussen et al. 2005). A 0.3 m layer of sediment, consisting of natural sediment from a nearby pond and sand, was mixed together and sieved to remove larger particles using standard methods before being added to each mesocosm (see Liboriussen et al. 2005 for details). Inlet water consisted of groundwater with known concentrations of total phosphorus (TP; 2–20 µg L^{-1} P), total nitrogen (TN; 51–70 µg L^{-1} N), and total iron (Fe; 0.10–0.62 mg L^{-1} Fe) from a local well. The retention time was approximately 2 months. High nutrient levels were obtained by addition of P (18.9 mg m^{-2} $week^{-1}$) and N solutions (189.7 mg m^{-2} $week^{-1}$ from August 2003 to December 2004 and 758.8 mg m^{-2} $week^{-1}$ from December 2004 to September 2008); the low nutrient level mesocosms received no extra nutrient additions. For more details see Liboriussen et al. (2005) and Nielsen et al. (2013).

Temperature acclimation

We conducted a 2-factorial (temperature × plant origin) laboratory experiment to study the short-term (weeks) effects of a temperature increase on the growth and biomass allocation patterns of *P. crispus* and *E. canadensis* subjected to long-term (5 years) acclimation to ambient and elevated (A2+50%) mesocosm temperatures. The experiment was performed during 2 time periods. The 2 species were sampled from the mesocosms on 29 September and 27 October 2008, when the ambient and A2+50% temperatures were 12 and 16 °C and 8 and 12 °C, respectively. In the lab, ~10 cm-long apical shoots of the plants were placed in aquaria with aerated water from the mesocosms and allowed to acclimate to experimental temperatures during a 1-week pre-incubation period. The aquaria were placed in climate chambers adjusted to the relevant temperatures. Half of the shoots from each combination of species and mesocosm temperature treatment was pre-incubated at ambient temperature (12 °C in September and 8 °C in October), and the other half was pre-incubated at the 4 °C higher temperature corresponding to the A2+50% scenario. Light intensity was 300 µmol m^{-2} s^{-1}.

After 1 week the shoots were mounted on nets and placed in aquaria with 5 L growth medium, which was modified from that described by Smart and Barko (1985) by increasing alkalinity from 0.85 to 1.2 meq L^{-1} and by adding 0.02 mM KH_2PO_4 and 0.2 mM NH_4NO_3. To this medium we added a commercial micronutrient solution (Plant Nutrition liquid, Tropica Aquacare). Throughout the experiment the aquaria were bubbled with atmospheric air. The medium was changed every other day to minimise growth of algae. Any filamentous algae associated with the plants were gently removed with a fine brush, when necessary. The light intensity was 300 µmol m^{-2} s^{-1} (16 h daylight/8 h night period) at the surface of the aquaria. Because the light source was placed at the side of the climate chamber, the position of the macrophytes within the aquaria was shifted every other day.

At the initiation of the experiment, 125 apical shoots without branches from each species type (long-term acclimated ambient and elevated mesocosm temperature) and pretreatment temperature were shortened to 5 cm. The shoots were mounted on nets (4 shoots of *P. crispus* and *E. canadensis* on each net) and incubated at the same temperature as during pre-incubation. The experiment was triplicated, and the plants were allowed to grow for 2 weeks before harvesting. Additionally, prior to the experiment, 10 shoots from each of the 4 plant origins were used to determine the initial wet weight/dry weight. The shoots were weighed and subsequently frozen for later freeze drying and determination of dry weight.

All shoots were harvested, and biomass allocation was measured as shoot length (main stem), number of leaves (*P. crispus*) or leaf verticils (*E. canadensis*), and branches per stem length. Dry weight (DW) of leaf and root biomass was determined on freeze-dried material, and the root to total shoot biomass ratio was calculated. Length growth was determined as increase in stem length per unit of time. The relative growth rate (RGR) was calculated as: $RGR = (\ln W_1 - \ln W_2)\, t^{-1}$, where W_1 and W_2 are the DW of shoot biomass prior to and after the growth period, and t is growth period in days.

To evaluate temperature acclimation of the 2 species, we calculated the relative response of each species and plant origin against that of control plants originating from ambient mesocosms and grown in the laboratory at ambient temperatures of 12 °C in September and 8 °C in October. Accordingly, in September the performance at 16 °C (A2+50% scenario) of the plants from ambient (12 °C) and heated mesocosms (16 °C, A2+50% scenario) was normalised to the performance of plants grown at experimental temperatures of 12 °C. Similarly, the performance of October plants at 12 °C (A2+50% scenario) was normalised to the performance of ambient plants grown at 8 °C.

The effects of temperature on shoot performance and the interaction between temperature and plant origin of *E. canadensis* and *P. crispus*, respectively, were analysed by 2-way analysis of variance (ANOVA). Homogeneity of variance was tested using Levene's test, and data were log-transformed if necessary.

Field mesocosm competition experiments

The field competition experiments were conducted in the low-nutrient–level mesocosms that received no additional nutrient additions apart from input from the groundwater added. *P. crispus* and *E. canadensis* were collected in November 2008 from the mesocosms run at ambient and +4 °C temperatures. Apical shoots of 12 cm in length were prepared and washed with tap water to remove accumulated sediments, debris, and epiphytes prior to the experiment. For *E. canadensis*, DW was 60.7 ± 14.2 and 57.5 ± 10.5 mg shoot^{-1} in the ambient mesocosms (n = 9) and the heated mesocosms (n = 9), respectively. For *P. crispus,* DW was 35.6 ± 2.0 and 30.2 ± 8.4 mg shoot^{-1} in the ambient temperature mesocosms (n = 9) and the heated mesocosms (n = 9), respectively.

For the experiment we used plastic pots with an inner diameter of 7 cm and a depth of 15 cm. Sediment was collected from a nearby nutrient-rich freshwater pond. To remove large fragments of vegetation and avoid uncontrolled introduction of vertebrates such as fish or amphibians, sediment was flushed through a 1 × 1 cm sieve and drained of excess water prior to mixing with washed sand with a volume ratio of 1:1.

A mixed sediment layer of 15 cm was placed evenly in the pots, and the shoots were planted with 4 cm of the stem embedded in the sediment and 8 cm stem above the sediment. *E. canadensis* and *P. crispus*, collected from the ambient mesocosms, were planted as monocultures in 6 pots for each species and in 6 pots as mixed cultures (18 total pots). Each pot contained 4 shoots of the same species in monocultures, whereas there were 2 *E. canadensis* and 2 *P. crispus* shoots per pot in the mixed cultures. To ensure similar conditions of competition from the beginning of the experiment, a stainless iron ring (inner diameter of 9 mm) was put around each plant stem to keep all 4 shoots in each pot close together. Next, the pots with macrophytes were placed into 2 frames, each containing 9 pots: 3 monoculture pots of *E. canadensis*, 3 monoculture pots of *P. crispus*, and 3 mixed culture pots. One frame was then placed 20 cm below the water surface in an ambient mesocosm and the other in a heated mesocosm (A2+50% scenario). *E. canadensis* and *P. crispus* collected from the heated mesocosms received the same treatment as described above but were only incubated in the heated mesocosm (A2+50% scenario). After 4 weeks, the macrophytes were harvested. The aboveground part of the plants was collected and washed on a 1 mm sieve to remove accumulated sediments, debris, and epiphytes and subsequently oven-dried at 80 °C until constant DW was attained.

Mesocosm plant decomposition experiment

The effect of heating on macrophyte decomposition was investigated in November 2008. Apical shoots (12 cm) of *P. crispus* and *E. canadensis* were collected from an ambient mesocosm and washed with tap water to remove accumulated sediments, debris, and epiphytes. Two shoots of *P. crispus* or *E. canadensis* were added to each of 6 brown plastic bottles and filled with 150 mL filtered water from the ambient mesocosm; 6 other bottles contained only filtered water and served as controls. In addition, a filtered water sample was taken to determine the initial P concentration. All bottles were tightly capped and placed in 2 frames, each frame containing 3 bottles with *P. crispus*, 3 bottles with *E. canadensis*, and 3 with just filtered water (controls). The 2 frames were anchored below the water surface in an ambient mesocosm and a heated mesocosm (A2+50% scenario), respectively. After a week, the frames were lifted and their lids left open for approximately 5 minutes and shaken gently to allow new oxygen to enter. Subsequently, the frames were returned to the mesocosms with closed lids. After 14 days, the frames were taken to the laboratory and macrophytes removed. The water in each bottle was analysed for TP, soluble reactive phosphorus (SRP), TN, and ammonium (NH_4^+-N). TP and TN were analysed after persulphate digestion (APHA 1992), SRP was determined by the ascorbic acid-molybdenum blue method according to Murphy and Riley (1962), and NH_4^+-N was determined by the phenol hypochlorite method according to Solórzano and Sharp (1980).

Comparisons of the means of plant biomass, relative growth rate, and shoot elongation, as well as nutrients, were performed using one-way ANOVA. If the difference was significant, a least significant difference (LSD) test was used to detect which treatments differed.

Results

Temperature acclimation

Warming generally affected the performance of *E. canadensis* (Fig. 1, Table 1). The plants acclimated to ambient and elevated mesocosm temperatures, respectively, were similarly affected by increased temperature as indicated by the nonsignificant temperature × type interaction (Table 1). In October, however, the plants from the elevated temperature mesocosms had significantly

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higher RGR and formed more branches per stem length than plants acclimated to ambient temperatures.

The RGR of *E. canadensis* varied between 0.01 and 0.077 d^{-1} across all temperatures and acclimatisation conditions. Plants collected from ambient temperature conditions in October (8 °C) more than doubled their RGR between 8 and 12 °C, whereas plants collected in September (ambient temperatures of 12 °C) were far less responsive to a +4 °C increase. The shoot elongation rate averaged 0.48 and 0.21 cm d^{-1} in September and October, respectively, and exhibited a 2-fold increase from low to high temperatures in both periods for *E. canadensis*. The average number of leaf verticils cm^{-1} varied from 7.3 to 6.5 at 8 °C and 12 °C in October and from 6.5 to 4.6 at 12 °C and 16 °C in September, being significantly affected by temperature but not by plant origin. The average number of branches by the end of the experiment ranged from 0.21 to 0.37 branches cm^{-1} in October where branching was unaffected by temperature and from 0.27 to 0.43 branches cm^{-1} in September where the plants had a significantly higher number of branches per stem length at 12 °C compared to 16 °C. Root allocation was affected by temperature, and in plants collected in September, root DW constituted a much higher proportion of total DW at high (16 °C) compared to low (12 °C) temperatures. In the October plants, no roots were formed at low temperature (8 °C) during the 2-week growth period; the root biomass ratio at 12 °C was similar to that at 12 °C in the September plants. Overall, plants that were acclimated to elevated temperatures in the mesocosms formed more roots than plants from ambient temperature conditions.

For *P. crispus*, there was no temperature effect on RGR or shoot morphology for the September plants, whereas the October plants responded significantly to temperature regarding all measured parameters except number of leaves per stem length (Fig. 1, Table 1). RGR varied between 0.035 and 0.072 d^{-1} across all temperatures and mesocosm acclimatisation temperatures (plant origin) and was lower at 8 °C than at 12 °C for the October plants and of similar magnitude at 12 °C and 16 °C in September. There was no effect of plant origin on RGR. As to shoot elongation rates, no temperature effect was observed for the September plants, but a stronger effect of plant origin was evident at higher elongation rates (0.33 cm d^{-1}) for shoots acclimated to ambient conditions than for shoots from elevated temperatures (0.23 cm d^{-1}). The October plants, however, showed a 2-fold increase in shoot elongation from 8 to 12 °C for both plant origins. The number of leaves was unaffected by temperature and only varied slightly (3.0–3.8 leaves cm^{-1}) between plant origins in September. The number of branches per stem length was unaffected by temperature for the September plants, whereas the October plants produced fewer branches per stem length at low (8 °C) than at high (12 °C) temperature. Significant temperature × plant origin interactions, however, indicated that branch formation in ambient plants was less sensitive to the low temperature treatment than plants from the heated mesocosm. Biomass allocation to root formation was low during the 2-week growth experiment. Hence, no or little root biomass was formed in plants grown at the low temperatures in September (12 °C) and October (8 °C), respectively, and the root biomass ratio remained <0.009 for the other temperature treatments.

The analysis of the relative response of growth and morphological parameters to temperature increase revealed that even though the 2 species reached similar absolute growth rates (Fig. 1), *E. canadensis* was much more responsive to a temperature increase than *P. crispus* within the temperature ranges studied (Fig. 2). For both species, stem elongation seemed to be sensitive to temperature changes, whereas leaf or branch number per stem length was much less plastic and did not contribute to the increased biomass growth at elevated temperatures to the same extent as stem elongation. For *E. canadensis*, the growth of shoots acclimated to elevated temperatures for 5 years was more responsive to elevated temperatures than shoots acclimated to ambient temperatures, particularly so in October where RGR increased 378% from 8 to 12 °C for shoots originating from heated mesocosms and less (122%) in the ambient mesocosms (Fig. 2C)

Mesocosm experiments

In the monocultures, warming increased the biomass and RGR of *E. canadensis* originating from the ambient mesocosms ($p < 0.05$) but had no effect on the biomass and RGR of *P. crispus* ($p > 0.05$; Fig. 3). Warming did not increase the RGR of *P. crispus* in any of the treatments ($p > 0.05$). Competition decreased the shoot elongation of *P. crispus* and the biomass and RGR of *E. canadensis* for plants transferred from the ambient to the heated mesocosms ($p < 0.05$). Warming in itself increased the elongation of *E. canadensis* pre-adapted to ambient conditions in both the monoculture and the mixed culture ($p < 0.05$; Fig. 3).

In the decomposition experiment, the concentrations of TP and N (including TN and NH_4^+-N) in water with *E. canadensis* were higher in the heated mesocosms than in the ambient mesocosms ($p < 0.05$) at the termination of the experiment (Fig. 4). No difference in concentrations was observed in the experiment with *P. crispus* at any of the temperatures ($p > 0.05$; Fig. 4). The concentrations of nutrients in water with *P. crispus* were higher than with *E. canadensis* in the ambient mesocosms ($p < 0.05$), whereas no difference in concentrations was observed in the heated mesocosms.

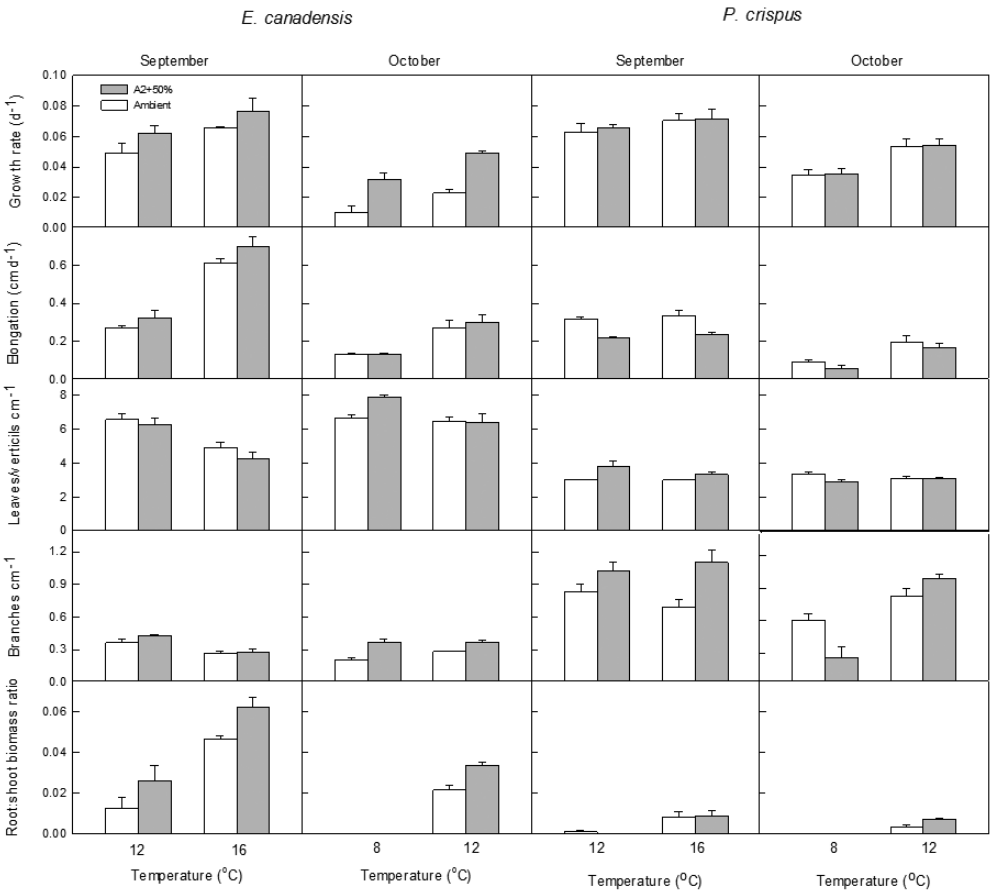

Fig. 1. Effect of temperature on relative growth rate, stem elongation rate, number of leaves, and branches per stem length and root to total shoot biomass ratio of *E. canadensis* and *P. crispus*. The plants were sampled in September and October from outdoor mesocosms with ambient and heated (+4 °C; A2+50%) temperatures. Mean ± SD, n = 3.

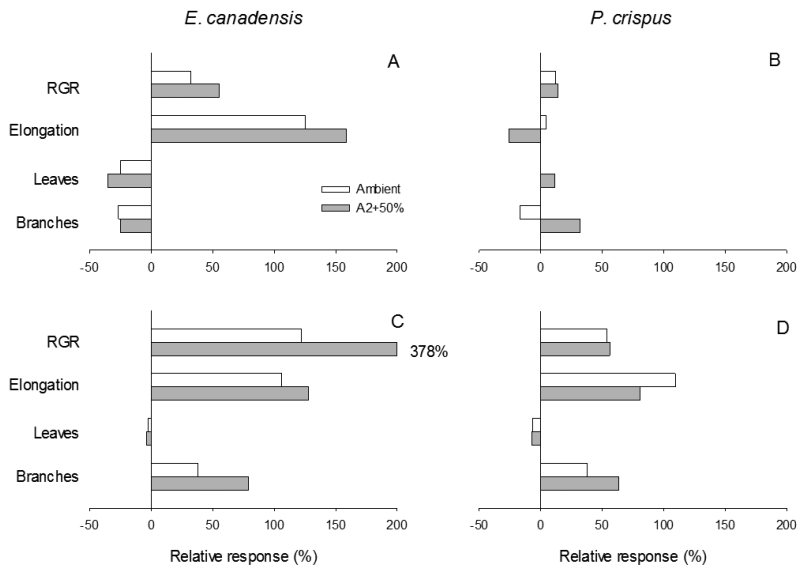

Fig. 2. The relative response of *E. canadensis* and *P. crispus* growth and morphology to a 4 °C temperature increase. Shoots were sampled in (A, B) September and (C, D) October from outdoor mesocosms with ambient (12 °C and 8 °C, respectively) and warmer (+4 °C; A2+50% scenario) temperatures. The relative responses are calculated against control plants collected from and subsequently grown at ambient temperatures of 12 °C in September and 8 °C in October.

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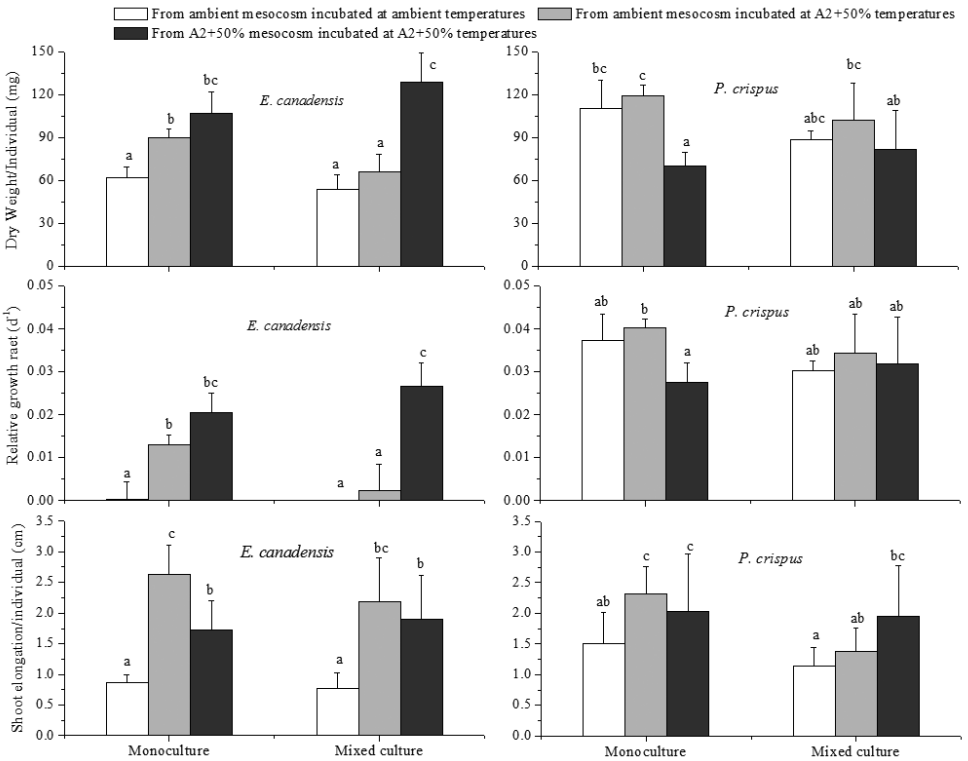

Fig. 3. Dry biomass (mean ± SD), relative growth rates (mean ± SD) and shoot elongation (mean ± SD) of the macrophytes in the mesocosm experiments. Different letters (a, b, c) indicate significant ($p < 0.05$) differences. The incubation time was 4 weeks.

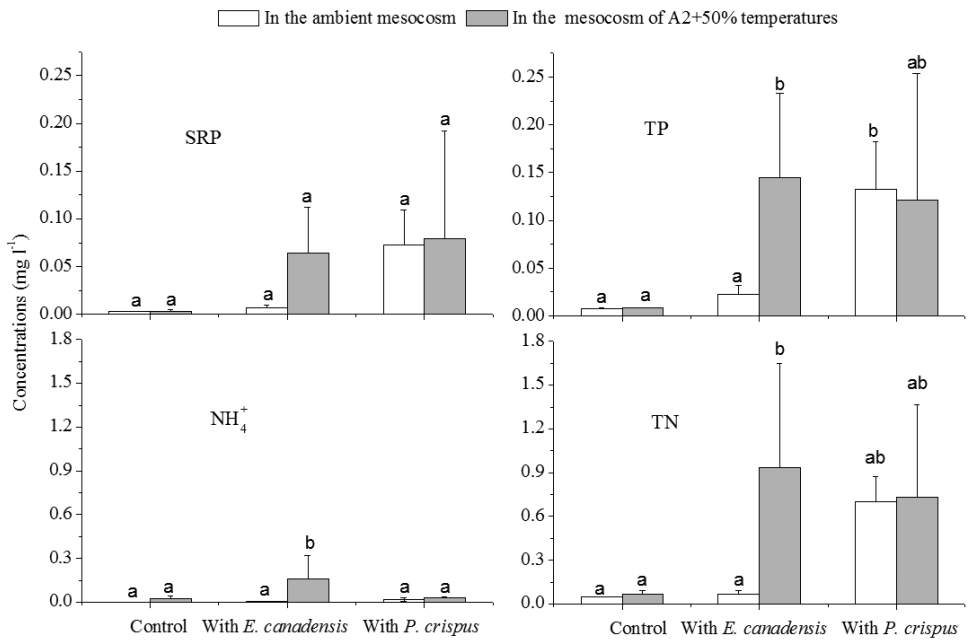

Fig. 4. Various phosphorus (unit as P, mean ± SD) and nitrogen (unit as N, mean ± SD) concentrations in the water of the mesocosm experiments. Different letters (a, b, c) indicate significant ($p < 0.05$) differences. The incubation time was 14 days.

Table. 1. Results of 2-way ANOVA (F-ratios) of the effects of temperature (September: 12 and 16 °C [A2+50% scenario]; October: 8 and 12 °C [A2+50% scenario]) and plant origin on growth and morphology parameters of *E. canadensis* and *P. crispus* (n = 3). Plant origin refers to the mesocosms from which the plants, acclimatised for 5 years to ambient and elevated temperatures, were collected for the experiment. One-way ANOVA was applied to analyse for effects of plant origin on root biomass ratio in October where no roots were formed at low temperatures.

			September	October
Species	Variable	Source	F-Ratio	F-Ratio
E. canadensis	Relative growth rate (d^{-1})	Temp.	6.82*	21.06**
		Origin	4.08	54.75***
		Temp. × Origin	0.01	0.52
	Elongation rate (cm d^{-1})	Temp.	115.81***	34.68***
		Origin	4.55	0.36
		Temp. × Origin	0.32	0.25
	Leaf verticils cm^{-1}	Temp.	26.16***	7.41*
		Origin	1.95	3.63
		Temp. × Origin	0.22	4.74
	Branches cm^{-1}	Temp.	23.68***	3.72
		Origin	1.81	40.63***
		Temp. × Origin	0.25	4.32
	Root biomass ratio	Temp.	44.08***	
		Origin	7.67*	15.41*
		Temp. × Origin	0.04	
P. crispus	Relative growth rate (d^{-1})	Temp.	1.90	19.94**
		Origin	0.19	0.04
		Temp. × Origin	0.04	0.00
	Elongation rate (cm d^{-1})	Temp.	0.74	24.34***
		Origin	34.27***	2.12
		Temp. × Origin	0.00	0.05
	Leaves cm^{-1}	Temp.	2.12	0.06
		Origin	11.53**	3.66
		Temp. × Origin	2.12	2.80
	Branches cm^{-1}	Temp.	0.11	44.08***
		Origin	11.34**	1.63
		Temp. × Origin	1.61	12.07**
	Root biomass ratio	Temp.	17.92**	
		Origin	0.01	13.16*
		Temp. × Origin	0.14	

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Discussion

Warming in late autumn stimulated the performance of both *E. canadensis* and *P. crispus*, although the response pattern of the 2 species differed. The RGR of *E. canadensis* was more sensitive to temperature, particularly at the low temperature studied (12 °C in September and 8 °C in October; Fig. 2), whereas the RGR of *P. crispus* showed no response to temperature for plants sampled in September. Hence, elevated temperatures during autumn may enhance the productivity of *E. canadensis* and thereby prolong the growing season, whereas *P. crispus* may be less affected.

Plant length also increased with increasing temperatures for *E. canadensis*, as earlier found by Barko et al.

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(1982), whereas the length of *P. crispus* increased from 8 to 12 °C (October) but remained unchanged from 12 to 16 °C (September). The morphology of *P. crispus*, here described by the number of leaves and branches per stem length, was not affected by temperature for plants collected in September. By contrast, the number of leaf verticils produced by *E. canadensis* seemed to be more sensitive to temperature with shorter distance between verticils at low temperature, as is also observed in winter when *E. canadensis* becomes shorter and more compact, with dense verticils.

Root allocation increased with temperature, most markedly for *E. canadensis*, whose root:shoot ratio at 16 °C was 7 times higher than for *P. crispus*. Similarly, for the majority of clones of *P. pectinatus* studied by Pilon and Santamaría (2002), an increase in root biomass allocation with temperature was found. For *E. canadensis*, an increase in root growth has been observed until ~16 °C, after which it declines (Barko et al. 1982). We emphasise, however, that in our experiment the plants had only 2 weeks to produce new roots because the original root mass was removed before initiating the experiment.

Freshwater macrophytes may acclimatise fast to temperature changes (Madsen and Brix 1997, Mckee et al. 2002); however, the difference in sensitivity to increased temperature between *E. canadensis* acclimated to ambient and A2+50% scenario temperatures in late autumn suggests that this species may become quiescent as temperature or photoperiod approaches a certain threshold in autumn. By contrast, *P. crispus* thrived better at low temperatures, as also found for *P. pectinatus* (Pilon et al. 2002). Neither *P. crispus* nor *E. canadensis* showed any sign of producing ecotypes during the 5-year mesocosm experiment; by contrast, both exhibited positive acclimatisation ability.

Our field experiments revealed that warming accelerated the decomposition rate of *E. canadensis*. Temperature is largely responsible for determining the rate and extent of decomposition of organic matter (Meentemeyer 1978, Petchey et al. 1999). Consequently, respiration processes may increase with warming in late autumn/early winter, resulting in enhanced oxygen consumption and nutrient release from the plants compared to the ambient conditions, as demonstrated in our experiment. Low oxygen may increase P release from sediments, lowering the water quality (Søndergaard et al. 2003, Hupfer and Lewandowski 2008). In addition, the faster decomposition may also contribute to increased P concentrations in the water in late autumn/early winter, at least in the short term. Because decaying macrophytes may act as an internal P source for lakes, they can add considerable quantities of P to water (Granéli and Solander 1988).

By contrast, warming did not alter the decomposition rate of *P. crispus*, demonstrating how species-dependent the decomposition process is (Shilla et al. 2006), reflecting differences in chemical composition of the macrophytes (Enríquez et al. 1993). In particular, the biochemical content of macrophytes, such as N and P, needed by decomposers affects the decomposition rate (Twilley et al. 1986); macrophyte species with high N content decompose faster (Godshalk and Wetzel 1978). Judging by the nutrient release from the decomposing macrophytes, the decomposition rate of *P. crispus* was, irrespective of temperature, similar to the rates of *E. canadensis* in the heated mesocosms.

Our results indicate that global warming may affect competition between species in the late season. In the heated mesocosms, we found the biomass of *E. canadensis* and the shoot elongation of *P. crispus* in the mixed culture from the ambient mesocosms to be lower than in the monocultures. In the heated mesocosms, all mixed-culture macrophytes, excepting *P. crispus* from the heated mesocosms, produced new roots (data not shown). In contrast, the macrophytes incubated at ambient temperatures did not provide evidence that warming changes macrophyte growth under competitive conditions. In the heated mesocosms, however, mixed culture *E. canadensis* produced new roots and *P. crispus* did not, suggesting that *E. canadensis* has an advantage over *P. crispus* by being a stronger competitor at warmer conditions because submersed macrophytes depend mainly on roots for nutrient uptake and attachment to the sediment (Carignan and Kalff 1980).

The changes in species composition and structure of macrophyte communities produced by warming have been suggested to have considerably greater impact on ecosystem decomposition rates than warming-induced phenotypic responses (Hobbie 1996). *E. canadensis* and *P. crispus* are considered tolerant species (Sainty and Jacobs 1981, Bolduan et al. 1994). Both are able to form dense macrophyte beds and are effective competitors, and, particularly, *E. canadensis* is able to outcompete other species (Rørslett and Berge 1986, Bolduan et al. 1994). One potential result of climate change may be an increased nutrient input and, in consequence, increased phytoplankton abundance in the water column (Jeppesen et al. 2009, 2011). We found that *E. canadensis* exhibited a large length increase at warmer temperatures. Likewise, *E. canadensis* exhibits adaptation, promoting the competition against phytoplankton as it uses the allocated energy to stretch the plants. Furthermore, the number of new side shoots did not increase any further between 12 and 16 °C, implying that also here the biomass allocation is used to increase macrophyte length. Moreover, in north temperate countries, *E. canadensis* can only propagate

vegetatively, which further stimulates fast colonisation, again favoured by the extensive root production at 16 °C. This finding suggests that *E. canadensis* under warmer conditions will be a better competitor against phytoplankton than in cold regions, although factors may favour the competitive capacity of phytoplankton in a warmer world, such as changes in trophic structure or an increase in nutrient levels (Jeppesen et al. 2009, 2014).

By contrast, *P. crispus* is more tolerant to colder temperatures (Bolduan et al. 1994). Growth early in the season is therefore a great advantage to this macrophyte, and it also exhibited much higher growth and length increase at 8 °C than *E. canadensis* in our experiment. Further, root growth increased significantly with increasing temperature but was more or less absent at 8 °C as the biomass allocation of *P. crispus* was used for upward growth. *P. crispus* also uses vegetative propagation in the form of winter turions, likewise promoting early spring growth. *P. crispus* exploits a special niche, enabling this cold-water strategist to compete with the phytoplankton in the water column (Nichols and Shaw 1986).

Conclusions

In the lab study we observed that both *Elodea canadensis* and *Potamogeton crispus* exhibited enhanced growth with increasing temperature in autumn. *P. crispus* generally had high temperature tolerance and showed acclimation to both cold and warm conditions but did not respond as markedly to temperature increases as *E. canadensis*. Neither of the 2 species showed any sign of developing ecotypes over the 5-year growth period in the mesocosms, but both species are capable of compensating for temperature changes by acclimatisation. The results of the mesocosm study suggest that *E. canadensis* will be a better competitor in a warmer climate, particularly in the late peripheral growing season, causing alterations in macrophyte community structure. Another consequence may be an increased oxygen demand due to increased decomposition rates with warming during autumn and winter, which potentially can have profound effects on lake ecosystems during winter.

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