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Growth of *Elodea canadensis* and *Elodea nuttallii* in monocultures and mixture under different light and nutrient conditions

Marie-Hélène Barrat-Segretain[1]

Claude Bernard University, Lyon, France

With 3 figures and 3 tables

Abstract: *Elodea canadensis* and *Elodea nuttallii* were used in indoor experiments to compare their survival and growth in monocultures and mixture, (1) under different light intensities and (2) in water enriched or not enriched with phosphate. In all cases, *E. nuttallii* grew better than *E. canadensis*. The growth of *E. canadensis* was affected by a reduction in light intensity, contrary to that of *E. nuttallii*. Increasing phosphate-content of water did not affect the stem elongation of *Elodea* species, but increased the growth rate of *E. nuttallii* calculated on dry weight. It is hypothesised that the formation of a canopy of *E. nuttallii* shading *E. canadensis* is a key factor in explaining the success of *E. nuttallii* in the field particularly under eutrophic conditions, differences in nutrient uptake between the two species being of secondary importance.

Key words: *Elodea*, environmental factors, growth interactions, invasive plant species.

Introduction

Elodea canadensis MICHAUX and *Elodea nuttallii* (PLANCHON) ST. JOHN (TUTIN et al. 1980) are two submersed freshwater plants native of temperate North America and introduced into Europe in the early nineteenth century (for *E. canadensis*) and in the middle of the twentieth century (for *E. nuttallii*) (COOK & URMI-KÖNIG 1985). Following its introduction, *E. canadensis* soon became a widely distributed and troublesome species in Europe (SIMPSON 1984), after which it often became integrated in the biocenosis (SIMPSON 1984). *E. nuttallii* was introduced in Europe in the 1940 s, and from this date

[1] **Author's address:** UMR CNRS 5023, Ecologie des Hydrosystèmes Fluviaux, Université Claude Bernard Lyon I, 69622 Villeurbanne cedex, France;
E-mail: barrat@univ-lyon1.fr

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on, it has actively been spreading in many parts of Europe. The spread of *E. nuttallii* has resulted in the displacement of *E. canadensis* from many localities where the latter was established (SIMPSON 1984, 1990, JAMES et al. 1998, BARRAT-SEGRETAIN 2001). Several authors have compared the life-history traits of the two species in order to explain this displacement. For example, photosynthesis and respiration of the two species over different conditions of pH, dissolved O_2 and inorganic C are quite similar (JONES et al. 2000, SIMPSON et al. 1980), whereas palatability and vegetative propagule establishment of *E. nuttallii* are slightly higher than those of *E. canadensis* (BARRAT-SEGRETAIN et al. 2002).

Among environmental factors controlling the growth of submersed macrophytes, light, temperature and nutrients are known to be of primary importance (BARKO & SMART 1981, ANDERSON & KALFF 1986). For the two *Elodea* species, optimal growth temperature is near 20 °C under low light intensities (POKORNY et al. 1984). However, KUNII (1981, 1984) showed that *E. nuttallii* can grow slightly even in winter if the daily mean water temperature is higher than 4 °C, whereas *E. canadensis* needs higher temperature for active growth. Therefore, *E. nuttallii* starts growing earlier than *E. canadensis*, which confers on it a competitive advantage. BARRAT-SEGRETAIN & ELGER (2004) investigated growth and competitive abilities of the two species cultivated in monocultures and mixture, and demonstrated that the growth of *E. canadensis* was negatively influenced by intra- and interspecific neighbours during a ten-weeks experiment, whereas that of *E. nuttallii* was not. They hypothesised that the growth characteristics of *E. nuttallii* enable it to produce a canopy shading out *E. canadensis* and probably inhibiting its development. SIMPSON (1990) also hypothesised that the formation of a canopy by *E. nuttallii* may contribute to the displacement of *E. canadensis* in the field.

Concerning effects of nitrogen and phosphorus concentrations on *Elodea* growth, OZIMEK et al. (1993) showed that the relative growth rate of both *Elodea* species is considerably improved in N-enriched water, if nitrogen concentration is lower than 4 mg/L. These authors have also reported that *Elodea* plants absorb great quantities of phosphorus. ROBACH et al. (1995, 1996) observed that *E. nuttallii* has higher abilities to accumulate phosphorus than *E. canadensis*, which could make it more competitive in eutrophic waters. EUGELINK (1998) reported that *E. nuttallii* has a higher growth rate than *E. canadensis*, but that phosphorus uptake by the leaves is higher in *E. canadensis* than in *E. nuttallii*.

Despite possible contradictions among them, all these observations conclude that the displacement of *E. canadensis* by *E. nuttallii* is probably due to differences in the response of the two species to environmental factors. However, except the study conducted by BARRAT-SEGRETAIN & ELGER (2004), no experiment was made on the growth of the two species cultivated together.

The aim of the present study was to compare the growth of *E. canadensis* and *E. nuttallii* in monocultures and mixture, (1) under three different light intensities and (2) in water enriched or not enriched with phosphate.

Material and methods

Laboratory experiments

The study was conducted at the University of Lyon, France. Plants of *E. canadensis* and *E. nuttallii* were collected in cut-off channels of the Rhône River where they co-occur. Monocultures and mixtures of *Elodea canadensis* and *Elodea nuttallii* were grown in indoor aquaria from 14 May to 8 July 2001 (experiment 1) and from 1 September to 21 October 2001 (experiment 2).

For both experiments the aquaria were 45 × 30 cm and 40 cm deep. Sediment (50 % sand, 35 % horticulture peat and 15 % clay) was placed at the bottom of each aquarium in an approximately 5-cm thick layer, above a 2-cm layer of field-collected sand. Five-cm long stem apices were used. The mean individual plant dry weight of such plant apices was measured at the start of the experiment (20 samples for each species) after drying at 70 °C for 48 h. This weight was considered as representing that of the apices planted in the aquaria (*E. canadensis*: 14.2 ± 1.05 mg (mean ± SD), *E. nuttallii*: 5.8 ± 0.86 mg).

In mixture, 8 stems of *E. canadensis* and 8 stems of *E. nuttallii* were equally spaced (approximately 4 cm between two consecutive stems), and stems of the two species alternated in the sediment without any separation. For monocultures, single stems of each species were placed in separate aquaria. During the first week, several stems of both species died and were replaced by new cuttings. Two weeks after the start of the experiment, the plants of both species were established, many of them having developed adventive roots. The surviving plants were counted periodically, and the lengths of all surviving plants of each species in each aquarium were measured from the sediment surface to the tip of the longest meristem. At the end of the experiment the plants were harvested, dried at 70 °C for 48 h and weighed.

Experiment 1: influence of light intensity

Water temperature in the aquaria was measured daily (mean 22.1 °C, range 19.8–24.6), and pH was measured weekly (mean: 8.01, range 7.95–8.07). Chemical characteristics of water were measured four times during the course of the experiment and revealed that water conditions were stable ([NH_4-N] = 0.075 mg/L, range 0.069–0.079; [NO_3-N] = 0.135 mg/L, range 0.124–0.142; [PO_4-P] = 0.031 mg/L, range 0.028–0.033). All these abiotic variables are adapted for the cultivation of both *Elodea* species (Pokorny et al. 1984, Simpson & Eaton 1986, Jones et al. 2000). Light was provided through daylight fluorescent lighttubes (60 W/m^2) with a 12: 12 photoperiod. According to the aquaria, light was provided by one, two or three tubes, which corresponded approximately to 1100, 1600 and 1900 lux under 30 cm of water (equivalent to roughly 28, 40 and 48 µmole photons m^{-2} s^{-1} PAR: low, medium or high light intensity). Each treatment was repeated four times for mixtures and eight times for monocultures.

Experiment 2: influence of P-concentration

Light was provided by two lighttubes with a 12 : 12 photoperiod. Water temperature was measured every three days (mean 20.8 °C, range 18.8–22.5). In half of the aquaria, water was enriched with phosphate by adding $(PO_4)_2Ca_3$ (0.15 g in each aquarium, which corresponds to an immediate increase of 1.67 mg/L in phosphate concentrations) one week after the plants were established. Each treatment (monocultures and mixture, phosphate-enriched water or not) was repeated 5 times. Chemical characteristics of the water in the aquaria were measured at different dates until the end of the experiment.

Data analysis

The relative growth rate (RGR) of the two species was calculated at the end of the experiment with the formula $RGR = (\ln X_2 - \ln X_1)/(t_2 - t_1)$, where X_1 and X_2 are the plant mean length (L) or plant dry weight (W) at times t_1 and t_2, respectively (HUNT 1990).

For each experiment, the effects of the treatment (light intensity or phosphate content) and of the culture pattern (monocultures or mixture) on the survival, and the RGR of the two *Elodea* species were compared using t-tests or ANOVA. The difference between the growth curves of the two species was tested with ANCOVA. Statistics on the proportion of surviving stems between the treatments were performed after arcsine-square root transformation.

A three-way ANOVA was impossible for the first experiment owing to different numbers of replicates, but one was performed (pattern × species × Phosphate) with Bonferroni error correction for the second experiment.

Results

Experiment 1: influence of light intensity

Survival

Survival of *E. canadensis* and *E. nuttallii* in monocultures was not significantly different, and was lower at low light intensity than at medium and high

Table 1. Effects of light intensity and species on the survival and on the Relative Growth Rate (RGR) calculated from length and dry weight in monocultures and mixtures analysed with two-way ANOVA. Data on survival were arc-sine square root transformed and data on RGR were log10 transformed before analysis. NS: Non significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	survival		RGR (length)		RGR (dry weight)	
	monocultures	mixtures	monocultures	mixtures	monocultures	mixtures
Species	NS	**	**	*	***	***
Light intensity	**	NS	*	NS	*	***
Species × light	NS	NS	NS	NS	NS	NS

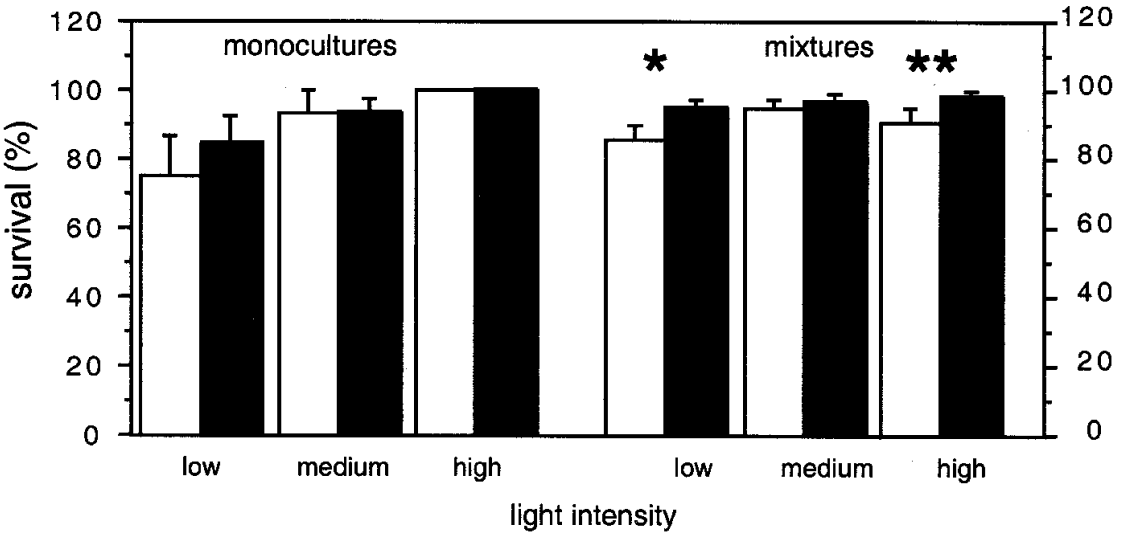

Fig. 1. Survival percentages (mean ± SD) of *Elodea* stems (open bars: *E. canadensis*; black bars: *E. nuttallii*) cultivated in monocultures and mixtures at different light intensities. Significant difference between species is indicated (t-test: * $P < 0.05$; ** $P < 0.01$).

light intensities (Fig. 1, Table 1). In mixtures, survival of *E. canadensis* was significantly lower than that of *E. nuttallii* at low and high light intensities.

Stem elongation

The stem elongation of *E. canadensis* was significantly lower than that of *E. nuttallii* whatever the light intensity, both in monocultures and mixtures (Fig. 2).

RGR calculated from length

The length RGR of *E. nuttallii* was significantly higher than that of *E. canadensis* both in monocultures and mixtures (Table 1). The difference between the species in mixtures was significant whatever the light intensity, but in monocultures only under high light intensity (Table 2). The light intensity influenced significantly the length RGR in monocultures. Both species had a higher RGR at high light intensity than at low and medium light intensities. In mixtures, the length RGR of *E. nuttallii* was higher at high light intensity than at low light intensity. Whatever the light intensity, the length RGR of each species did not differ according to the culture pattern (Table 2).

RGR calculated from dry weight

Species and light intensity had a significant effect on dry weight RGR in both culture patterns (Table 1). The dry weight RGR of *E. nuttallii* was higher than

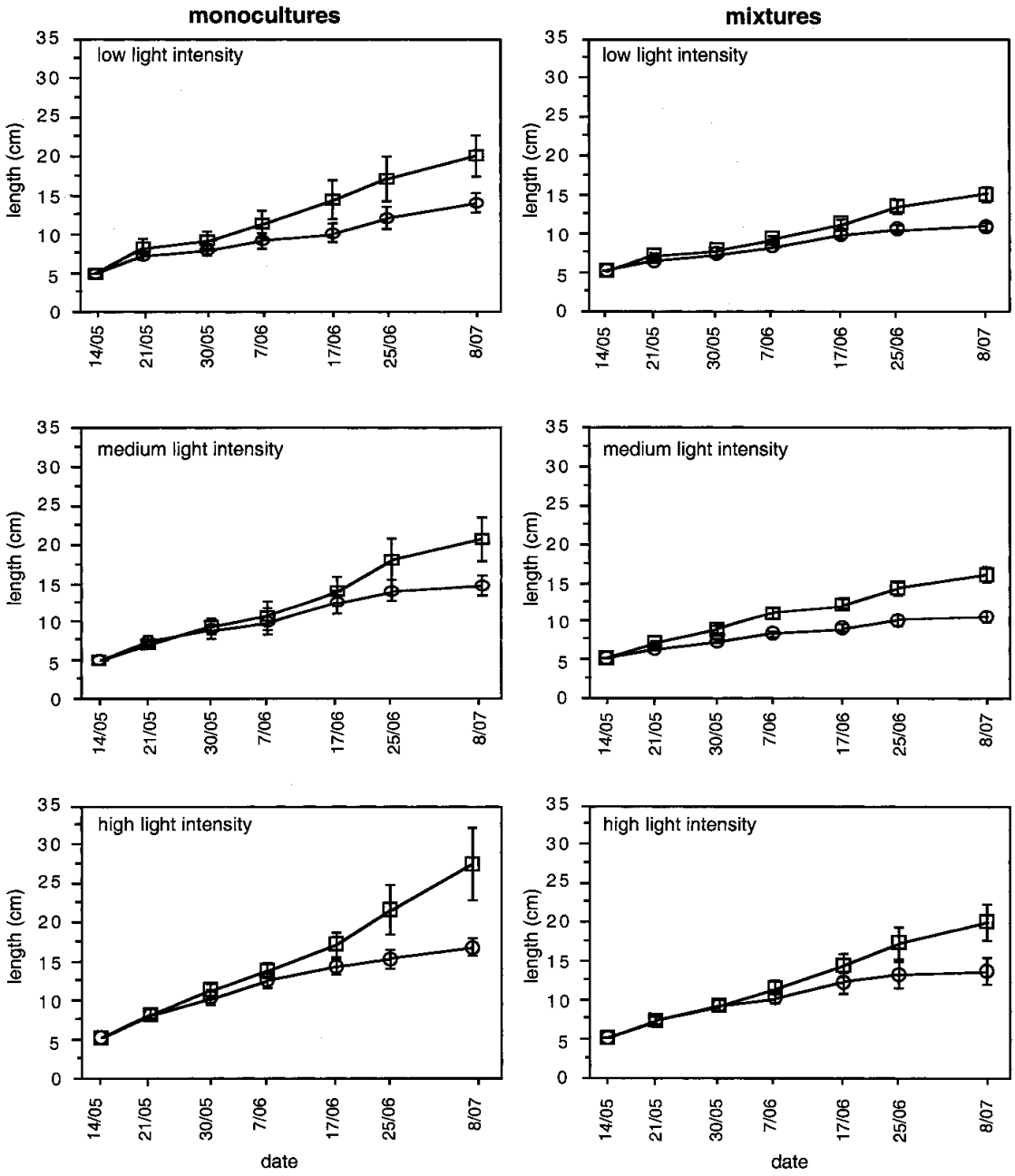

Fig. 2. Growth (mean ± SD) of *Elodea* stems (circles: *E. canadensis*; squares: *E. nuttallii*) cultivated in monocultures (n = 8) and mixtures (n = 4) at different light intensities. In each graph, slopes of the lines are significantly different (ANCOVA, $P < 0.001$).

that of *E. canadensis* under all conditions, except in monoculture and at low light intensity (Table 2). The dry weight RGR of both species increased with light intensity in both culture patterns. The dry weight RGR of *E. canadensis* was always lower in mixtures than in monocultures, whereas that of *E. nuttallii* was not influenced by culture pattern (Table 2).

Table 2. Relative Growth Rate (RGR) [mean (SD)] of both species of *Elodea* calculated from length and dry weight under different culture patterns and light intensities. *, ** $P < 0.05$ and $P < 0.001$ (paired t-test) for comparison between species in each culture pattern. In bold, values significantly different (paired t-test, $P < 0.05$) between culture pattern for a given species. Different letters in each column show a statistical difference between light treatments (t-tests, $P < 0.05$).

Light intensity	RGR (length)			
	monocultures (n = 8)		mixtures (n = 4)	
	E. canadensis	*E. nuttallii*	*E. canadensis*	*E. nuttallii*
Low	0.0167 (0.0005) a	0.0228 (0.0062) a	0.0137 (0.0024) a**	0.0194 (0.0034) a**
Medium	0.0178 (0.0047) a,b	0.0231 (0.0071) a	0.0131 (0.0031) a**	0.0209 (0.0028) a, b**
High	0.0216 (0.0029) b*	0.0290 (0.0050) b*	0.0172 (0.0063) a**	0.0241 (0.0060) b**
Light intensity	RGR (dry weight)			
	monocultures (n = 8)		mixtures (n = 4)	
	E. canadensis	*E. nuttallii*	*E. canadensis*	*E. nuttallii*
Low	**0.0429 (0.0038)** a	0.0555 (0.0100) a	**0.0167 (0.0085)** a**	0.0440 (0.0124) a**
Medium	**0.0423 (0.0032)** b**	0.0669 (0.0076) b**	**0.0269 (0.0028)** b**	0.0612 (0.0111) b**
High	**0.0478 (0.0042)** c**	0.0762 (0.0095) c**	**0.0355 (0.0069)** c**	0.0716 (0.0054) c**

Table 3. Relative Growth Rate (calculated from dry weight) values [mean (SD), n = 5] for *Elodea* species in monocultures and mixtures and phosphate-enriched or not-enriched water. Different letters in each row show significant difference between species (paired t-test, $P < 0.05$). *, ** significant difference for paired t-test between phosphate treatments for each species in each culture pattern (* $P < 0.05$; ** $P < 0.01$).

Water	monocultures		mixtures	
	E. canadensis	*E. nuttallii*	*E. canadensis*	*E. nuttallii*
not enriched	0.0411 (0.0013) a	0.0624 (0.0019) b*	0.0339 (0.0024) a	0.0600 (0.0053) b*
phosphate-enriched	0.0407 (0.0016) a	0.0698 (0.0018) b*	0.0374 (0.0025) c	0.0679 (0.0034) d*

Experiment 2: influence of P-concentration

The addition of calcium phosphate to the water resulted in an increase of [PO_4-P] from 0.015 (oligotrophic conditions) to 0.66 mg/L (eutrophic conditions) because part of the phosphate added was fixed in the substratum. Then [PO_4-P] content decreased and reached 0.27 mg/L at the end of the experiment (Fig. 3).

The stems of *E. canadensis* were shorter than those of *E. nuttallii* under all conditions and at each date (Fig. 3, ANCOVA, $P < 0.001$), but for each species no difference appeared between the two phosphate treatments.

A three-way ANOVA after $\log_{10}$ transformation testing the effects of species, culture pattern and phosphate enrichment on the dry weight RGR revealed that only species had a highly significant effect ($F_{1,8} = 43.132$, $P < 0.01$).

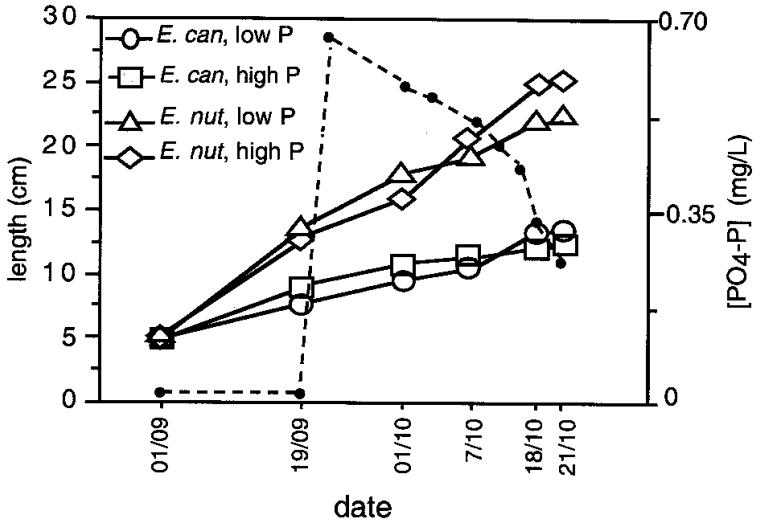

Fig. 3. Length growth (mean ± SD, n = 5) of *Elodea* stems cultivated in mixture in water enriched or not enriched with calcium phosphate. The dashed line indicates $[PO_4\text{-}P]$ concentration in phosphate-enriched water. At each date after the start of the experiment, the difference between the two species was highly significant (t-test, $P < 10^{-4}$).

Under all conditions (monocultures or mixtures, water enriched with phosphate or not), the dry weight RGR of *E. canadensis* was lower than that of *E. nuttallii*. This confirms the results of the first experiment under medium light intensity. In contrast there was no significant difference between the dry weight RGR of the species cultivated in monocultures and mixtures.

The dry weight RGR of *E. canadensis* did not differ according to the phosphate enrichment of water. However, the dry weight RGR of *E. nuttallii* was higher in phosphate-enriched water, both in monocultures and mixtures (t-tests, $P < 0.01$ and $P < 0.05$, respectively).

Discussion

Cook & Urmi-König (1985) and Dethioux (1989) reported that *E. canadensis* tolerates high levels of light (the optimum being at about 16,000 lux), but both *Elodea* species are considered to be adapted to low light intensities (Rolland 1995) and have a seasonal adaptation to light availability (Simpson & Eaton 1986). The light intensities used in the present experiments were lower than values obtained under field conditions (we measured a light intensity of 10,000 lux at a water depth of 30 cm during a sunny winter day) but they were similar to those used by other authors for *Elodea* culture (Abernethy et al. 1996, James et al. 1998, Jones et al. 2000). Our results allow to compare the growth of the two *Elodea* species under given conditions. The present study shows their lower survival at low light intensity, probably because photosyn-

thesis is not efficient under these conditions. In addition, we used very small stems (5 cm), which need high light intensity to survive at the start of the experiment. The lower survival of *E. canadensis* in mixture was probably due to shading by *E. nuttallii* which grew more rapidly (higher length RGR), particularly at low light intensity that was unfavourable for both species.

The occasional differences obtained between length and weight RGRs can be explained by the fact that the production of axillary stems was not taken into account in the length measurement. Therefore, a simple and long stem may have had the same weight as a short and ramified one. Our experiment showed that the RGRs of *E. canadensis* were more influenced by the culture pattern than those of *E. nuttallii*, which confirms the results of BARRAT-SEGRETAIN & ELGER (2004) on growth interactions between *E. canadensis* and *E. nuttallii, E. canadensis* being more influenced by the presence of neighbours than *E. nuttallii*.

For several conditions, the RGR and the stem elongation of *E. canadensis* were lower than those of *E. nuttallii.* ABERNETHY et al. (1996) observed that high shade did not affect mean length and mean biomass of *E. canadensis* plants, but this was not verified in our results. On the contrary, both species developed better at high light intensity, and *E. canadensis* was affected by a reduction in light intensity. SIMPSON (1990) reported that *E. nuttallii* has a greater stem elongation than *E. canadensis*, and our results confirm this observation. If light intensity is compatible with *E. nuttallii*'s growth, this species grows rapidly and forms a canopy, thus restricting light availability for species growing beneath its canopy, lowering their growth and survival as was the case for *E. canadensis*. The great difference in weight between 5-cm long stems of the two species means that the *E. nuttallii* shoots are more slender than the *E. canadensis* shoots. At the same development stage (same dry weight), *E. nuttallii* is higher than *E. canadensis*, which supports the conclusion as to its shading canopy.

Phosphate concentrations used in the present experiment correspond to those found in the field in stations where *E. nuttallii* outcompetes *E. canadensis*. For example in North-East France *E. canadensis* is found in stations with $[PO_4\text{-}P] = 0.04$ to 0.214 mg/L, and *E. nuttallii* in stations with $[PO_4\text{-}P] = 0.04$ to 0.63 mg/L (THIÉBAUT et al. 1997). BARRAT-SEGRETAIN (2001) also reported the presence of both species in oligotrophic waters ($[PO_4\text{-}P] = 0.015$ mg/L). The survival of both species was high at intermediate light intensity, which allowed to use this light level to test the effect of phosphate enrichment. Greater phosphate content of the water increased the growth rate (calculated from dry weight) of *E. nuttallii*, but the stem elongation of the plants were not affected. The decrease in phosphate-content of the water after the date of enrichment can be explained by fixation in the substratum and the capacity of both species to take up phosphorus from the water (EUGELINK 1998). As the ability to ac-

cumulate phosphorus is higher in *E. nuttallii* than in *E. canadensis* (ROBACH et al. 1995, 1996), we could have expected a greater elongation of *E. nuttallii* in enriched water and then the faster formation of a canopy. However, our results show that the elongation was independent of the trophic level of the water, at least for the time of the experiment, whereas biomass increased at high phosphate content. Therefore, a high phosphate content favours the formation of lateral branches of *E. nuttallii* which may also smother neighbouring plants.

Conclusion

The growth of *E. nuttallii* was higher than the growth of *E. canadensis* in all experiments, both in monocultures and mixture. Light intensity affected the stem elongation of both species, whereas an increase in phosphate-content only affected the increase in biomass of *E. nuttallii*. In addition, it is well known that high trophic levels in the field favour proliferation of plankton and algae in water, therefore reducing light availability for submersed species. In eutrophic water, the difference in sensitivity to phosphate concentration may contribute to the success of *E. nuttallii* over *E. canadensis* both by direct and indirect effects. The present results confirm that competition for light, and the formation of a canopy shading the other species (particularly early in the season) are probably one key factor in explaining the success of *E. nuttallii*, at least in eutrophic waters. However, the replacement of *E. canadensis* by *E. nuttallii* also observed in non-eutrophicated waters cannot be elucidated by results from the present study. In addition, our observations were made over a relatively short period of time, and the reduction in the growth of *E. canadensis* in the presence of *E. nuttallii* in experimental tanks is not sufficient to conclude on a real competitive exclusion of *E. canadensis* by *E. nuttallii*. To be final, our conclusions need to be completed by experiments over a longer period of time, to evaluate whether the replacement of *E. canadensis* by *E. nuttallii* observed in the field would also occur under experimental conditions.

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