

# Comparison of three life-history traits of invasive *Elodea canadensis* Michx. and *Elodea nuttallii* (Planch.) H. St. John

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## Abstract

Three life-history traits, regeneration and colonisation of vegetative plant fragments, resistance to water current and palatability to a generalist herbivore were compared in two invasive macrophyte species, *Elodea canadensis* Michx. and *Elodea nuttallii* (Planch.) H. St. John. Few differences in traits were found between these species. Both species showed similar resistance to water current, whilst fragment regeneration and colonisation and palatability were only slightly higher in *E. nuttallii* than in *E. canadensis*. These small differences do not explain the displacement of *E. canadensis* by *E. nuttallii* as observed in the field.

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## 1. Introduction

Invasion of habitats by non-native species is a global phenomenon with serious ecological, economic and social consequences. To date our ability to predict which species will make successful invaders has been limited (Rejmanek, 1996; Rejmanek and Richardson, 1996). Factors that have been suggested as predictors of invasive success include abundance and range in the native habitat, taxonomic isolation, intrinsic rate of natural increase and life-history traits such as reproductive and genetic characteristics (Williamson, 1996). Analysis of the life-history traits of such invasive species will therefore lead to a better understanding of the invasion process.

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*Elodea canadensis* Michx. and *Elodea nuttallii* (Planch.) H. St. John are two of the three *Elodea* species native to North America and were introduced to Europe in the 19th and 20th centuries. Both species have similar distribution patterns in North America. Following its introduction into the British Isles in 1836, *E. canadensis* soon became a widely distributed and troublesome species in Europe (Simpson, 1984), after which it often became integrated in the biocœnosis (Simpson, 1984; Dutartre, 1986). The introduction of *E. nuttallii* into the British Isles in 1939 resulted in the displacement of *E. canadensis* from many European waterways where the latter had been well established (Simpson, 1990; Thiébaud et al., 1997). In general, displacement can result from disturbance events (eg. floods and dredging; Barrat-Segretain, 2001) or perhaps from competitive interactions between individuals (Simpson, 1990). Several authors have suggested that this displacement was due to physiological differences in the responses of the two species to environmental variables, and have compared selected life-history traits between the two species. The ability to accumulate phosphorus seems to be greater in *E. nuttallii* than in *E. canadensis* in eutrophic waters (Robach et al., 1995). In contrast, rates of photosynthesis and respiration in *E. nuttallii* (Jones et al., 2000) and *E. canadensis* (Simpson et al., 1980) under different conditions of pH, O<sub>2</sub> and dissolved inorganic carbon, appear quite similar. In addition, James et al. (1998) demonstrated that pH tolerance by the two species is also comparable. Therefore, the displacement of *E. canadensis* by *E. nuttallii* is not readily explained by these physiological traits. Very few studies have investigated other life-history traits of the two species. Simpson (1990) reported that *E. nuttallii* has a greater rate of stem elongation and axillary stem production over a given period of time than *E. canadensis*, which allows it to rapidly produce a canopy inhibiting the development of *E. canadensis*.

The aim of the present study is to examine differences in three life-history traits of the two *Elodea* species. These traits are related to species production and plant survival factors, which are particularly important to consider in the analysis of the invasive or competitive success of the species (Williamson, 1996). As unspecialised fragments have long been recognised to play a key role in the propagation of *Elodea* species (Cook and Urmi-König, 1985; Nichols and Shaw, 1986; Cook, 1987), the regeneration (regrowth into viable plants) and colonisation (establishment in the sediment) abilities of vegetative fragments of the two species were compared in a laboratory experiment. Barrat-Segretain et al. (1998, 1999) and Barrat-Segretain and Bornette (2000) investigated the regeneration and colonisation abilities of several macrophyte species, including *E. canadensis*, but so far no one has compared the recolonisation abilities of the two *Elodea* species.

Resistance to water current was also compared in the two species. We estimated the minimum force to break stems as well as drag resistance (which integrates morphology, flexibility and leaf reconfiguration processes; Vogel, 1989) for several individuals under known flow conditions. A greater resistance to water current for one species may make it more persistent to peak discharges, whereas a species more easily uprooted or fragmented by water current may have greater colonisation ability.

Finally, as herbivory can be of primary importance in modulating biodiversity of communities (Crawley, 1989; Van et al., 1998) and because invasiveness is often related to the lack of specialist herbivores in the newly colonised area (Room, 1990; Piper, 1996), the palatability of the two species to a generalist herbivore (*Lymnaea stagnalis* L.) was also investigated through laboratory experiments.

## 2. Materials and methods

### 2.1. Colonisation and regeneration abilities of *Elodea* fragments

The following protocol has already been used by Barrat-Segretain et al. (1998) and by Barrat-Segretain and Bornette (2000). *Elodea* plants were collected in May 2000 for the spring experiment and in September 2000 for the autumn experiment, from a former channel of the Rhône River (France), which is patchily scoured by floods approximately 40 days a year, and where rapid recolonisation occurs after each flood or after experimental disturbance (Barrat-Segretain and Amoros, 1996). Plants were carefully collected and placed in water collected on site in open plastic containers and immediately brought back to the laboratory for use in the experiment.

Later the same day, in the greenhouse, 32 samples of three types of vegetative fragments were collected from plants of each species: (1) the whole plant (above-ground and under-ground parts), (2) above-ground parts of the plant, (3) fragments of shoot consisting of four internodes. All these fragments are frequently found in the field after floods have removed the sediment and fragmented the aquatic vegetation; they can therefore be expected to have significance for recolonisation. Fragments were placed on the surface of plastic pans (24 cm × 18 cm × 10 cm) containing 1 cm of sand covered with 1 cm of sediment (sandy silt) and 7 cm of water, all collected on the sampling site. For each species and each fragment type, four pans ( $n = 4$ ) containing eight fragments were randomly placed in the greenhouse.

Greenhouse temperature was maintained at 10 °C during the night (from 6 p.m. to 10 a.m.) and at ambient temperature during the day (from 20 to 22 °C). Light was provided simultaneously by natural light and fluorescent white tubes at a constant light intensity of 2000 lx ( $\approx 36 \mu\text{mol}/(\text{m}^2 \text{ s})$ ) from 8 a.m. to 10 p.m. Groundwater collected at the sampling site was regularly added to the pans to compensate for evaporation and to maintain a constant water level. Permanent oxygen supply was maintained in the pans (through small air-pumps and plastic tubes) to avoid anaerobic conditions. Any dead plant material was removed from the pans.

Each experiment was monitored every week over a 10 week period, and several parameters were recorded for each fragment: survival (dead or alive), position in the pan (at the water surface, on the sediment surface or within the water layer), development of new buds (a few millimeters long), the number of these buds, development of roots and possible rooting in the sediment. Fragments that had rooted successfully were counted as survivors and transplanted to other pans so that their development would not inhibit growth of other fragments by competition for light or nutrients. When a new bud developed on a fragment and became detached from it, it was counted as a new individual, and its growth was recorded as for other fragments. In the following results, all percentages correspond to mean percentages calculated for four pans with eight original fragments.

Influence of season on survival, regeneration and colonisation abilities of fragments and comparison between the two *Elodea* species were studied using Student's *t*-tests. Standard deviations (S.D.) using percentages were calculated after arc-sine transformation. The effects of season and species were also assessed using a two-way ANOVA.

## 2.2. *Elodea palatability*

*E. canadensis* and *E. nuttallii* were collected from two former channels of the Rhône River. They were stored in a greenhouse, in aerated tap water at below 16 °C, for a period not exceeding 3 days. All the experiments used young plant tissues without any signs of grazing or necrosis. Fragments were rinsed and epiphytic flora and marl coverage were removed by hand before feeding experiments were conducted.

We recorded consumption rates by the pond snail *Lymnaea stagnalis* (L.). This animal has been used previously in laboratory studies (Smits, 1994; Elger et al., 2002), and it is assumed to be a good model for assessing plant palatability to generalist invertebrate grazers (Elger and Barrat-Segretain, 2002). The snails were bred in aquaria and fed ad libitum with lettuce before the start of the experiment. The mean ( $\pm$ S.D.) shell length of the snails used in palatability tests was  $30.5 \pm 1.0$  mm.

The 80 small plastic containers (8 cm  $\times$  8 cm  $\times$  16 cm) filled to a depth of 12 cm with breeding water were put in a growth chamber (22 °C; LD 16:8). The 40 of the containers were left grazer-free (gf). In each of the other 40 (with grazer: wg), one individual of *L. stagnalis* was added and kept without food for the first 24 h. At the end of this period, apical shoots (about 6 cm) of the *Elodea* species of the two localities were randomly allocated to each container after blotting them with paper towels to remove excess water and weighing them to the nearest 0.1 mg (initial fresh weight, noted FW0). The plant biomass provided (200–400 mg) was sufficient to ensure unlimited food for snails. Snails were removed after 24 h of grazing and plant fragments remaining in each container were dried (48 h at 70 °C) and the dry weight remaining (DW1) determined. The experiment was done twice (June and September 2000).

The linear relationship between DW1<sub>gf</sub> and FW0<sub>gf</sub> was assessed separately for each combination of species, date and site. For each pair of containers, the estimated coefficients were used to calculate  $DW1'_{gf} = aFW0'_{gf} + b$ , where  $FW0'_{gf} = FW0_{wg}$ , and the dry weight consumed was determined by  $DW1'_{gf} - DW1_{wg}$ . Body dry weight (in g) of *Lymnaea* individuals was estimated from shell length (SL, in mm), using an allometric model established before the experiment on 64 snails (dry weight =  $0.0103 \exp(0.0826 \text{ SL})$ ,  $r^2 = 0.78$ ). A comparison of consumption rates (dry weight consumed per body dry weight of *Lymnaea*) between the two *Elodea* species was performed using Student's *t*-tests. The effects of season, site and species on consumption rate were assessed using a three-way ANOVA.

## 2.3. *Hydrodynamic abilities*

The forces acting on five shoots of each *Elodea* species under given flow conditions were measured in an experimental flume with the drag-measuring device used by Statzner et al. (1999). The flume was 8.75 m long, 0.25 m wide and 0.40 m high. It was fed by a centrifugal pump, which had a maximal discharge of approximately 260 m<sup>3</sup>/h. Flow conditions were controlled by adjusting discharge and flow depth (by a tailgate).

Each plant was fixed in a hollow base (15.0 cm long  $\times$  9.5 cm wide  $\times$  5.0 cm high) by its base in such a way that only the stem and leaves were exposed to the flow. The base was placed on the drag-measuring device. Raising the bottom (with panels of smooth PVC) all along the flume and around the drag-measuring device ensured that the top of the

base was level with the bottom of the flume. The drag-measuring device consisted of two units (produced by Techniques Modernes d'Extensiométrie, Orgeval, France) containing strain gauges, which measured the deformation of flexible parts of the units. This apparatus was linked to a conditioner (Analog Devices, model 1B31), which displayed in real time the drag force applied to the “plant + device” system. To estimate the drag caused by the device, preliminary measurements were made with the device alone at different current velocities. Plant drag values were evaluated as the difference between the plant + device drag and the device drag at the same velocity. Although such an estimation presents theoretical problems (see Hoerner, 1965), the results remained comparable as all samples were similarly conditioned.

Flow velocities were measured with a propeller (Nixon Stream flow with helix no. 403), approximately 1 m upstream from the position of the drag-measuring device (i.e. to avoid flow disturbance during the drag measurements) and at a water depth of 40% from the bottom (which is commonly described as the mean velocity value of the water column in an open channel, Gordon et al., 1992).

For each shoot, the drag was measured at 12–14 different current velocities ranging from 0.20 to 1.16 m/s. During all the experiments, water depth in the flume varied from 0.165 to 0.193 m (mean  $\pm$  S.D. =  $0.176 \pm 0.006$ ;  $n = 125$ ). The values used for drag and velocity were the means of 10 and 30 values, respectively, collected over 30 s in stable flow conditions.

The lengths (in mm) of the portions of the shoots exposed to flow (i.e. length of stem + leaves) were as follows: 160, 229, 234, 279 and 358 for *E. canadensis* and 144, 180, 267, 276 and 427 for *E. nuttallii*. To ensure a hydrodynamic comparison between shoots of different lengths (i.e. to avoid size effects), we used a dimensionless variable, the drag coefficient ( $C_d$ ) of the shoots, calculated from  $C_d = 2D/\rho SU^2$ , where  $D$  = drag (N),  $r$  = water density ( $=1000 \text{ kg/m}^3$ ),  $S$  = projected shoot area when laid on a flat surface and viewed from above ( $\text{m}^2$ ), and  $U$  = water velocity (m/s) (Vogel, 1994). Under comparable flow conditions, shoots with low  $C_d$  values would be more hydrodynamic than shoots with high  $C_d$  values.  $C_d$  can thus be considered as a synthetic variable (i.e. integrating body shape, flexibility, leaf configuration with respect to hydraulic constraints, etc.), affecting the ability of a shoot to withstand current forces (Koehl, 1996).

As the projected shoot area is not easily measured, this was estimated from the shoot dry mass ( $\text{DM}_S$ , in kg) using the equation given by Schutten and Davy (2000) (standard errors, S.E., in brackets):  $S = 15.91 (\pm 0.77) \text{DM}_S + 0.0004 (\pm 0.0002)$ . Shoots were dried at  $70^\circ\text{C}$  for 48 h to obtain dry weights.

To describe the flow conditions inside the experimental flume during drag measurements, we used another dimensionless variable, the Reynolds number ( $Re$ ), calculated from  $Re = Uh/\nu$ , where  $h$  = water depth (m) and  $\nu$  = kinematic viscosity of water (approximated as  $1 \times 10^{-6} \text{ m}^2/\text{s}$  as the water temperature during all the experiments was approximately  $21^\circ\text{C}$ ).  $Re$  represents the relative importance of inertia to viscous forces for a particular flow situation (i.e.  $Re$  is proportional to the flow turbulence).

As generally used to compare the hydrodynamic abilities of different organisms in given flow conditions (Webb, 1975; Vogel, 1994; Koehl, 1996; Sagnes et al., 2000), we expressed the  $C_d$  values of the different shoots with respect to the  $Re$  values during drag measurements (note that, as water depth was essentially constant during all the experiments,  $Re$  values were

directly correlated with velocity values). Theoretically,  $C_d$  values decrease exponentially as  $Re$  values increase. For rigid bodies at high  $Re$  values (between  $(1.0 \text{ and } 2.5) \times 10^5$ , see Vogel, 1994),  $C_d$  values drop abruptly and then gradually increase with  $Re$ .

2.4. Minimum breaking force

We determined the minimum force needed to break 18 shoots of each species (mean length  $\pm$  S.D. =  $202.5 \pm 11.2$  mm for *E. canadensis* and  $200.7 \pm 14.6$  mm for *E. nuttallii*). For this purpose, we firmly anchored one end of the shoot and pulled on the other end longitudinally (i.e. following the axis of the stem) with a graduated spring balance. The pulling increase was about 0.1 N/s. We noted the force at which the stem broke (minimum breaking force =  $BF_m$ , in N with a precision of about 0.02 N), and the stem diameter ( $R_d$ , in mm) at the breaking point.

3. Results

3.1. Colonisation and regeneration abilities of *Elodea* fragments

*Survival:* We found a high survival rate (from 88 to 100%, Fig. 1) for whole plants after 10 weeks for both *Elodea* species and in both seasons. The two-way ANOVA for species and seasons and their interactions as sources of variance (Table 1) showed that there was an interactive effect of species and season on the survival of plants without roots. The survival of plants without roots of *E. nuttallii* was significantly higher (100%) than that of

Table 1  
Two-way ANOVAs performed on survival, colonisation and regeneration abilities of the three fragment types for the two *Elodea* species and in the two seasons

Source of variance		d.f.	Survival		Colonisation		Regeneration	
			M.S.	P	M.S.	P	M.S.	P
Whole plant	Species	1	89.114	0.3977	225.08	0.3068	395.811	0.0168
	Season	1	89.114	0.3977	0.000	0.9999	5819.401	<0.0001
	Species $\times$ season	1	422.303	0.0804	899.85	0.0541	81.993	0.4428
	Residual	12	115.87		197.55		130.195	
Plants without roots	Species	1	0.000	0.9998	460.75	0.0488	136.890	0.135
	Season	1	123.488	0.2590	41.746	0.5214	363.474	0.023
	Species $\times$ season	1	3148.052	<0.0001	9255.4	<0.0001	10.240	0.669
	Residual	12	87.957		95.82		53.302	
Four-internode fragment	Species	1	89.019	0.5446	14.251	0.7784	333.702	0.0274
	Season	1	3577.834	0.0019	2206.7	0.0038	8879.764	<0.0001
	Species $\times$ season	1	89.019	0.5446	599.03	0.0867	62.687	0.2979
	Residual	12	228.998		172.11		52.949	

Statistical analyses were performed after arc-sin square-root transformation.

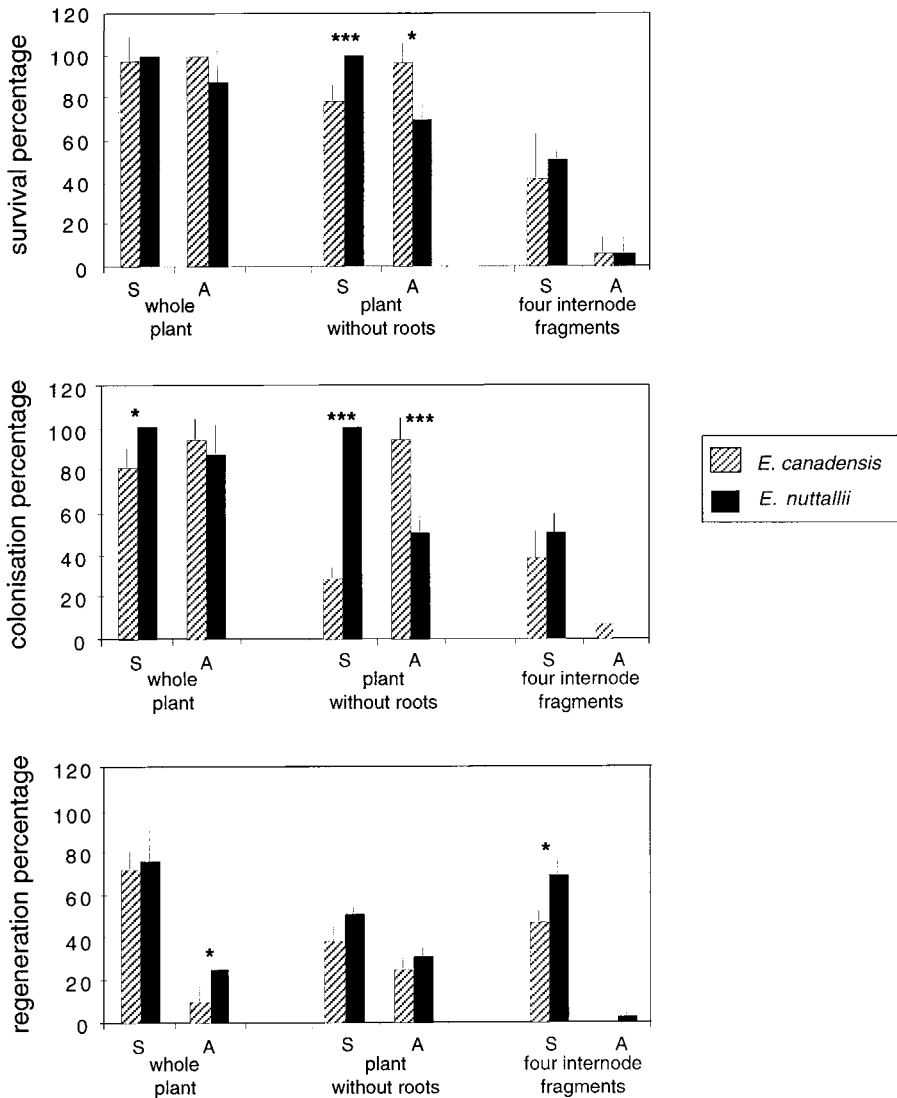


Fig. 1. Mean percentages ( $\pm$ S.E.) of survival, colonisation (rooting in the sediment) and regeneration (development of propagules) of fragments of two *Elodea* species after experimental periods of 10 weeks in spring (S) and in autumn (A). Standard errors of percentages were calculated after arc-sine square-root transformations. Statistical comparisons of differences between the characteristics of both *Elodea* species were made using ANOVA. \* $P < 0.05$ ; \*\*\*  $P < 0.001$ .

*E. canadensis* (78%) in spring, but the reverse was found in autumn (96% for *E. canadensis*, 69% for *E. nuttallii*). There was no significant difference between species in the survival rates of four-internode fragments, but these fragments survived significantly better in spring than in autumn (e.g. 50% in spring and 6% in autumn for *E. nuttallii*).



**Colonisation:** Rooting of whole plants into the sediment was higher for *E. nuttallii* (100%) than for *E. canadensis* (81%) in spring, but there was little difference between the two species in autumn (94% for *E. canadensis*, 88% for *E. nuttallii*). However, an interaction between species and season significantly affected the colonisation of plants without roots (Table 1), which was higher for *E. nuttallii* (100%) than for *E. canadensis* (28%) in spring, and higher for *E. canadensis* (94%) than for *E. nuttallii* (50%) in autumn. The colonisation ability of four-internode fragments was very similar in both species but significantly higher in spring than in autumn.

**Regeneration:** Percentage regeneration of whole plants was higher in spring (71.87 and 75% for *E. canadensis* and *E. nuttallii*, respectively) than in autumn (9.37 and 25%, respectively). Plants without roots and four-internode fragments of both species had higher regeneration rates in spring than in autumn. Four-internode fragments of *E. nuttallii* had higher regeneration rates than *E. canadensis* in spring, whereas there was virtually no regeneration for such fragments in autumn.

### 3.2. *Elodea palatability*

Overall mean ( $\pm$ S.E.) consumption rates amounted to  $45.7 \pm 3.8$  mg/g per day for *E. nuttallii* and  $25.6 \pm 4.6$  mg/g per day for *E. canadensis* ( $P = 0.0013$ ; Fig. 2). The three-way ANOVA ( $r^2 = 0.32$ ) showed that the effects of both season and plant species were highly significant ( $P = 0.0009$ ;  $P = 0.0005$ ). In contrast, there was little correlation between consumption rate and site ( $P = 0.0951$ ). Interactions of these factors and consumption rate were not significant.

### 3.3. *Hydrodynamic abilities*

Drag values measured on each shoot depended strongly on the square of the flow velocity (Table 2), which is consistent with theory (see Vogel, 1994). As a long shoot offers more resistance to flow than a short one under comparable flow conditions, the slope of the equations in Table 2 would be expected to be positively correlated with shoot length. This correlation was not significant for *E. canadensis* ( $r^2 = 0.72$ ,  $P = 0.067$ ), owing to the small number of replicates, whilst it was significant for *E. nuttallii* ( $r^2 = 0.90$ ,  $P = 0.013$ ).

For a comparison of hydrodynamic abilities between species, we therefore had to eliminate the short size effect, by using the  $C_d$  values of the shoots. *E. nuttallii* and *E. canadensis* showed no differences in their hydrodynamic abilities (i.e. in their  $C_d$  values) in the  $Re$ -range studied (Fig. 3). The overall shape of the scatter plot of  $C_d$  versus  $Re$  for the two species was in accordance with the theoretical curves of  $C_d$  versus  $Re$ : an exponential decrease was observed for  $Re$  values between  $(5 \text{ and } 20) \times 10^4$ . Low  $C_d$  values at  $Re < 5 \times 10^4$  were undoubtedly due to errors in drag measurements at low flow velocities: in such experimental conditions, shoot drag was very low compared to measuring device drag and a small error on the total drag value would lead to a significant error in the shoot drag value. For  $Re > 20 \times 10^4$ ,  $C_d$  values suddenly increased. Visual observations during the experiments confirmed that, at such  $Re$  values, the flow regime became torrential, which induced flapping of the shoots and which therefore led to a rapid increase in drag values as  $Re$  increased.



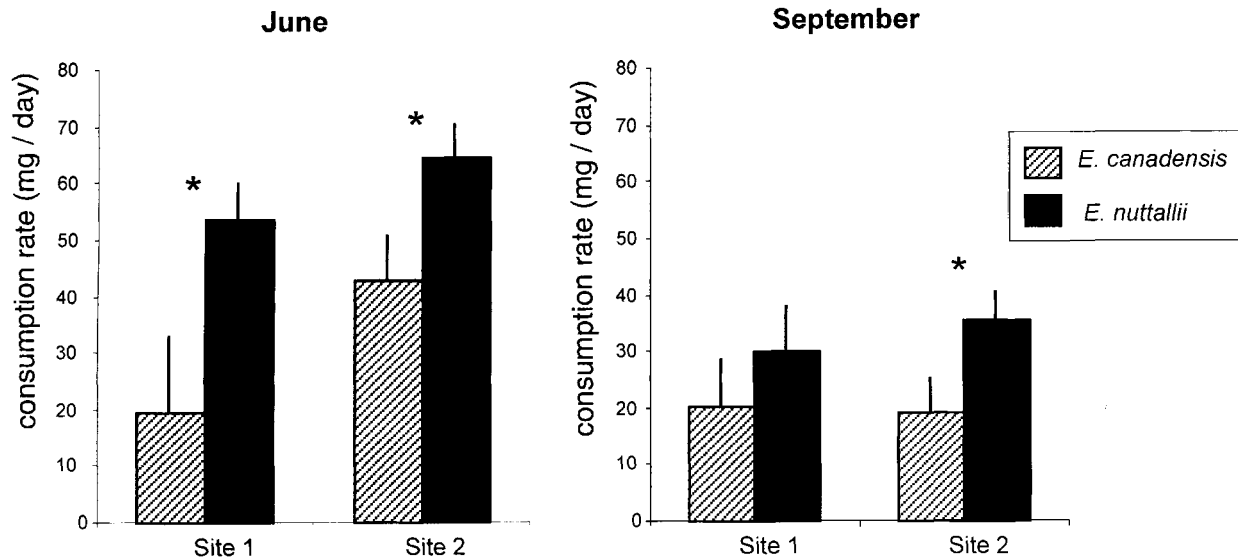


Fig. 2. Mean consumption rates ( $\pm$ S.E.) of the pond snail *Lymnaea stagnalis* (L.) for both *Elodea* species collected at two sites and at two different seasons.

Table 2  
Quadratic polynomial curve function parameters for the relation between drag ( $D$ , in N) of different *Elodea* shoots vs. flow velocity ( $U$ , in m/s) in an experimental flume

Shoot	Length	$a$ ( $\pm$ S.E.)	$b$ ( $\pm$ S.E.)	$n$	$r^2$
<i>E. canadensis</i>					
1	160	0.109 ( $\pm$ 0.015)	+0.014 ( $\pm$ 0.010)	12	0.85
2	229	0.147 ( $\pm$ 0.019)	+0.036 ( $\pm$ 0.012)	12	0.86
3	234	0.082 ( $\pm$ 0.012)	+0.029 ( $\pm$ 0.008)	12	0.82
4	279	0.151 ( $\pm$ 0.017)	+0.028 ( $\pm$ 0.011)	13	0.88
5	358	0.285 ( $\pm$ 0.018)	+0.032 ( $\pm$ 0.012)	12	0.96
<i>E. nuttallii</i>					
1	144	0.080 ( $\pm$ 0.015)	+0.017 ( $\pm$ 0.011)	12	0.73
2	180	0.121 ( $\pm$ 0.023)	+0.018 ( $\pm$ 0.015)	13	0.71
3	267	0.143 ( $\pm$ 0.016)	+0.014 ( $\pm$ 0.010)	13	0.87
4	276	0.193 ( $\pm$ 0.028)	+0.003 ( $\pm$ 0.018)	14	0.80
5	427	0.235 ( $\pm$ 0.018)	+0.021 ( $\pm$ 0.012)	12	0.94

Equations were of the type:  $D = aU^2 + b$  and all were highly significant ( $P$  always  $< 5 \times 10^{-4}$ ). Shoot lengths (in mm) represent the portion of the shoots exposed to flow (i.e. length of stem + leaves);  $n$  is the number of drag measurements, carried out at different flow velocities.

3.4. Minimum breaking force

$BF_m$  was independent of shoot length for both species (linear regression,  $P = 0.72$  and  $P = 0.85$  for *E. canadensis* and *E. nuttallii*, respectively). In contrast,  $BF_m$  was linearly related to  $R_d$  for *E. canadensis* ( $BF_m (\pm S.E.) = 1.437 (\pm 0.556) R_d - 0.581 (\pm 0.756)$ ;  $r^2 = 0.30$ ;  $P = 0.02$ ) whilst  $BF_m$  was independent of  $R_d$  for *E. nuttallii* (linear regression,  $P = 0.12$ , mean ( $\pm S.E.$ ) =  $1.398 \pm 0.060$ ).

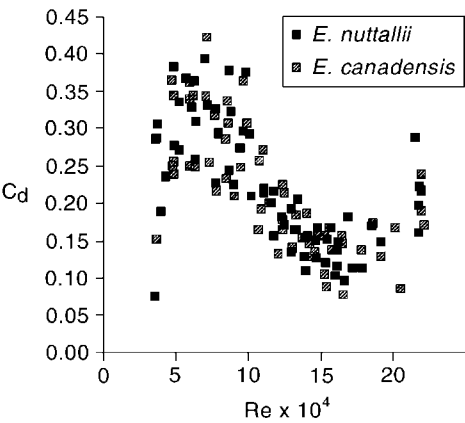


Fig. 3. Drag coefficient ( $C_d$ ) vs. the Reynolds number ( $Re$ ) for different shoots of *Elodea* species.  $C_d$  values were calculated from drag measurements in an experimental flume. The surface area used as reference in the  $C_d$  calculations is the projected shoot area.

With the exception of one  $BF_m$  value of 0.098 N for a specimen of *E. canadensis* (certainly due to weakened tissues), the lowest  $BF_m$  values obtained were approximately 0.736 N. Such forces were never reached during the drag measurements (maximum drag value obtained = 0.432 N for the 358 mm long *E. canadensis* at a flow velocity of 1.13 m/s). As a confirmation, no plant breakage was observed during the drag experiments. From the equations in Table 2, we can estimate the minimum flow velocity needed to break the different shoots. For example, for a  $BF_m$  of 1.398 N as stated above, the 144 and 427 mm long *E. nuttallii* should break in mean flow velocities of 4.15 and 2.42 m/s, respectively.

#### 4. Discussion

Fragments of both *Elodea* species have high survival rates which allow them to be dispersed over long distances, therefore increasing their invasion capabilities. In general, fragments produced by both species possess high regeneration and colonisation abilities in comparison with other species (Barrat-Segretain et al., 1999). This is not surprising, since these two species are known to reproduce and disperse principally by vegetative means (Sculthorpe, 1967; Cook, 1987).

The colonisation ability of *E. canadensis* is higher in autumn than in spring, whereas the reverse is true for *E. nuttallii*. Therefore, the hierarchy in the abilities of the species is modified according to season. *E. nuttallii* has an advantage over *E. canadensis* in spring and conversely in autumn. As regeneration percentages in both species are much greater in spring than in autumn, over the whole year we can say that *E. nuttallii* has greater colonisation and regeneration abilities than *E. canadensis*. Regeneration and colonisation of *E. canadensis* during both seasons, as shown in the present study, are similar to the findings previously reported by Barrat-Segretain and Bornette (2000), who demonstrated that these abilities can be related to recolonisation patterns of bare patches observed in the field. The capacity to disperse and establish itself may be important in the overall distribution of a plant species (Keddy, 1976), and particularly in an invasive species. A great number of *Elodea* propagules enter cut-off channels frequently disturbed by floods (Cellot et al., 1998). The significantly higher survival and colonisation rates of *E. canadensis* in autumn should give this species an initial advantage over *E. canadensis* at the start of the spring season by ensuring greater habitat saturation of over-wintering plant fragments. However, this advantage is probably compensated for by greater stem elongation in *E. nuttallii*, thus permitting the formation of a canopy which inhibits the development of *E. canadensis* (Simpson, 1990). Both species have great dispersal abilities but, over the whole year, the greater colonisation and regeneration abilities of *E. nuttallii*'s propagules together with their greater growth rate (Simpson, 1990) ensure greater invasive potential.

Once a species has reached a site it must establish itself in that habitat. When abiotic conditions are favourable for its establishment, the new species also has to face biotic conditions, such as competition and herbivory. Herbivory is recognised as playing an important part in structuring aquatic macrophyte communities (Lodge and Lorman, 1987; Sheldon, 1987; Van et al., 1998). In a previous study under similar experimental conditions and involving eight macrophyte species of the Rhône River floodplain, the consumption rates recorded with *L. stagnalis* ranged from 3.6 (*Nuphar lutea*) to 63.6 mg/g per day (*Berula*

*erecta*, Elger et al., 2002). Applying these values, the two *Elodea* species can be classified as species of intermediate palatability, but *E. nuttallii* is more palatable than *E. canadensis*.

Both *Elodea* species are more palatable in early summer, during their active growth period (fastest growth rate, as shown by the experiment on colonisation and regeneration). The principle of allocation states that because organisms are ultimately resource limited, trade-offs will exist between competing abilities such as growth, maintenance and reproduction (Gadgil and Bossert, 1970). It is likely that *E. nuttallii* allocates more resources to regeneration and colonisation (our results) and rapid growth (Eugelink, 1998) than *E. canadensis*, therefore allocating less resources to deterring herbivores through morphological or chemical adaptations. In this context, seasonal differences in *Elodea* palatability illustrate the trade-off between growth and synthesis of anti-herbivore defences. Indeed, several studies have shown a positive correlation between relative growth rate of some plant species and their palatability (Sheldon, 1987; Coley, 1988). The greater palatability of the two *Elodea* species in summer is probably compensated for by their greater growth rate in this period. One can generalise from the observed patterns of *Elodea* palatability, at least at a regional level, as they are independent of site. It is difficult to compare these results with field observations; on the whole, *E. canadensis* is poorly consumed by invertebrates (Smirnov, 1962; Gaevskaya, 1969; Gross et al., 2001). Sushkina (1949, cited by Gaevskaya, 1969) indicated that, under field conditions, *Lymnaea* sp. avoids pure *E. canadensis* beds and only consumes this plant when it is an obligatory food. In contrast, *E. canadensis* may be intensively eaten by some vertebrates, as indicated in studies focusing on fish gut content (Gaevskaya, 1969; Prejs, 1984). Unfortunately, no similar data are available concerning *E. nuttallii*.

Under comparable flow conditions, the hydrodynamic abilities of the “stem + leaves” system are the same for *E. canadensis* and *E. nuttallii*. For both species, the shoot portion exposed to flow presents the same resistance to current in the range of Reynolds number considered. Nevertheless, the real hydrodynamic abilities of a plant also depend on the type of substrate it colonises (on a fine substrate, susceptible to erosion, a plant would be more easily uprooted) and on its anchoring ability. Both *Elodea* species studied here grow on similar substrate types (fine sediment such as silt and sand: Dethioux, 1989) and show the same type of root organisation. Therefore, minimum uprooting forces should be comparable for shoots of *E. canadensis* and *E. nuttallii* of similar size.

Minimum breaking forces were different for shoots of comparable diameter for the two species studied. As  $BF_m$  is linearly related to  $R_d$  for *E. canadensis* but not for *E. nuttallii*, thin shoots of *E. canadensis* are more fragile than thin shoots of *E. nuttallii*, whereas thick shoots of *E. canadensis* are less breakable than thick shoots of *E. nuttallii*. We estimated that, for the largest *E. nuttallii* studied, the first shoot breaks would appear for flow velocities above 2.4 m/s. This estimate is based on the drag experiments, which were conducted in clear water. Under natural conditions, such high flow velocities would lead to the transport of large quantities of solids which increases both the water viscosity and also the mechanical constraints applied to the plants (Daubenmire, 1959). Thus, in the field, shoots should break at lower flow velocities than those estimated here.

As (1) the hydrodynamic abilities of the “stem+leaf” system are the same for *E. canadensis* and *E. nuttallii* and (2) the conditions required to break stems of deep-rooted *Elodea* species are still not clearly described in their natural habitat, both species should be equally resistant to an increased flow velocity (flood disturbance).

It is interesting to compare the life-history traits of both *Elodea* species with their success in the field. Their invasive abilities associated with their abilities to regenerate and colonise by vegetative fragments are quite similar, with a small advantage for *E. nuttallii*. The palatability of *E. nuttallii* is slightly higher than that of *E. canadensis*, which is a disadvantage, because a higher palatability may decrease the competitive ability of freshwater plants (Van et al., 1998; Gross et al., 2001). Both species have a similar resistance to water current. Therefore, the slightly higher regeneration and colonisation ability of *E. nuttallii* is the sole biological trait out of the three examined in the present study that provides a possible explanation for the displacement of *E. canadensis* by *E. nuttallii* in the field. Further studies must be carried out, in particular on the growth rates of both species, on their growth timing and on differences in their tolerance to environmental conditions.

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