

Morphological variations of natural populations of an aquatic macrophyte *Elodea nuttallii* in their native and in their introduced ranges

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Received 28 November 2008; accepted in revised form 5 February 2009; published online 12 February 2009

Abstract

Introduced plant species appear often more vigorous than their conspecifics in the native range. We investigated the morphological variations of *Elodea nuttallii* (Planch.) St John and its behaviour in its native and in its introduced habitats. We assessed eight morphological traits of 24 populations in the native North America range and 16 populations in the introduced European range. The introduced taxa can be very distinct in their growth form and size from counterparts in their native range. The shorter broad-leaved phenotype typically occurs in shallow streams, whereas the longer narrow-leaved phenotype occurs in lakes. Larger leaf width and higher number of lateral shoots - when nutrients are not limiting- may enhance plant performance. The European populations grow more vigorously than their American relatives, possibly because of different selection pressures.

Key words: morphological variations, biological traits, vitality, aquatic macrophytes, *Elodea nuttallii*, Europe, North America

Introduction

Several factors that may influence the susceptibility of a community to invasion have been identified (Crawley 1987; Lonsdale 1999; Davis et al. 2000). The reasons that some species become invasive following introduction, and which traits allow these species to disrupt the ecosystems they invade, have become topics of considerable interest and debate (Blossey and Nötzold 1995; Callaway and Aschehoug 2000; Keane and Crawley 2002; Müller-Schärer et al. 2004). While all non-native plants may carry some risk of becoming natural invaders, the taxonomic analysis of Daehler (1998) suggests that plants with amongst the highest risk of becoming natural invaders worldwide include species that are primarily aquatic or semi-

aquatic. Furthermore, invaders characterized by higher leaf area and greater phenotypic plasticity appear to be “super invaders” (Daehler 2003). For example, the variation of populations of *Elodea nuttallii* (Planch.) St John, a well known invasive species, is such that the two extremes of its morphological range appear to be distinct taxa in Europe, one with long, completely plane leaves, and the other with shorter, broader, strongly reflexed leaves (Simpson 1988; Vanderpoorten et al. 2000).

Understanding the basis for invasiveness is critical in assessing the risks associated with new or spreading invasive species. Apart two flora comparisons (Crawley 1987; Thébaud and Simberloff 2001) the available literature does not provide sufficient empirical data to suggest that increased vitality in invasive populations is a

common phenomenon. A previous work, based on literature data, established that there is no general tendency for aquatic plants to be more vigorous in their introduced ranges (Thiébaud 2007). The aim of our study was to collect empirical data for one of the most rapid current invader of Europe in water bodies, *Elodea nuttallii*. Native to North America, *E. nuttallii* was introduced into Europe in 1939 (Simpson 1984). Only female plants were observed initially, introduced via the trade in live aquarium plants (Cook and Urmi-König 1985). The spread of *E. nuttallii* has resulted in its displacement of *E. canadensis* Michaux from many localities where the latter had previously become well established in Europe (Simpson 1990; Thiébaud et al. 1997; Barrat-Segretain 2001; Larson 2007). In the long term, *E. canadensis* and *E. nuttallii* therefore appears redundant enough to coexist within the sites (Héroult et al. 2008). The different invasiveness patterns of *Elodea* species could be solely due to the ecological drift (Héroult et al. 2008). In North America, *E. nuttallii* is concentrated around the St Lawrence Valley, the Great Lakes, and the Pacific West Coast, but is more common further south. *E. nuttallii* populations are rarely troublesome in natural habitats in North America, but plants can become dominant in altered or created aquatic systems, especially when bicarbonate, reduced iron, and phosphorus are plentiful. *E. nuttallii* is listed in southern Ontario (Argus and White 1977), southern British Columbia and southern Quebec (Bouchard et al. 1983). Remarkably little is known about the ecology of *E. nuttallii* within its native range. Studies indicate that *E. nuttallii* is present at different stages in the eutrophication of a lake (Lawrence 1976).

The distribution of the aquatic plants in North America and in Europe has been documented in the literature and by consulting herbariums in Museum in Canada (Montreal, Quebec) and in the USA (Albany, New York State). Even though the climate was generally more continental in North America, all regions were characterized by a temperate climate. For a representative comparison of North American and European regions, a total of 90 populations were visited during the summers of 2003 and 2004. The populations were distributed through four main regions in both continents: thirty European populations were located in Britain, north-eastern France, Switzerland and Belgium, while 60 North American populations were located in

Canada and the United States (30 sites in Quebec and 30 in New York State; Annex 1). We investigated field morphological variations of natural populations of *E. nuttallii* in their native (North America) and in their introduced ranges (Europe).

Material and Methods

Morphological variation of E. nuttallii

To measure the morphological variation of *Elodea nuttallii* in its native ranges and in its introduced ranges, 16 sites were selected in Europe from among the 30 European sites visited, while of the 60 North American sites visited, 11 and 13 sites, respectively, were chosen in Canada (Quebec) and the USA (New York State). Among them, five and ten of the sites in Canada and USA respectively were lakes whilst eight of the sites in Europe were also lakes. Within each region, the populations were sampled according to a geographical gradient (samples were distributed evenly in the East-West and South-North areas of each sampling region). Records made for each population included geographical location, the most frequent species in the accompanying flora and the type of water body (lake or stream). The criteria used to identify the *Elodea* species in North America and in Europe were the criteria defined by Simpson (1988). Field trips were carried out in the summer (from mid-July to mid-August). Thirty plants were randomly collected at each site to investigate the morphological variations. Measurements of morphological traits were realized in the laboratory. The presence or absence of fruits in each plant was investigated. The main traits are illustrated in the Figure 1.

Eight morphological traits were measured on each plant: (1) main shoot length; (2) number of lateral shoots - Lateral shoots included the initial lateral shoot which developed from the nodes on the original apical shoot and the other lateral shoots that developed either from the same nodes or from the nodes on the lateral shoots - ; (3) cumulated length of lateral shoots (initial + secondary); (4) bulk, measured as the ratio between dry mass of the plant and total length of all shoots; (5) internode length, defined as the length of ten internodes below the three-cm long apex; (6) length of a leaf located at the sixth whorl; (7) width of a leaf located at the sixth whorl; (8) area of a leaf located at the sixth whorl. The leaf fully expanded was fixed on a

paper, and its length, its width and its area were calculated by using a Scion image V. 1.63 programme).

Only sites sampling several times were selected to represent base flow chemistry. Twelve sites (five rivers and seven lakes) and thirteen sites (six streams and seven lakes) were respectively chosen in North America and in Europe. Conductivity and pH were measured using a combined glass electrode. Soluble reactive phosphorus (SRP) was determined using the ascorbic acid method for SRP (APHA 1992),

while ammonium was analyzed using the phenol hypochloride method (Wetzel and Likens 1991). Nitrate, sulfate and chloride analyses were determined with ion chromatography.

For lakes, we added two parameters: water clarity and Chlorophyll *a*. Water clarity was estimated by Secchi disk according to standard methods. Chlorophyll *a* is measured by filtering a sample water through a glass fiber filter. The filter is ground up in an acetone solution and Chlorophyll *a* quantified using a spectrophotometer.

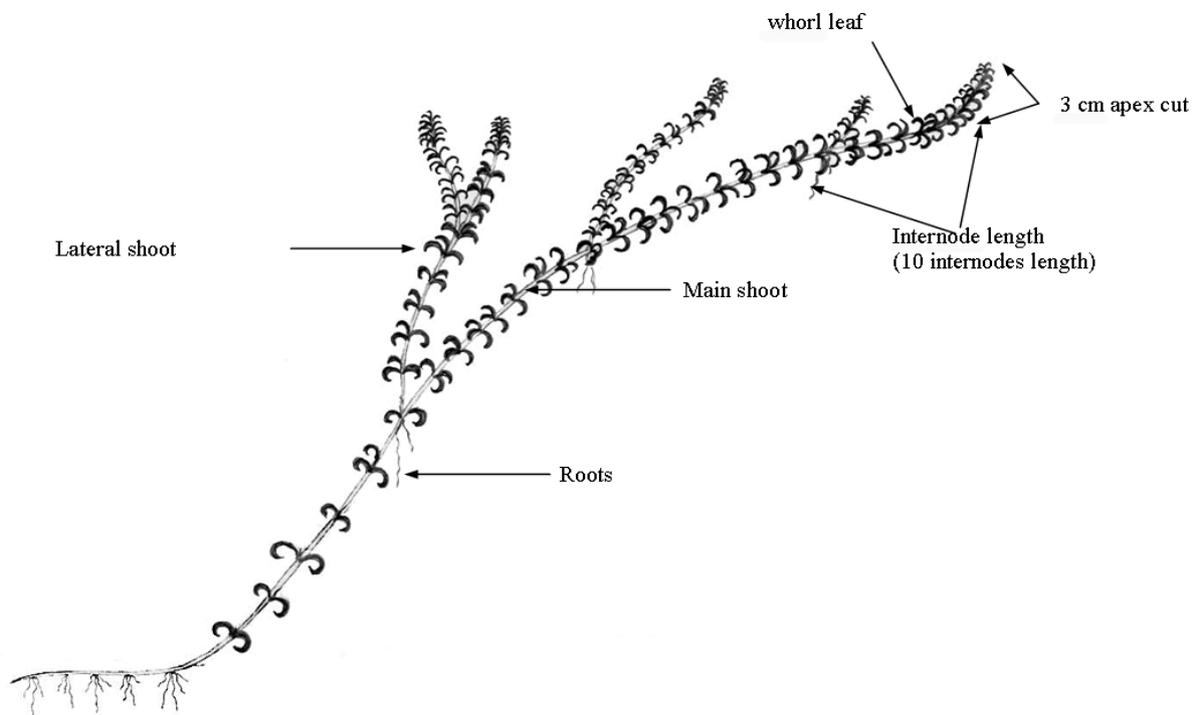


Figure 1. Diagram illustrating *E. nuttallii* and its morphological traits

Statistical analyses

We used analysis of variance (two-factor ANOVAs) methods for testing for differences in plants traits between continents and type of water body. Data were log transformed to normalize their distribution prior to analysis. Tukey HDS tests were used as a post-hoc test. They were set at a significance level of 0.05.

Spearman's coefficients of correlation were calculated between chemical variables and

independent morphological traits. Relationships with the traits "leaf area" and "bulk" were not considered because of their correlations with other traits.

Canonical Correspondence Analysis (CCA) based on raw data was used to elucidate the relationships between morphological traits (except the area leaf and bulk) and environmental variables. Significance of the canonical axes was tested using Monte-Carlo permutations of samples.

Results

The species *E. nuttallii* typically form dense monospecific stands in the lower littoral zone of lakes in the prospected sites in Canada, whereas it was often mixed with *Elodea canadensis* (38% of the sites) in eastern USA. The two *Elodea* species were only found together in 6.7 % of the European sites. In the introduced range, *E. nuttallii* often covered the littoral zone of the shallow basin or streams with dense mats, but it is most commonly associated with European

native aquatic vascular plants (e.g. *Callitriche* species, *Ranunculus* species, *Myriophyllum spicatum* L.).

Morphological variation of E. nuttallii in Europe and in North America

All morphological traits significantly differed between Europe and North America and between lakes and streams (Tables 1, 2). The average population size (main shoot length, internode length), bulk, branching (number and length) and

Table 1. Morphological differences between European and American populations of *Elodea nuttallii*
P-values (Mean± Standard deviation)

		Europe		North America		P
trait 1	Shoot length cm	57.12	± 30.26	31.28	± 17.43	< 0.01
trait 2	Number lat.shoot	7.65	± 4.67	5.50	± 4.64	< 0.0001
trait 3	Length lat.shoot cm	61.82	± 63.0	35.64	± 39.4	< 0.0001
trait 4	Bulk (mg cm ⁻¹)	2.31	± 1.2	1.73	± 0.95	< 0.0001
trait 5	Internode length cm	0.74	± 0.33	0.56	± 0.28	< 0.0001
trait 6	Length leaf cm	1.17	± 0.31	0.96	± 0.28	< 0.0001
trait 7	Width leaf cm	0.22	± 0.09	0.15	± 0.05	< 0.01
trait 8	Leaf area cm ²	0.17	± 0.11	0.09	± 0.05	< 0.01

Table 2. Morphological differences between populations of *Elodea nuttallii* in lakes and in streams
P-values (Mean± Standard deviation, ns: not significant)

		Lake		Stream		P
trait 1	Shoot length cm	41.77	± 1.01	40.92	± 1.24	ns
trait 2	Number lat.shoot	5.82	± 0.18	7.14	± 0.22	< 0.0001
trait 3	Length lat.shoot cm	49.89	± 1.95	39.94	± 2.40	< 0.0013
trait 4	Bulk (mg cm ⁻¹)	1.82	± 0.04	2.17	± 0.05	< 0.0001
trait 5	Internode length cm	0.66	± 0.01	0.58	± 0.06	< 0.0001
trait 6	Length leaf cm	1.03	± 0.01	1.06	± 0.01	ns
trait 7	Width leaf cm	0.15	± 0.15	0.21	± 0.001	< 0.01
trait 8	Leaf area cm ²	0.09	± 0.001	0.17	± 0.001	< 0.01

leaf traits (area, length, and width) were significantly higher in European than in American populations (Table 1). A highly significant difference was established between streams and lakes, except for main shoot length and length leaf (traits 1, 6, Table 2). The interactions between the continent and the type of waterway were significantly different for the

morphological traits tested, with the exception of length of lateral shoots (two-factor ANOVAs, Table 3).

Linking species and environmental variables

The number of lateral shoots, bulk and width leaf were mainly correlated with nutrients (traits 2,

7), whereas the main shoot length, length of lateral shoots and the internode length were correlated with the Secchi Disk (traits 1, 3, 5; Table 4).

The CCA showed that a high percentage of the traits-environment relation (96.7%) was explained by the first two canonical axes (Figure 2). Monte Carlo permutation tests on the first eigenvalues indicated that the relation between the traits and the environmental variables selected by the model were significant. These results suggest that morphological traits of *Elodea nuttallii* in the European and North

American sites can be explained by the variables included in the model. The first axis was defined positively by leaf width (trait 7) and in lesser extend by number of lateral shoots (trait 2). The second axis was characterised negatively by main shoot length (trait 1), in lesser extend by the length of leaf (trait 6) and by internode length (trait 5). A clear opposition was established between native population traits and introduced population traits (Figure 2). Three European populations corresponding on recently introduced species are close to North American populations.

Table 3. Two-factor ANOVAs used to test the continent and water bodies effects on each trait (ns: not significant)

			F	P	Degree of freedom
trait 1	Main shoot length (cm)	Type of water body	2,90	0,0888	1
		Continent	298,62	< 0,0001	1
		interaction	15,52	0,0001	1
trait 2	Number of lateral shoots	Type of water body	10,95	0,0010	1
		Continent	67,53	< 0,0001	1
		interaction	20,60	< 0,0001	1
trait 3	Length of lateral shoots (cm)	Type of water body	13,19	0,0003	1
		Continent	89,70	< 0,0001	1
		interaction	2,03	ns	1
trait 4	Bulk (mg cm ⁻¹)	Type of water body	2,90	0,0888	1
		Continent	109,14	< 0,0001	1
		interaction	33,44	< 0,0001	1
trait 5	Internode length (cm)	Type of water body	42,96	< 0,0001	1
		Continent	164,37	< 0,0001	1
		interaction	8,77	0,0031	1
trait 6	Length leaf (cm)	Type of water body	0,46	ns	1
		Continent	115,41	< 0,0001	1
		interaction	20,30	< 0,0001	1
trait 7	Leaf width (cm)	Type of water body	152,19	< 0,0001	1
		Continent	173,73	< 0,0001	1
		interaction	79,66	< 0,0001	1
trait 8	Leaf area (cm)	Type of water body	92,53	< 0,0001	1
		Continent	122,46	< 0,0001	1
		interaction	9,29	0.0024	1

Table 4. Coefficient of correlation between water chemical parameters and plant traits of *Elodea nuttallii* in bold: significant values

	pH	Conductivity	Phosphate	Ammonium	Nitrate	Sulfate	Chloride	Chl. a	Secchi Disk
Shoot length (cm)	0.07	0.06	0.23	-0.08	0.38	-0.13	-0.23	-0.07	0.54
Nbr lat.shoot	0.004	-0.26	0.59	0.55	0.15	-0.31	-0.33	0.14	-0.01
Length lat.shoot (cm)	0.24	0.14	0.06	-0.09	0.27	-0.17	-0.19	-0.00	0.60
Bulk (mg cm ⁻¹)	-0.04	-0.02	0.55	0.24	0.41	-0.14	-0.26	0.006	0.33
Internode length (cm)	0.32	0.38	-0.04	-0.18	0.23	0.27	0.24	-0.05	0.39
Length leaf (cm)	-0.01	0.25	0.23	0.003	0.30	0.18	0.11	0.003	0.18
Width leaf (cm)	-0.54	-0.34	0.78	0.49	0.23	-0.12	-0.33	0.05	-0.11

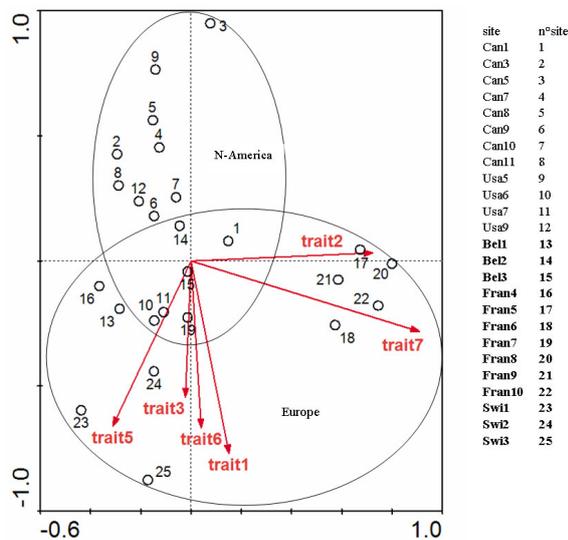


Figure 2. Ordinations obtained by Canonical Correspondence Analysis based on morphological traits. The relative position and magnitude of the biological traits are represented by arrows. The sites are positioned as points in the C.C.A. diagram. Trait 1: main shoot length; trait 2: number of lateral shoots; trait 3: length of lateral shoots; trait 5: internode length; trait 6: leaf length; trait 7: leaf width

Discussion

Morphological variation of E. nuttallii in Europe and in North America

Despite considerable variation between populations within continents, there were pronounced differences between continents; the vitality (main shoot length, branching,) was significantly higher in European than in American populations. Introduced plant species that became successful invaders appear often more vigorous and taller than their counterparts in the native range (Thebaut and Simberloff 2001; Leger and Rice 2003; Stastny et al. 2005). This seems to contradict the results of Daehler (2003) who reviewed the performance of co-occurring native and alien species but did not find higher growth rates, competitive ability nor fecundity to be characteristics of the latter. The seemingly contradictory conclusions of Daehler's review (2003) could be due to fact that his review was not confined to congeners (Pysek and Richardson 2007).

The introduced *Elodea nuttallii* populations appeared to perform better in Europe, possibly because of changed selection pressures (no selective herbivores for example). Johnson et al.

(1998) suggested that *Acentria ephemera*, an European aquatic moth larva, can potentially feed on *Elodea* species in North America. However when the density of these grazers is high, herbivory by *Acentria ephemera* causes severe damage to the European species *Myriophyllum spicatum*. Moreover, Lake and Leishman (2004) showed that both invasive exotic and non-invasive exotic species had significantly lower levels of leaf herbivory than native species, implying that release from pests alone cannot account for the success of invasive species. This is congruent with our results. We observed no leaf damage in the European populations, whereas limited damages were observed in the leaves of few American populations (6.7 % of the sites). *Elodea nuttallii* suffer less herbivory than native species in Europe (Thiébaud and Gierlinski 2007). The vitality of invasive plants may be associated with changes in resistance as well as tolerance to herbivory and that both types of anti-herbivore defence may need to be examined simultaneously to advance our understanding of invasiveness.

Biological traits of E. nuttallii in native and in introduced areas

There seem to be some traits commonly associated with successful invaders: growth rate, resistance and tolerance to disturbances, high fecundity and efficient dispersal of seeds or vegetative fragments.

North American and European populations of *E. nuttallii* showed pronounced differences in reproduction. *E. nuttallii* was characterized by no sexual reproduction in their introduced range, whereas fruits were observed in 6.7 % of the USA sites. Fruiting specimens are very rare in North America (Lawrence 1976) and very few fully mature fruits were noticed in Canada (Catling and Wojtas 1986). Although *E. nuttallii* reproduces both sexually and asexually by vegetative clonal propagation in North America, vegetative reproduction seems to be the dominant method of propagation. To our knowledge, no study has been undertaken to investigate the speed and extent of vegetative reproduction and propagation of *E. nuttallii* in North America. In the introduced range, Barrat-Segretain et al. (2002) showed that when introduced to a new habitat, the establishment of *Elodea* buds is rapid, since the propagules sank into the sediment and grew rapidly. However, it

is difficult to draw any conclusion regardless the role of the sexual versus vegetative reproduction on the propagation of *E. nuttallii* in their native and introduced ranges.

The clearest consistent difference that Lake and Leisham (2004) found between invasive exotic and non-invasive exotic species was in specific leaf area, suggesting that large specific leaf area facilitates invasiveness. Due to infrequent and ephemeral flowering, together with the minute size of the flowers, leaf morphology is often the trait used to differentiate *Elodea* species in North America (Catling and Wojtas 1986; Lawrence 1976). Unfortunately there is overlap in the characters and there is little agreement among authors on the nature of these characters. According to Catling and Wojtas (1986) leaf width partially separates male plants of *Elodea canadensis* and *Elodea nuttallii* but not female plants. Determination of sterile *Elodea* species has also been an area of controversy in Europe. The European populations of *E. nuttallii* have a higher specific leaf length (1.17 cm) and leaf width (0.22 cm) and internode length (0.74 cm) than in native ones (0.96 cm, 0.15 cm, 0.56 cm respectively). The leaves are either linear or linear-lanceolate and the shape of the leaf apex is narrowly acute to acuminate in *E. nuttallii*'s European populations. By changing leaf width, individuals maximize growth under a variety of environmental conditions and have the potential to intensify the development of lateral shoots and of resource-acquiring structures in the more favourable microhabitats of a heterogeneous environment. Larger leaf width and higher number of lateral shoots were produced in streams (Table 3) because there is a stimulating effect of moderate flow, a response to flow constraints or simply as a function of greater nutrient supply in rivers (mean values: [ammonium] = 32 µg/l; [SRP] = 51 µg/l) than in lakes ([ammonium] = 48 µg/l; [SRP] = 16 µg/l).

Invaders seems often have higher phenotypic plasticity than natives, and this plasticity probably allows invaders to succeed in a wider range of environments (Daehler 2003). A greater phenotypic plasticity is particularly advantageous in disturbed environments. Plastic "general-purpose genotypes" could have a fitness advantage in founding populations where local adaptation has not yet occurred (Sexton et al. 2002), or cannot occur because of a lack of genetic variation. Genetic differentiation in introduced populations may occur in any

ecological trait that is beneficial under the novel selection conditions, given that there is genetic variation for it. Our results established that *E. nuttallii* exposed to environmental stresses showed a wide range of morphological variations. The shorter broad-leaved phenotype typically occurs in shallow streams, whereas the longer narrow-leaved phenotype occurs in deeper waters. The latter may also be present near the surface when light intensity is reduced due to turbidity of the water. High phenotypic plasticity is really a key ingredient of invasiveness of plants in aquatic environments. For example, Di Nino et al. (2007) showed that genetically uniform populations of *E. nuttallii* develop a common phenotype under similar environmental conditions. However, with increasing water nutrient enrichment, *E. nuttallii* showed increases in leaf area with decreases in internode length (Di Nino et al. 2007). These plastic responses may enhance plant performance. To detect evolutionary change in invaders, comparative studies of native versus introduced populations are needed. A combination of field and common garden studies is needed to fully understand evolutionary change in *E. nuttallii*.

Implication for management

On the basis of our results (a high plasticity, allocation of resources to growth and a foliar investment), *E. nuttallii* should be regarded as having a high risk of being invasive, and we recommend that it is nominated as a priority target for eradication or control in new sites. Different studies established that *E. nuttallii* is probably in an expansion phase in Europe and will likely spread to new areas (Simpson 1984; Thiébaud et al. 1997; Barrat-Segretain 2001, Larson 2007). In general, the priority of biological invasion control is to prevent new infestations from taking hold, especially for the fastest-growing and most disruptive species. It should be noted that most stakeholders and decision makers have a limited perception of the problem (Garcia-Llorente et al. 2008). The prevention approach would include greater investment in prevention: preventing organisms from entering a particular pathway, and preventing organisms that are transported from being released or escaping alive. Stronger enforcement of existing laws coupled with an intensive public education campaign is needed to prevent further *Elodea* species introduction.

Conditions where invaders had the largest performance advantages (high or fluctuating nutrient loading, flow regime alteration, industrial contamination) are generally associated with degraded habitats. Biological invasions could be seen as one of a syndrome of traits that characterize degraded aquatic ecosystems (Wilby 2007). The European Water Framework Directive requires the restoration of degraded freshwaters (Wilby 2007). A basic recommendation is to foster good ecological conditions in water masses as a self-defence measure for aquatic ecosystems against the colonising pressure of *Elodea* species. Specific emphasis on hydromorphological as well as nutrient-related pressures, combined with the delivery of programmes on a catchment scale, should support the environmental improvements needed to sustain reduction of *Elodea* species.

Acknowledgements

We are grateful to Prof. Jacques Haury (ENSA, Rennes) and to Gisèle Verniers (GEREA, Belgium), Prof. Philippe Kuepfer (University of Neuchâtel, Switzerland), Prof. Laure Giamberini (University of Metz), Prof. Michèle Trémolières (University of Strasbourg) for their helpful assistance in collecting *Elodea nuttallii* samples. Many thanks to Dr Dan Molloy from the New York Museum and to Dr Jacques Brisson from the Plant Biology Research Institute of Montreal and the Botanical Gardens of Montreal for information on the distribution of *Elodea canadensis* and *E. nuttallii* in North America. This project was sponsored by the “Biological Invasions” program of the French Ministry of Ecology and Sustainable Development.

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Annex 1

Location of sampling sites in North America and in Europe

	Type	Location	Label	Coordinates (Latitude/Longitude)
Canada	Lake	Lac Renaud	Can1	45.56 N 74.12 W
Canada	Lake	lac Buckingham	Can2	45.35 N 75.25 W
Canada	Lake	Grand Mère:	Can3	46.37 N 72.41 W
Canada	Lake	Lac Ouimet	Can4	45.50 W 74.10 W
Canada	Lake	Tremblant Lake	Can5	46.15 N 74.38 W
Canada	Stream	Magog river	Can6	45.16 N 72.09 W
Canada	Stream	Saint Jerome	Can7	45.47 N 74.00 W
Canada	Stream	rivière Rouge	Can8	45.39 N 74.42 W
Canada	Stream	Saint-François river: Pierville	Can9	46.04 N 72.45 W
Canada	Stream	châteaugay river: Huntlington	Can10	45.05 N 74.10 W
Canada	Stream	Yamaska	Can11	45.17 N 72.55 W
USA	Lake	Pond Eddy	Usa1	41.27 N 74.49 W
USA	Lake	Chautauqua lake	Usa2	42.12 N 79.27 W
USA	Lake	Greenwood lake	Usa3	41.11 N 74.19 W
USA	Lake	lake Canandaigua	Usa4	42.49 N 77.16 W
USA	Lake	lake Cassayuna	Usa5	43.11 N 73.34W
USA	Lake	lake Champlain: port Henry	Usa6	44.03 N 73.28 W
USA	Lake	lake Erie Buffalo	Usa7	42.54 N 78.53 W
USA	Lake	lake George Bolton	Usa8	43.35 N 73.35 W
USA	Lake	Sandy pond lake Ontario	Usa9	43.39 N 76.05 W
USA	Lake	Troy pond	Usa10	42.43 N 73.40 W
USA	Stream	little Salmon river	Usa11	43.34 N 76.03 W
USA	Stream	Hudson river Saugerties	Usa12	42.45 N 73.57 W
USA	Stream	mohawk river troy cohoes	Usa13	42.46 N 73.42 W
Belgium	Lake	Eau d'Heure Lake 1	Bel1	50.14 N 4.24 E
Belgium	Lake	Eau d'Heure Lake 2	Bel2	50.14 N 4.24 E
Belgium	Lake	Eau d'Heure Lake 3	Bel3	50.14 N 4.24 E
France	Lake	Talmont	Fran1	46.28 N 1.37 W
France	Stream	Derval:Don river 1	Fran2	47.40 N 1.40 W
France	Stream	Derval:Don river 2	Fran3	47.40 N 1.40 W
France	Lake	Corny	Fran4	49.03 N 6.04 E
France	Stream	Philipsbourg	Fran5	48.57 N 7.38 E
France	Stream	Niederbronn les Bains	Fran6	48.57 N 7.38 E
France	Stream	Bitche	Fran7	49.03 N 7.26 E
France	Stream	Ingwiller	Fran8	48.52 N 7.29 E
France	Stream	Wimmenau	Fran9	48.55 N 7.25 E
France	Stream	Wingen sur Moder	Fran10	48.55 N 7.22 E
Switzerland	Lake	Genève	Swi2	46.42 N 6.09 E
Switzerland	Lake	Lausanne	Swi3	46.31 N 6.38 E
Switzerland	Lake	Neuchatel	Swi1	46.59 N 6.56 E