Chapter eleven

Non-indigenous aquatic and semiaquatic plant species in France

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INTRODUCTION

The invasion of natural communities by introduced plants constitutes one of the most serious threats to biodiversity (Heywood 1989). What is the current situation in France? What do we know about these invasions and their consequences? What measures have been implemented to manage non-indigenous plant species populations? To respond to these questions, the French Ministry for Ecology and Sustainable Development has supported various biological invasion research projects (''INVABIO'') and the National Museum of Natural History entrusted Muller *et al*. (2004) to evaluate plant species invasiveness in metropolitan France.

While the invasibility of riparian plants communities, patterns, and causes of river corridor invasion by non-indigenous plant species have been studied (Planty-Tabacchi *et al*. 1995, 2001, Tabacchi and Planty-Tabacchi 2002), significantly less attention has been paid to the introduced aquatic and semiaquatic plants. Biological invasion research in freshwater systems has focused on a few plants such as *Fallopia* taxa (Schnitzler and Muller 1998, Bailey and Schnitzler 2003), *Elodea* species (Thiébaut *et al*. 1997, Barrat-Segretain 2001, 2004, 2005, Barrat-Segretain *et al*. 2002, Greulich and Trémolières 2002) or *Ludwigia* sp. (Dutartre and Oyarzabal 1993, Dutartre *et al*. 1997, 1999, 2002, Cazaubon *et al*. 2002, Cornier *et al*. 2002, Dandelot *et al*. 2005). To elucidate the reasons for the success of non-indigenous species (NIS), studies have gathered

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data on the biology and ecology of emblematic, non-indigenous macrophytes. Numerous studies and reports have focused on the management of invaders such as *Ludwigia* sp. (Dutartre and Oyarzabal 1993, Damien 2002, Fournier and Oyarzabal 2002, Pipet 2002, Rebillard *et al.* 2002, Grillas 2004) and, to a lesser extent, *Elodea* species (Di Nino *et al.* 2005).

NON-INDIGENOUS AQUATIC AND SEMIAQUATIC MACROPHYTES IN FRANCE

Compilation of a species list

The term ‘‘aquatic macrophyte’’ is commonly used for all macroscopic forms of aquatic vegetation including algae, bryophytes, some pteridophytes, and many flowering plants (angiosperms). This assemblage contains extremely heterogeneous species which survive in similar habitats but result from fundamentally different evolutionary pathways. Non-indigenous aquatic plants do not belong to one distinct taxonomic group, but rather form a collection of many plant taxa.

This chapter does not claim to be an exhaustive review of introduced plants in metropolitan France, but rather an overview of the present situation. This review covers aquatic macrophytes in inland waters, excluding marine algae, such as *Caulerpa taxifolia* (Vahl.) C. Agardh, as well as woody species (except for *Hibiscus roseus*). Some taxa, regarded as non-indigenous by certain authors (although with a wide margin of doubt), have been included here: *Acorus calamus*, *H. roseus* (three European populations; E. Tabacchi 2005, personal communication), and *Azolla mexicana* (formerly known as *Azolla caroliniana* Willd). The status of several species from southern Europe varies according to the author: *Vallisneria spiralis*, *Stratiotes aloides*, *Scirpus mucronatus*, and *Scirpus pungens* are protected locally, whereas Dutartre *et al.* (1997) considered these species non-indigenous. In addition, van der Velde *et al.* (2002) considered *Salvinia natans* and *Octodiceras fontanum* as non-indigenous in the Netherlands, while they are protected in France. Some NIS are well-established, whereas others are found only occasionally in aquatic environments.

For aquatic macrophytes, several regional floras (Abbayes *et al.* 1971, Corillion 1982, Bournerias 1984, Lambinon *et al.* 1992) and local scientific journals (Bulletin de la Société Scientifique de Bretagne, Bulletin de la Société d’Histoire Naturelle de Moselle, Bulletin de la Société Linnéenne de Normandie, Bulletin de l’Association Philomathique d’Alsace Lorraine, Bulletin de la Société des Sciences de Nancy, le Monde des Plantes) were consulted. They provided information about plant histories in the geographical area, specifically on whether it is an indigenous or an NIS. Several sources containing information on NIS were also used (Dutartre *et al.* 1997, Aboucaya 1999, Muller *et al.* 2004).

NIS taxonomic groups and eco-morphological types

My resulting list of NIS, representing 24 families and 58 species in metropolitan France (Table 1), includes species found occasionally as well some hybrids. Some aquatic families are well represented, such as *Lemnaceae* and *Hydrocharitaceae*. Furthermore, numerous non-indigenous semiaquatic species were also present, such as *Poaceae* and *Cyperaceae*. As compared to Wallentinus's list (Wallentinus 2002), 10 additional species, including two bryophytes, have been identified as NIS in France.

Table 1 List of non-indigenous aquatic and semiaquatic plant species in France and their vectors of introduction: (a) escaped from aquaria, (b) arrived on seagoing vessels (ballast water, timber trade), (c) introduced intentionally (ornamentals, pond gardens, medicinal plant), (d) seed or grain contaminant, (e) wool industry, (f) natural expansion, (?) unknown source.

	Family	Vectors
Alga		
Hydrodictyon reticulatum (L.) Lagerh.	Hydrodictyaceae	?
Bryophyta		
Dumortiera hirsuta (Sw.) Nees	Marchantiaceae	f
Octodiceras fontanum (Bach. Pyl) Lindb.	Fissidentaceae	f
Pteridophyta		
Azolla filiculoides Lam	Azollaceae	a
Azolla mexicana C. Presl	Azollaceae	a
Salvinia natans (L.) All.	Salviniaceae	a?
Vascular plants (monocots and dicots)		
Acorus calamus L.	Araceae	c
Althernanthera philoxeroides (Martius) Griseb	Amaranthacea	a
Aponogeton distachyos Thunb.	Aponogetonaceae	c
Callitriche peploides Nutt.	Callitrichaceae	?
Callitriche terrestris Rafin	Callitrichaceae	?
Cortadaria selloana (Schultes and Schultes fil.) Ascherton and Graebner	Poaceae	c
Cotula coronopifolia L.	Asteraceae	c?
Cyperus difformis L.	Cyperacea	?
Cyperus eragrostis Lam.	Cyperacea	c
Cyperus esculentus L.	Cyperacea	e
Cyperus reflexus Vahl	Cyperacea	e
Egeria densa Planchon	Hydrocharitaceae	a
Eichhornia crassispes (Mart.) Solms	Pontederiaceae	c
Eleocharis bonariensis Nees	Cyperaceae	?

Table 1 Continued.

	Family	Vectors
Elodea canadensis Michaux	Hydrocharitaceae	a/b
Elodea ernstiae H. St. John	Hydrocharitaceae	a
Elodea nuttallii (Planchon) H. St. John	Hydrocharitaceae	a
Fallopia japonica (Houtt.) Ronse Decraene	Polygonaceae	c
Fallopia sachalinensis (F. Schmidt Petrop.) Ronse Decraene	Polygonaceae	c
Fallopia x bohemica Chrtek and Chrtkova	Polygonaceae	f
Glyceria striata (Lam.) A. S. Hitchc	Poaceae	d
Heracleum mantegezzianum Sommier and Lev	Apiaceae	c
Hibiscus roseus Thore	Malvaceae	c
Hydrilla verticillata (L.f.) Royle	Hydrocharitaceae	a/c
Hydrocotyle ranunculoides L.fil	Apiacae	a/c
Impatiens balfouri Hooker fil.	Balsaminaceae	c
Impatiens glandulifera Royle	Balsaminaceae	c
Juncus tenuis Willd.	Juncaceae	?
Lagarosiphon major (Ridley) Moss	Hydrocharitaceae	a
Lemna aequinoctialis Welw.	Lemnacaeae	f?
Lemna minuta H.B.K.	Lemnacaeae	f?
Lemna perpusilla Torrey	Lemnacaeae	f?
Lemna turionifera Landolt	Lemnacaeae	f?
Lindernia dubia (L.) Pennel	Scrophulariaceae	f
Ludwigia grandiflora subsp. hexapetala (Hook. and Arn.) Nesom and Kartesz	Onagraceae	c
Ludwigia peploides subsp. montevidensis (Spreng.) Raven	Onagraceae	c
Myriophyllum aquaticum (Velloso) Verdcourt	Haloragaceae	a
Myriophyllum heterophyllum Michaux	Haloragaceae	a/c
Najas graminea Delile	Najadaceae	f?
Paspalum dilatatum Poiret	Poaceae	e
Paspalum distichum L	Poaceae	f?
Pistia stratiotes L.	Araceae	a/c
Pontederia cordata L.	Pontederiaceae	c
Sagittaria latifolia Willd.	Alismataceae	a/c
Schoenoplectus prolifer Rottb.	Cyperaceae	?
Scirpus mucronatus L.	Cyperaceae	?
Scirpus pungens Valh.	Cyperaceae	?
Spartina alterniflora Loisel	Poaceae	b/c
Spartina x townsendii H. and J. Groves	Poaceae	f
Spirodela oligorhiza (Kurz) Hegelm.	Lemnacaeae	f/a
Stratiotes aloides L.	Hydrocharitaceae	c
Vallisneria spiralis L.	Hydrocharitaceae	a

The composition of the non-indigenous aquatic flora is illustrated in Fig. 1A, with one alga (hydrodictyaceae), two bryophytes (Marchantiaceae, Fissidentaceae), three pteridophytes (Azollaceae and Salviniaceae), and 52 vascular plants (34 monocotyledons and 18 dicotyledons). More NIS are monocots than dicots proportionally, perhaps due to the monocots' high incidence of rhizomatous growth.

Of these non-indigenous plants, helophytes, amphiphytes, floating, and submersed species represented 20, 20, 19, and 16% of the introduced macrophytes, respectively (Fig. 1B). Helophytes are emergent plants which occupy permanent, standing water, or wet soil. Floating macrophytes are not rooted in sediment, but live unattached in the water. The life forms within this group included very small floating or submersed plants with few or no roots (*Lemna minuta* and the water fern *Azolla* sp.). Submersed macrophytes include many flowering plants, for example *Elodea nuttallii* and *Egeria densa* which complete their life cycle under water.

Invasion histories and pathways

Many aquatic macrophytes were introduced more than a hundred years ago, while others are more recent arrivals. The majority of introductions took place at the end of the 19th and at the beginning of the 20th centuries (Table 2). Of all the introduced species listed here, more than 50% came from America and almost 40% came from Asia and/or Africa (Table 2).

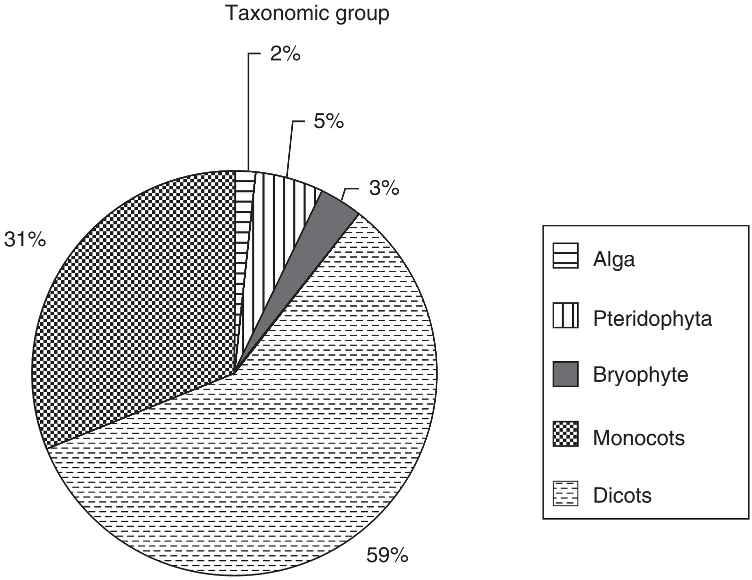

Fig. 1A Taxonomic groups of non-indigenous aquatic and semiaquatic plants in France.

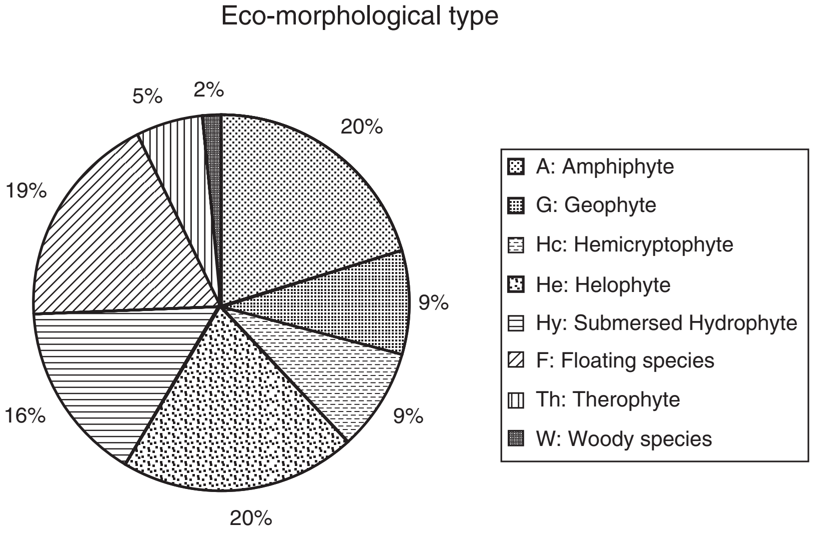

Fig. 1B Eco-morphological types of non-indigenous aquatic and semiaquatic plants in France.

Some NIS are only reported occasionally, like *Eichhornia crassipes* (Planty-Tabacchi 1993) or *Althernanthera philoxeroides* in south-west France (Dupont 1989, Georges 2004) or *Pistia stratiotes*; *Pontederia cordata* and *Hydrilla verticillata* were observed only once in an aquatic environment.

The time-lag phenomenon, during which a given population remains small and geographically restricted, is well documented for riparian species (e.g. *Impatiens glandulifera, Fallopia japonica, Fallopia sachalinensis*) or amphiphytes, such as *Ludwigia grandiflora* subsp. *hexapetala* and *Ludwigia peploides* subsp. *montevidensis* (Dutartre and Oyarzabal 1993). The fact that certain introduced species became aggressive after a lag phase is ecologically significant.

The invasion histories of some NIS are well known:

- The hybrid *Spartina x townsendii* was first observed in France in 1906 along the Atlantic Coast. The first sighting in south-west France occurred in 1985 and then spread quickly via mud flats, resulting in hundreds of hectares being colonised by this species. Moreover, a second North American species, *Spartina versicolor* Fabre, not included in our list, has been reported occasionally. *Spartina alterniflora* spread, but only around the Bay of Brest (Goulletquer *et al.* 2002).
- The two Japanese Knotweed taxa (*F. japonica* and *F. sachalinensis*) have been expanding throughout Europe ever since their deliberate introduction in the 19th century. The spread has increased dramatically since the 1980s: *F. japonica* and *F. sachalinensis* and hybrids have developed in large

Table 2 NIS origin and introduction date in France. (? = unknown).

	Origin area	First found
Alga		
Hydrodictyon reticulatum (L.) Lagerh.	Cosm. subtropic.	1989
Bryophyta		
Dumortiera hirsuta (Sw.) Nees	N. America	before 1997
Octodiceras fontanum (Bach. Pyl) Lindb.	S-Europe	?
Pteridophyta		
Azolla filiculoides Lam.	N. America, S. America, Australia	1880
Azolla mexicana C. Presl.	N. America	1901
Salvinia natans (L.) All.	S. Europe, India, Japan.	before 1997
Vascular plants (monocots and dicots)		
Acorus calamus L.	Asia, N. America, India	XIV
Althernanthera philoxeroides (Martius) Griseb	S. America	1971
Aponogeton distachyos Thunb.	S. Africa	1830
Callitriche peploides Nutt.	N. America	before 1997
Callitriche terrestris Rafin	N. America	before 1997
Cortadaria selloana (Schultes and Schultes fil.) Ascherton and Graebner	S. America	before 1977
Cotula coronopifolia L.A	S. Africa	before 1980
Cyperus difformis L.	Pan-tropical	1850
Cyperus eragrostis Lam.	S. America	XIX
Cyperus esculentus L.	Tropical Asia and Africa	1952
Cyperus reflexus Vahl	Tropical America	2003
Egeria densa Planchon	S. America	1961
Eichhornia crassispes (Mart.) Solms	S. America	before 1993
Eleocharis bonariensis Nees	S. America	1750
Elodea canadensis Michaux	N. America	1845
Elodea ernstiae H. St. John	S. America	1959
Elodea nuttallii (Planchon) H. St. John	N. America	1959
Fallopia japonica (Houtt.) Ronse Decraene	Asia	1825
Fallopia sachalinensis (F. Schmidt Petrop.) Ronse Decraene	Japan	1869
Fallopia x bohemica Chrtek and Chrtkova	Hybrid	before 2003
Glyceria striata (Lam.)A. S. Hitchc	N. America, Central America	1906
Heracleum mantegezzianum Sommier and Lev	Caucasus	1993
Hibiscus roseus Thore	Europe ?	before 1995
Hydrilla verticillata (L.f.) Royle	Australia, Asia, Africa	before 1997
Hydrocotyle ranunculoides L.fil	N. and S. America	1820
Impatiens balfouri Hooker fil.	Himalayas	1943

Table 2 Continued.

	Origin area	First found
Impatiens glandulifera Royle	Himalayas	1842
Juncus tenuis Willd	N. America	XIX
Lagarosiphon major (Ridley) Moss	S. Africa	1960
Lemna aequinoctialis Welw.	S. America	?
Lemna minuta H.B.K.	N. and S. America	1965
Lemna perpusilla Torrey	Asia, N. Africa and S. America	before 1997
Lemna turionifera Landolt	N. America	1992
Lindernia dubia (L.) Pennel	N. America	before 1997
Ludwigia grandiflora subsp. hexapetala (Hook. and Arn.) Nesom and Kartesz	S. America	1820–1830
Ludwigia peploides subsp. montevidensis (Spreng.) Raven	S. America	1820–1830
Myriophyllum aquaticum (Velloso) Verdcourt	S. America	1880
Myriophyllum heterophyllum Michaux	N. America	before 1997
Najas graminea Delile	S. Europe to E. Asia ?	before 1997
Paspalum dilatatum Poiret	S. America	1937
Paspalum distichum L.	Trop. America	1965
Pistia stratiotes L.	S. America	?
Pontederia cordata L.	N. America	?
Sagittaria latifolia Willd.	N. America	1936
Schoenoplectus prolifer Rottb.	S. Africa, Australia?	1920
Scirpus mucronatus L.	Paleo Subtrop.	1859
Scirpus pungens Valh.	S. America	1849
Spartina alterniflora Loisel	N. America	1906?
Spartina x townsendii H. and J. Groves	hybrid	1906
Spirodela oligorhiza (Kurz) Hegelm.	Asia, Australia	?
Stratiotes aloides L.	S. Europe, Asia	1834
Vallisneria spiralis L.	S. Europe, N. Africa, Asia	1787

patches along many riparian and man-made habitats, often far from the original introduction point (Bailey and Schnitzler 2003).

- Coming from South America, *Ludwigia* sp. (*L. grandiflora* and *L. peploides*) were introduced by accident in southern France in the 1820s. Long restricted to the southern part of the country, from Camargue to Aquitaine, they have been migrating north for nearly 30 years. Today, *L. peploides* has reached the Belgian border. Others have been observed at sites in Belgium and in the Netherlands (Dandelot 2004).
- In a similar pattern, *E. densa*, a species first observed in France in 1960 (Feuillade 1961a, b), has spread along the entire Atlantic coast (Dutartre *et al.* 1999).

- An indigenous of North America, *Elodea canadensis*, first recorded in the early 19th century in the British Isles (Simpson 1984, 1990), is now naturalized and widespread in Europe. *Elodea canadensis* became a persistent weed following its naturalization, choking waterways before declining to its present, less-abundant (but still common) level (Thiébaut *et al.* 1997, Barrat-Segretain 2001).
- Another species from North America, *E. nuttallii* was first found in Belgium in 1939 and had spread into northern France by the end of the 1950s (Sell 1959). For the past 30 years it has been colonizing numerous ponds and streams in metropolitan France, except in the south-east (G. Thiébaut 2006, unpublished data). *Elodea nuttallii* is replacing *E. canadensis* at many sites (Mériaux 1979a, b, Thiebaut *et al.* 1997, Barrat-Segretain 2001). Although *E. canadensis* and *E. nuttallii* have been spreading for several years in eastern France, this species is relatively more problematic in other European countries. For example, *E. nuttallii* was classified as one of the ''top ten'' invasive species in Germany (F. Klingenstein 2005, personal communication); colonies have been expanding in Lake Leman in Switzerland since 1993 (Demierre and Perfetta 2002), in numerous ponds, reservoirs, and streams in Brittany (Simpson 1990), in Belgium (G. Verniers 2004, personal communication), as well as in Sweden (D. Larson 2006, personal communication).

I have come to the conclusion that most invasive plant species arrived in France as a result of human intervention (aquarium plants, ornamental use). Of all the plants, 38% are ornamentals, by far the dominant vector for introduced plants (Table 1). Another 17 of the introduced plant species are sold for use in freshwater aquaria (29% of the aquatic and semiaquatic plants; Table 1). Among the well-known examples of aquarium plants are certain hydrocharitaceae species (*E. densa, Elodea sp., Lagarosiphon major, H. verticillata*) and some other taxa (*Myriophyllum aquaria*). Plants which escaped from aquaria (Hydrocharitaceae, *Ludwigia* sp., *Myriophyllum* sp.) easily colonized freshwater environments. Highly invasive aquatic and semiaquatic species, including *Ludwigia* sp. and *Fallopia* taxa, have resulted to a large extent from either intentional introduction for ornamental use (outdoor ponds) or use as ornamentals after the initial introduction (Table 1). A few species are medicinal plants (e.g. *A. calamus*). *Spartina alterniflora* from the East coast of North America was introduced accidentally in ship ballast at the end of the 19th century in southern England, but it was also intentionally introduced into France to stabilize sand dunes, given its ability to increase sediment accumulation.

NIS distribution in France

Plant distribution varies according to the different climate in each of three biogeographical zones (Atlantic A, Continental C, Mediterranean M). For example, the diploid *L. peploides* colonises mainly the Mediterranean region of France (except for the south-eastern part), while the polyploid *L. grandiflora* predominates in all the other regions (Dandelot 2004). These data are taken primarily from Aboucaya (1999), from other publications (Felzines and Loiseau 2003, Muller *et al.* 2004, Felzines 2004), and from personal data (Table 3).

Of the 11 taxa present in the three biogeographical areas, there are five widespread invasive and one potentially invasive plants: three riparian species (*F. japonica*, *F. sachalinensis*, *I. glandulifera*), two floating species (*Azolla filiculoides*, *L. minuta*), and a single amphibious species (*L. grandiflora*). *Ludwigia* species are considered to be the most invasive aquatic plants in France. For

Table 3 Classification of NIS according to their invasiveness in France. Data taken primarily from Aboucaya (1999) and from: Felzines and Loiseau (2003), Muller *et al.* (2004), Felzines (2004), and personal data.
M: Mediterranean area, A: Atlantic area, C: Continental zone.

	Invasive		Potentially invasive	
	widespread	restricted	widespread	restricted
Acorus calamus L.				AC
Althernanthera philoxeroides (Martius) Griseb				M?
Aponogeton distachyos Thunb.				A
Azolla filiculoides Lam			MAC	
Azolla mexicana C. Presl				AC
Callitriche peploides Nutt.				?
Callitriche terrestris Rafin				?
Cortadaria selloana (Schultes and Schultes fil.) Ascherton and Graebner		M		A
Cotula coronopifolia L. A		M		A
Cyperus difformis L.				M
Cyperus eragrostis Lam.				C
Cyperus esculentus L.				A
Cyperus reflexus Vahl				A
Dumortiera hirsuta (Sw.) Nees				A?
Egeria densa Planchon		A		
Eichhornia crassispes (Mart.) Solms				M
Eleocharis bonariensis Nees				AC
Elodea canadensis Michaux		C		MA
Elodea ernstiae H. St. John				C
Elodea nuttallii (Planchon) H. St. John		C		A
Fallopia japonica (Houtt.) Ronse Decraene	MAC			
Fallopia sachalinensis (F. Schmidt Petrop.) Ronse Decraene	MAC			

Table 3 Continued.

	Invasive		Potentially invasive	
	widespread	restricted	widespread	restricted
Fallopia x bohemica Chrtek and Chrtkova			MAC	
Glyceria striata (Lam.)A. S.Hitchc				AC
Heracleum mantegezzianum Sommier and Lev		AC		
Hibiscus roseus Thore				A
Hydrilla verticillata (L.f.) Royle				MA?
Hydrocotyle ranunculoides L.fil				AC
Hydrodictyon reticulatum (L.) Lagerh.			MAC?	
Impatiens balfouri Hooker fil.				AC
Impatiens glandulifera Royle	MAC			
Juncus tenuis Willd		AC		
Lagarosiphon major (Ridley) Moss		A		
Lemna aequinoctialis Welw.				M
Lemna minuta H. B. K.	MAC			
Lemna perpusilla Torrey				M
Lemna turionifera Landolt		C		
Lindernia dubia (L.) Pennel		AC		M
Ludwigia grandiflora subsp. hexapetala (Hook. and Arn.) Nesom and Kartesz	MAC			
Ludwigia peploides subsp. montevidensis (Spreng.) Raven				C
Myriophyllum aquaticum (Velloso) Verdcourt		A		M
Myriophyllum heterophyllum Michaux				?
Najas graminea Delile				?
Octodiceras fontanum (Bach. Pyl) Lindb.				?
Paspalum dilatatum Poiret		MA		C
Paspalum distichum L.		MA		C
Pistia stratiotes L.				M
Pontederia cordata L.			MAC?	
Sagittaria latifolia Willd.				AC
Salvinia natans (L.) All.				MA?
Schoenoplectus prolifer Rottb.				A
Scirpus mucronatus L.			MAC	
Scirpus pungens Valh.				AC
Spartina alterniflora Loisel				A
Spartina x townsendii H.and J. Groves				A?
Spirodela oligorhiza (Kurz) Hegelm.				A
Stratiotes aloides L.				AC
Vallisneria spiralis L.			MAC	

the 567 sites investigated in France by Dutartre (2004), *Ludwigia* sp. were found in rivers with low water velocity in summer (29%), in shallow wetlands (20%), in ditches and channels (20%), in ponds and on lake shores (13%), in oxbows (9%), and in wet meadows (4%).

Many of the NIS listed have a restricted invasion range in France: for example the hybrid *S. x townsendii* along the Atlantic Coast or *S. alterniflora* in Bay of Brest (Goulletquer *et al.* 2002). Fifteen species are restricted to Atlantic sites only, 10 to the Mediterranean zone, and eight to the Continental area. Twelve species have been observed in both Atlantic and Continental areas, whereas only five taxa were listed for both Atlantic and Mediterranean areas (Table 3). Plants normally found growing in rice-fields were often limited in range to southern France, since the warm climate they need is not found further north. Invasibility potential is highest in the Atlantic area. In many cases, tropical–subtropical species thrived in Mediterranean and Atlantic areas but were absent in colder, northern France.

Numerous NIS (e.g. *A. philoxeroides, E. crassipes, P. stratiotes)* have spread worldwide, but are restricted to the Mediterranean zone in France. These species, sold in the aquarium trade, are potentially invasive (Table 3). Other species, such as *Cotula coronopifolia*, are invasive in some habitats (salt marshes, estuaries) but their low actual invasiveness allows them to be considered as potentially invasive in the Atlantic area. The number of sites at which a species occurs is a misleading indicator for degree of invasiveness. Some species, such as the non-indigenous *Lemna* sp. or water fern, which are found at a much more restricted number of sites than *Elodea* species, for example, are in fact highly invasive and spreading at those sites.

NIS MANAGEMENT IN FRANCE

Some invasive species are considered to cause ‘‘nuisance growth’’, where the degree of nuisance is judged in relation to the water body management aim (for transportation, recreation, fishery management, or conservation). The ultimate goal is to prevent the establishment of new invasive species proactively, while setting control priorities for established plants. The action plan takes into account the plants’ actual and potential impact on ecosystem functioning, as well as the indigenous species and communities present, particularly if rare and/or ecologically important species are targeted for conservation. Action is recommended only after careful analysis indicates that leaving the spreading species unchecked will result in greater damage than that caused by control efforts.

In general, the biological invasion control priority is to prevent new infestations from taking hold, especially for the fastest growing and most disruptive species. NIS that are not rapidly increasing in numbers, proliferating in undisturbed habitats, or interfering in areas recovering from disturbance have a lower priority for control. Large infestations of plants which cause considerable environmental impact, such as *Ludwigia* spp. or Hydrocharitaceae (*L. major, E. densa*) have the highest priority for control.

Each site has its own management plan based on individual characteristics. Hand-pulling has been tested to limit unwanted proliferation of *E. nuttallii* in a small stream (Di Nino *et al.* 2005). In order to fight *Ludwigia* sp., various solutions adapted to individual sites were tested: manual removal and/or treating with herbicides (Dutartre and Oyarzabal 1993, Damien 2002, Fournier and Oyarzabal 2002, Pipet 2002, Rebillard *et al.* 2002). The removal operation was manual at the beginning of *Ludwigia* sp. colonisation. When it became well-established, mechanization was necessary (Dutartre and Oyarzabal 1993, Dutartre *et al.* 1999). Although chemical treatment can replace or enhance manual removal operations, it has been used only as a last resort, where water use and environmental considerations made it possible. In some wetlands in southern France, salt water has been used to eradicate salt-sensitive *L. peploides* (Grillas 2004).

Management plans established early on were the first steps towards sustainable management of aquatic environments. However, these efforts are compromised as long as invasive aquatic plant species continue to be sold to individuals. Stronger enforcement of existing laws, coupled with an intensive public education campaign, is needed to prevent further NIS introduction.

INVASIBILITY AND INVASIVENESS

Habitat invasibility

Invasibility is an emergent property of an environment, the outcome of several factors including the region's climate, the environmental disturbance regime, and the competitiveness of the resident species (Lonsdale 1999). The actual invasion of an environment by a new species is influenced by three additional factors: the number of propagules entering the new environment, the characteristics of the new species, and the susceptibility of the environment to invasion (Lonsdale 1999).

For example, whether or not cut-off channels are connected to the main river is probably the essential parameter of colonization by *E. canadensis* and *E. nuttallii* in the Rhône River flood plain. These two species colonize new areas most often by vegetative fragments transported by water currents (Barrat-Segretain 2001). Flood disturbances can, in particular, damage or destroy some resident vegetation and allow for the introduction of *Fallopia* taxa. In some cases, restoration work or river management efforts may be considered as disturbances that facilitated NIS invasion (Schnitzler and Mulller 1998).

Fluctuation in resource availability is identified as another key factor controlling habitat invasibility (Davis *et al.* 2000). In a previous study, I established that the eutrophication process increases the invasibility of *Elodea* species while inducing competition between *Elodea* species and indigenous macrophyte species. *Elodea nuttallii* and *E. canadensis* take advantage of eutrophication because they are adapted for the quick nutrient uptake necessary for growth and can avoid turbidity by covering the water's surface (Thiébaut 2005). However, when increased levels of eutrophication induced the disappearance of submersed macrophytes as a result of phytolankton blooms and increased turbidity, they were replaced by free-floating plants such as duckweed. This type of vegetation allowed *Azolla* species to invade, particularly *A. mexicana* and *A. filiculoides. Azolla* species live in symbiosis with the nitrogen-fixing cyanobacterium *Anabaena azollae* Strass and are therefore efficient phosphorus removers in the absence of nitrate.

Life history traits of invasive plants

Many studies have focused on identifying plant traits that define invasiveness (e.g. Goodwin *et al.* 1999, Vaźquez 2005). There have been many attempts in invasion biology to predict outcomes by focusing on the traits of potential invaders and of the invaded community. Unfortunately, most of these attempts have been unsuccessful (Vásquez 2005).

Below is my review of the studies that have evaluated the relationship between the traits of some emblematic species in France and their invasion success (Barrat-Segretain *et al.* 2002, 2004, Barrat-Segretain 2004, 2005, Barrat-Segretain and Elger 2004, Dandelot 2004, Petit 2004, Thiébaut 2006). However, less is known about the invasiveness of the majority of NIS and the invasibility of aquatic habitats.

Biological attributes as key factors for invasion

Ploidy level: Invasion outcomes might be influenced by variations in clonal architecture and ecological attributes of emergent hybrids, as well as differentiated abilities for sexual reproduction. Effective hybridization is known to increase a species' invasive potential in its secondary distribution area, if the parents themselves are invasive (Bailey 2003). For example, hybridization with local *S. maritima* (Curtis) Fernald resulted in a sterile hybrid, *S. alterniflora* being the seed parent in the cross. Chromosome doubling in this hybrid gave rise to a new fertile allopolyploid species, *S. x townsendii*. This new species, genetically isolated from its parents, is very aggressive (Petit 2004). Similarly, the ploidy level of *Fallopia* taxa was studied in north-eastern France. All plants were hybrid *Fallopia x bohemica* and male fertile. The population analysed was a mixture of hexaploids, octoploids, and aneuploids. The seedlings found were octoploids, indicating the ability of octoploid plants to produce seeds (A. Schnitzler 2006, personal communication). A possible outcome of hybridization is heterosis or ''hybrid vigour''. Although dissolution of heterosis can occur in hybrid populations that retain sexual reproduction, vegetatively reproducing aquatic plants can propagate hybrid genotypes indefinitely. Molecular data demonstrate clearly that invasive water milfoil populations in North America have resulted from hybrization between NIS and indigenous species. These observations suggest that invasiveness in these aggressive NIS may be linked to heterosis maintained by vegetative propagation (Moody and Les 2002). In France, no plant morphologically intermediate between the indigenous *M. spicatum* Linnaeus and the non-indigenous *Myriophyllum heterophyllum* has been discovered yet, but the potential exists.

Reproductive biology: The reproductive biology of numerous aquatic NIS, especially in their foreign ranges, is relatively poorly understood. Levels of inbreeding and other mating-system parameters have been measured in several emergent species but are lacking for free-floating or submerged taxa. Invasion capacity may be influenced by the balance between sexual versus clonal reproduction. The relative importance of sexual versus clonal recruitment may vary among populations of clonal plants because reproduction allows populations to persist in habitats or regions where sexual reproduction cannot occur. For example, the spread of dioecious *E. canadensis* or *E. nuttallii* across Europe involved only female plants, and male and female *S. aloides* plants tend to be confined to different parts of the species' European range so that sexual reproduction is not possible in most populations.

Sexual reproduction generates genotypic diversity which may increase the adaptive evolution rate during expansion into new habitats. The seeds produced by sexual reproduction are also more likely to participate in long-distance colonization than vegetative clonal propagules which are often larger, more vulnerable to desiccation, lack dispersal and dormancy mechanisms, and therefore have less capacity for dispersal (Eckert 2002). Asexual reproduction includes both seed production without fertilization and vegetative reproduction (rhizomes, turions, tubers, and stolons). Asexual reproduction is important in the establishment, growth, and maintenance of NIS. Each aquatic species has followed a unique evolutionary path representing a complex balance between sexual and asexual reproduction, levels of genetic variation in offspring, and the ability to maximize survival. Because of the highly diverse evolutionary histories of aquatic plants, it is difficult to identify general evolutionary models.

Dispersal of propagules: Gene flow in aquatic plants may be greatly affected by the discrete and patchy nature of many aquatic habitats and the directional transport of propagules in running water. Transport of vegetative fragments may lead more frequently to successful gene establishment than seed dispersal and may, in part, explain the extensive geographical ranges of many clonal aquatic species (Barret *et al.* 1993). Semiaquatic invaders differ from many aquatic invaders in that seeds are often dispersed *via* water, whereas aquatic plants and plant fragments can be dispersed *via* flotation. In aquatic species, reproduction occurs primarily from asexually rooting plant fragments. *Ludwigia grandiflora* produces viable seeds and plantlets in the south of France (Dutartre *et al.* 1997, Dandelot 2004). Stem fragmentation is the main dispersal mode for *Ludwigia* spp., *Elodea* sp. and *E. densa*. After establishing themselves in the bank or channel bottom, prostrate stems grow laterally, rooting adventitiously at nodes. Water plants excel in this capacity with a variety of vegetative structures that are highly specialized to function efficiently as propagules, some being even capable of long-distance dispersal (Dutartre *et al.* 1997, Thiébaut *et al.* 1997, Dandelot 2004). Life history traits, regeneration (regrowth into viable plants) and colonization (establishment in the sediment) of vegetative plant fragments, and resistance to water current were compared in two invasive macrophyte species, *E. canadensis* and *E. nuttallii* (Barrat-Segretain *et al.* 2002). Both species showed similar resistance to currents, while fragment regeneration and colonization were only slightly higher in *E. nuttallii* than in *E. canadensis*.

Physiological traits as key factors for invasion

Allelopathy: NIS are considered less vulnerable than indigenous species to phytophagous animals, due to a lack of natural herbivores in their introduced range or efficient defence mechanisms. For example, *Ludwigia* spp. are consumed less by herbivores probably due to their high content of saponins and calcium oxalate (Dandelot 2004). In the same way, a slightly higher palatability was established for *E. nuttallii* than for *E. canadensis* (Barrat-Segretain *et al.* 2002, Barrat-Segretain and Elger 2004). The difference in palatability between the two *Elodea* species was also partly related to the smaller dry matter content of *E. nuttallii*. At an intraspecific level, the effect of time of year is also fully explained by the temporal variability in dry matter content for the *Elodea* species (Elger and Wilby 2005). Palatability is a multi-factorial feature of plants, resulting from chemical (e.g. nutrient content and amount of secondary compounds) and physical (e.g. toughness and hairiness) tissue characteristics. Despite these studies, there is no comprehensive view of biotic interactions occurring in fresh waters.

Competition: The success of invasive species has also been attributed to their ability to displace other species by direct competition. The formation of an *E. nuttallii* canopy which shades *E. canadensis* is a key factor in explaining the success of *E. nuttallii*, particularly under eutrophic conditions (Barrat-Segretain and Elger 2004). Later, Barrat-Segretain (2005) established that both spatial pattern and development stage of *E. canadensis* may influence the outcome of competition with *E. nuttallii*. The coexistence of the two *Elodea* species is enhanced by river disturbances (Barrat-Segretain 2001), whereas *E. nuttallii* dominates in less-disturbed waters as a result of its higher growth rate.

Phenotypic plasticity: NIS have been shown to modify resource allocation through changes in their morphology and physiology. Plant plasticity when facing fluctuating resources is one characteristic that contributes to competitiveness and invasibility. By changing leaf area, *E. nuttallii* individuals can maximize growth and reproduction under a variety of environmental conditions (F. Di Nino 2006, unpublished data). Phenotypic plasticity may play a key role in the adaptation of organisms to changing environmental conditions. This trait is especially important for aquatic plant species which often spread asexually and thus lack genetic variation.

A broad ecological tolerance: Wide ecological amplitude seems necessary because any changes in the water potentially influence all plants in contact with it; for example, *Ludwigia* sp. has rather good resistance to frost in Europe. The growth of *E. canadensis* is affected by reduced light intensity, contrary to that of *E. nuttallii*. Increasing water phosphate levels increased the growth rate of *E. nuttallii* (Barrat-Segretain 2004). *Elodea nuttallii* and *E. canadensis* have wide amplitude in nutrient levels (Dendène *et al.* 1993, Robach *et al.* 1995, Rolland *et al.* 1999, Thiébaut and Muller 2003, Thiébaut 2005). Adaptation to dynamic water conditions is apparent in widespread aquatic species such as *Lemna aequinoctialis* and *L. turionifera* which can tolerate extreme ranges in pH from 3.2 to more than 9.0 (Landolt 1986).

CONCLUDING REMARKS

This review shows that a total of 58 plant species has been introduced into aquatic environments in France over the last three centuries. Most NIS arrived in France through human intervention (aquarium or ornamental plant use). Plant distribution varies according to the different climates in three biogeographical zones.

Despite several recent contributions concerning biology and ecology in the rapidly developing field of invasion biology, less is known about the invasiveness characteristics of aquatic or semiaquatic species and the specific features associated with habitat invasibility. This synthesis highlights the gaps in our understanding and contributes to identifying areas for further research which should be encouraged in order to prevent biological invasions of aquatic and semiaquatic species in France, other parts of Europe, and the world.

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