Biological Invasions (2007) 9:1–12
DOI 10.1007/s10530-006-9000-1

# Invasion success of non-indigenous aquatic and semi-aquatic plants in their native and introduced ranges. A comparison between their invasiveness in North America and in France

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Received 22 June 2005; accepted in revised form 8 February 2006

*Key words:* biological traits..., France, invasive plants, North America

## Abstract

Aquatic and semi-aquatic plants comprise few species worldwide, yet the introduction of non-indigenous plants represents one of the most severe examples of biological invasions. My goal is to compare the distribution and the biology of aquatic and semi-aquatic plants in their introduced ranges and in their native ranges. The primary objective of this study is to test the hypothesis that invasive species have evolved traits likely to increase their success in the new range. I made two reciprocal comparisons, i.e. I compared European species in France and in North America, and North American species in France and in North America. Twenty-seven species were classified according to their invasiveness in their introduced area. I found six invasive macrophyte species in France native to North America and 17 invasive species in North America native to Europe. Four species are invasive in both areas. There is no general tendency for macrophytes to be more vigorous in their introduced ranges. Most non-indigenous aquatic and semi-aquatic species are potentially invasive or widespread and well-established in their introduced country, while few species seem to be restricted in their distribution.

## Introduction

Invasion biology has received considerable attention during the last decades (Crawley 1987; Lodge 1993; Williamson 1996; Lonsdale 1999). Most botanical studies have attempted to identify traits that confer invasiveness to plants. There are a number of predictions that can be made as to which attributes are likely to confer success for invasive species. Sutherland (2004) compared ten life history traits to determine if there were significant life history traits that distinguish weed species from non-weeds, non-indigenous plants from native weeds, and invasive non-indigenous plants from non-invasive non-indigenous weeds in the USA. A major challenge for invasive plant research is to develop the ability to predict the invasiveness of species and the invasibility of habitats (Kareiva 1996). The critical questions for invasive plant research are: what attributes make invasive species successful? Why do only some introduced species become invasive and does the type or severity of disturbance affect the invasiveness of species? What makes a community or ecosystem invasible?

Much attention has been directed to the threats posed by invasive species to: biodiversity, ecosystem integrity, and human health. Hybridisation can increase genetic variation, and can lead to transgressive phenotypes that may be more suitable and fit to live in a transformed environment. Two main factors have been invoked to underlay the invasive success of a species, i.e. (1) ecological processes such as new environments (human-altered or natural, e.g. disturbances, nutrient regime, community structure) or the release from biotic constraints (specialized natural enemies, competitive superior neighbours, pathogens), and (2) evolutionary processes such as post-invasion evolution of increased competitive ability due to altered selection in the new range (EICA hypothesis, Blossey and Nötzold 1995). However, there is a lack of knowledge concerning the patterns followed by all types of biological invaders. This gap of knowledge is greater for macrophytes than for many other groups.

The present distribution of aquatic and semi-aquatic non-indigenous plants, at the continental or at the worldwide scales, is primarily the result of human activities. Carpenter and Lodge (1986) reviewed the effects of submersed macrophytes on the physical environment (light extinction, temperature, hydrodynamics, substrate), chemical environment (oxygen, inorganic and organic carbon, nutrients), and the biota (epiphytes, grazers, detritivores, fishes). In North America, macrophyte species, both native and non-indigenous, may have parallel distributions. The invasion of non-native species has occurred since the mid-eighteenth century as a result of the migration and settlement of European people on the North American continent. In Canada and in the north-eastern United States, the percentage of non-indigenous species ranges from 20 to 30%. In the United States, those states in the northeast that have been occupied the longest by European colonists have percentages near or over 30%, the highest percentage known being 36% from the state of New York. A range of 20–30% is found in those mid-western states that most extensively are involved in agriculture, while more northern and western states have values below 20%. These differences reflect the history of migration and settlement of the European people as they moved westward across the North American continent, and of the agricultural, industrial, and recreational practices that have been developed since then (Flora of North America 1993; Stuckey 1993).

While much is known about the problems caused by the flux of European plants into North America, less attention has been paid to the American species that have been introduced into Europe over the same time period. In fact, more than 6000 species from North, Central and South America have been introduced into Europe over the past 400 years. Many of these species are now naturalized, the ornamental and terrestrial species being the majority.

My goal here is to re-examine the EICA hypothesis that there is a tendency for introduced aquatic and semi-aquatic plant species to be more vigorous in their introduced than in their native ranges. I made two reciprocal comparisons, i.e. I compared the European species in France and in North America, and North American species in France and in North America.

## Material and methods

I assembled a list of invasive (as defined by Pysek et al. 2004) aquatic and semi-aquatic plants either in North America or in France. These species are arranged in three categories: (1) native to North America and introduced into France, (2) native to Europe and introduced into North America, (3) native to South America and introduced into France and North America (Table 1). We found a total of 27 species distributed in both France and North America.

The introduced plants were only aquatic species (with two forms, one aquatic and one terrestrial) in France, whereas in North America helophyte species were also introduced. Aquatic species with two forms coming from South America were introduced into both North America and France (Table 1). There was a detectable but inconsistent tendency for species that invade areas to come from particular families (e.g. Hydrocharitaceae, Lemnaceae, Azollaceae) in France. At the genus level, in France there was usually a tendency for area invaders to come from taxa that were not represented in the native flora (e.g. *Elodea*). The genus *Azolla* is probably the only genus of introduced floating ferns found in France, whereas the fern *Marsilea quadrifolia* was introduced into North America. *Trapa* is the only genus that is exclusively non-indigenous to North America. Two genera (*Myriophyllum, Potamogeton*) have problematic taxa comprising

*Table 1.* List of invasive and aquatic plants in France and in North America.

| | | Code | Family | USA | First found in USA | First found in Canada | France | First found in France |
|---|---|---|---|---|---|---|---|---|
| Group I | *A. caroliniana Willd.* | *Acar* | Azollaceae | N | | | E | no data |
| | *Azolla filiculoides Lam.* | *Afil* | Azollaceae | N | | | E | 1880 (Deux-Sèvres) |
| | *E. nuttallii* (Planchon) H. St. John | *Enut* | Hydrocharitaceae | N | | | E | 1959 (Alsace) |
| | *E. canadensis* Michaux | *Ecan* | Hydrocharitaceae | N | | | E | 1845 |
| | *L. minuta* H.B.K. | *Lminu* | Lemnacaeae | N | | | E | 1965 (Pyrénées-Atlantiques) |
| | *Lemna turionifera Landolt* | *Ltur* | Lemnacaeae | N | | | E | 1992 (Alsace, Lorraine) |
| Group II | *A. calamus* L. | *Acal* | Aracae | E | 1600 | | N | |
| | *Butomus umbellatus* L. | *Bumb* | Butomaceae | E | | 1905 (St, Lawrence R, QUE) | N | |
| | *C. stagnalis* Scop. | *Csta* | Callitichaceae | E | 1861 (New York) | | N | |
| | *G. maxima* (Hartman) Holmberg | *Gmax* | Poaceae | E | 1975 (Wisconsin), | 1956 (Ontario) | N | |
| | *H. morus-ranae* L. | *Hmor* | Hydrocharitaceae | E | | 1932 (Ontario) | N | |
| | *I. pseudacorus* L. | *Ipseu* | Iridaceae | E | < 1980 (Washington, DC); | 1961 (colombie britannique) | N | |
| | *M. quadrifolia* | *Mqua* | Marsilaceae | E | 1860 (Bantam Lake, CT) | | N | |
| | *M. spicatum* L. | *Mspi* | Haloragaceae | E | 1942 (Washington, DC) | 1960 (Ontario) | N | |
| | *Myosotis scorpioïdes* L. | *Msco* | Boraginaceae | E | | | N | |
| | *Nasturtium officinale* R.Brown | *Noff* | Brassicaceae | E | < 1826 | | N | |
| | *Najas minor All.* | *Nmin* | Najadaceae | E | 1934 (Hudson river) | | N | |
| | *N. peltata* O. Kuntze | *Npel* | Menyanthaceae | E | 1882 (Winchester, MA) | ? (Rideau river) | N | |
| | *P. arundinacea* L. | *Paru* | Poaceae | E | | 1800 | N | |
| | *P. crispus* L. | *Pcri* | Potamogetonaceae | E | 1859 (Wilmington, DE) | < 1956 (Ontario) | N | |
| | *R. amphibia* (L.) Besser | *Ramp* | Brassicaceae | E | 1831 | | N | |
| | *T. natans* L. | *Tnat* | Trapaceae | E | < 1879 (Middlessex Co, MA) | | N | |
| | *Veronica beccabunga* L. | *Vbec* | Scrophulariaceae | E | 1876 (Hudson Co, NJ) | | N | |
| Group III | *E. densa*[a] Planchon | *Eden* | Hydrocharitaceae | E | 1893 (Long Island, NY); | | E | 1961 (Manche) |
| | *L. peploides*[a] (Kunth) P.H. Raven | *Lpep* | Onagraceae | E | | | E | 1820–1830 (Montpellier) |
| | *L. hexapetala*[a] (Hook and Arn) E.M. Zardini, H.Y.Gu et P.H. Raven | *Lhex* | Onagraceae | E | | | E | 1820–1830 (Montpellier) |
| | *M. aquaticum*[a] (Velloso) Verdcourt | *Maqu* | Haloragaceae | E | 1890 (Haddonfield, NJ) | | E | 1880 (Bordeaux) |

[a] Native from South America.

Q: questionable origin: considered by some to be native, but probably exotic and naturalized in the US.

N = native.

E = exotic.

*Table 2.* Species traits and modalities of aquatic macrophytes used for for aquatic plants.

| No. | Species traits | No. | Modality |
|---|---|---|---|
| 1 | Size | 1 | ≤ 20 cm |
| | | 2 | 20–50 cm |
| | | 3 | 50–70 cm |
| | | 4 | 70–150 cm |
| | | 5 | 150–250 cm |
| | | 6 | > 250 cm |
| 2 | Leaf length | 1 | ≤ 1 cm |
| | | 2 | 1–3 cm |
| | | 3 | 3–5 cm |
| | | 4 | 5–20 cm |
| | | 5 | 20–80 cm |
| | | 6 | > 80 cm |
| 3 | Leaf width | 1 | ≤ 2 mm |
| | | 2 | 2–4 mm |
| | | 3 | 4–12 mm |
| | | 4 | 12–20 mm |
| | | 5 | 20–40 mm |
| | | 6 | > 40 mm |
| 4 | Flower width | 1 | ≤ 3 mm |
| | | 2 | 3–10 mm |
| | | 3 | > 10 mm |
| 5 | Propagation | 1 | fragmentation |
| | | 2 | rhizomes |
| | | 3 | stolons |
| | | 4 | winterbuds |
| | | 5 | seeds |
| | | 6 | other |
| 6 | dissemination | 1 | hydrochory |
| | | 2 | zoochory |
| | | 3 | anemochory |
| | | 4 | anthropochory |
| 7 | Biological type | 1 | hydrophyte |
| | | 2 | helophyte |
| | | 3 | amphiphyte |
| 8 | Growth form | 1 | free |
| | | 2 | anchored |
| | | 3 | floating leaves |
| | | 4 | support tissue |
| | | 5 | submersed |

both native and non-indigenous species in North America, whereas the genus *Potamogeton* comprises only indigenous species in Europe.

To define the status of a plant species in France and in North America, we indicated whether the taxon is native or non-indigenous to that region (origin status, Table 1).

## *Species traits*

Traits of each species were documented almost entirely on the basis of information from the existing literature (in particular: Flora of North America 1993; Aboucaya 1999; Muller et al. 2004). More than 50 references were used. For poorly documented species in France, we used data collected by myself, particularly for morphological characteristics. Available information on traits varied considerably among the different species. This information gathered from a very large and scattered bibliography was reduced to eight species traits (=variables). For each of these traits, the different modalities (=categories) of the 27 species were considered in France and in North America.

The eight selected traits are: trait 1 'maximal size' (=stem length); 2: leaf length, 3: leaf width; 4: flower width; 5: propagation type (seeds, stolons, rhizome, tubers, winterbuds...), 6: dissemination technique (anemochory, hydrochory, zoochory, anthropochory); 7: biological type (hydrophyte, helophyte, amphiphyte); 8: growth form (free-floating leaves, floating leaves, support tissue, submersed). For each species, the sources generally listed a range of normal lengths, occasionally with in-parentheses value for an especially large or small individual. We used the upper limit of the normal range, as did Crawley (1987) and Thebaud and Simberloff (2001). The eight traits were reached in France and in North America (Tables 2–4).

## *Data analysis*

The information was structured using 'fuzzy coding' (see Bornette et al. 1994; Chevenet et al. 1994; Usseglio-Polatera 1994) in the following way: 0, the species had no link with a modality; 1, the species had a link with the modality. This technique of fuzzy coding helped to compensate for different types and levels of information available for different species (Chevenet et al. 1994). The modalities (=categories) of these eight traits have been adapted to a range appropriate for plants defining the contents of each variable (Tables 2–4). For traits that exhibited a gradient, modality 1 is the lowest. The species traits are scored all in one sense from the less to the better adaptive (e.g. the modality 1 was attributed to hydrophytes).

The two previous matrices (species × traits in Europe and species × traits in North America)

*Table 3.* Species traits and modalities of aquatic plants used in this analysis in North America.

| North America | *Modality* | Size | | | | | | Leaf length | | | | | | Leaf width | | | | | | Flower width | | | Propagation | | | | | | Dissemination | | | | Biological type | | | Growth form | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 1 | 2 | 3 | 4 | 5 |
| *A. calamus* | Acal | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *A. caroliniana* | Acar | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *A. filiculoïdes* | Afil | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *B. umbellatus* | Bumb | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *C. stagnalis* | Csta | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *E. densa* | Eden | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *E. nuttallii* | Enut | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *E. canadensis* | Ecan | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *G. maxima* | Gmax | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *H. morsus-ranae* | Hmor | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *I. pseudacorus* | Ipseu | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *L. minuta* | Lminu | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *L. turionifera* | Ltur | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *L. hexapetala* | Lgra | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *L. peploides* | Lpep | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. quadrifolia* | Mqua | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *M. scorpioïdes* | Msco | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. aquaticum* | Maqu | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. spicatum* | Mspi | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *N. minor* | Nmin | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *N. officinale* | Noff | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *N. peltata* | Npel | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *P. arundinacea* | Paru | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *P. crispus* | Pcri | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *R. amphibia* | Ramp | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| *T. natans* | Tnat | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *V. beccabunga* | Vbec | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |

See Table 2 for modalities.

were analysed using the methods described by Chevenet et al. (1994). Multiple Correspondence Analysis 'MCA analysis' (i.e the simultaneous ordination of both matrices) was used to check for a relationship between species traits in Europe and in North America.

## Results

Species traits that are best explained by successive factorial axes can be identified using correlation ratios (Figure 1). The F1 axis is mainly (cf. correlation ratios with axis F1) related to maximal size (variable 1), leaf length and width (variables 2 and 3), biological type (variable 7), and growth form of the plant (variable 8). Positive values on the F1 axis are related to small and non-anchored hydrophytes. The F2 axis is mainly related to leaf length (variable 2) and biological type (variable 7).

Eigenvalues denote the importance of the first axis in explaining the variability of total inertia (17%) in the correspondence analysis of the fuzzy codes species traits (Figures 1–3). The axis F2 explained 11.6% of the variability of the first axis. The first two axes explain only 30% of the total variation.

No significant difference was found between traits in introduced and in natives ranges when all non-indigenous species traits were considered; in fact, group 1 is close to group 2 (Figure 2). On the contrary, there was a significant difference when the data were independently analyzed for traits (Figure 3). The first two axes separate three groups of species on the basis of their traits

*Table 4*. Species traits and modalities of aquatic plants used in this analysis in France.

| North America | *Modality* | Size | | | | | | Leaf length | | | | | | Leaf width | | | | | | Flower width | | | Propagation | | | | | | Dissemination | | | | Biological Type | | | Growth form | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 1 | 2 | 3 | 4 | 5 |
| *A. calamus* | Acal | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *A. caroliniana* | Acar | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *A. filiculoïdes* | Afil | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *B. umbellatus* | Bumb | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *C. stagnalis* | Csta | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *E. densa* | Eden | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *E. nuttallii* | Enut | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *E. canadensis* | Ecan | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *G. maxima* | Gmax | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *H. morsus-ranae* | Hmor | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *I. pseudacorus* | Ipseu | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *L. minuta* | Lminu | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *L. turionifera* | Ltur | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *L. hexapetala* | Lgra | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *L. peploides* | Lpep | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. quadrifolia* | Mqua | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *M. scorpioïdes* | Msco | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. aquaticum* | Maqu | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *M. spicatum* | Mspi | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *N. minor* | Nmin | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *N. officinale* | Noff | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| *N. peltata* | Npel | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| *P. arundinacea* | Paru | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| *P. crispus* | Pcri | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *R. amphibia* | Ramp | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 |
| *T. natans* | Tnat | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| *V. beccabunga* | Vbec | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |

See Table 2 for modalities.

in North America and in France (Figure 3). Group A consists of non-anchored plants such as *Lemna minuta* H.B.K. Most of these species are small and have floating leaves. No difference in biological traits was observed between native and introduced ranges. Group B is mainly composed of plastic species which show differences in both their introduced and native ranges. This group includes helophyte species (e.g. *Phalaris arundinacea* L.) on the lower left side and amphiphytes (i.e *Myriophyllum aquaticum* (Velloso) Verdcourt) on the upper left side. Group C comprises mainly submersed anchored macrophytes such as *Potamogeton cripus* L. One can distinguish species which differed significantly in North America and in France (e.g. *Trapa natans* L.) and species which are similar in the two areas, such as *Elodea canadensis* Michaux in group C.

The 27 species were classified according to their invasiveness in their introduced area (Table 5). Originally from South America, the submersed hydrophytes *Egeria densa* Planchon, *Ludwigia peploides* (Kunth) P.H. Raven, and *Ludwigia hexapetala* (Hook and Arn) E.M.Zardini, H.Y.Gu and P.H. Raven were found in North America and in France. These species are invasive in both areas. *T. natans* is considered as a noxious aquatic weed in North America, whereas it is extirpated or endangered in much of Europe. However, the distribution of the species can be similar in the native and in the introduced ranges: e.g. *Myriophyllum spicatum* L. is a widespread invasive species in North America and a spreading native aquatic macrophyte in Europe. Most non-indigenous aquatic species are potentially invasive or widespread and well-established in their introduced

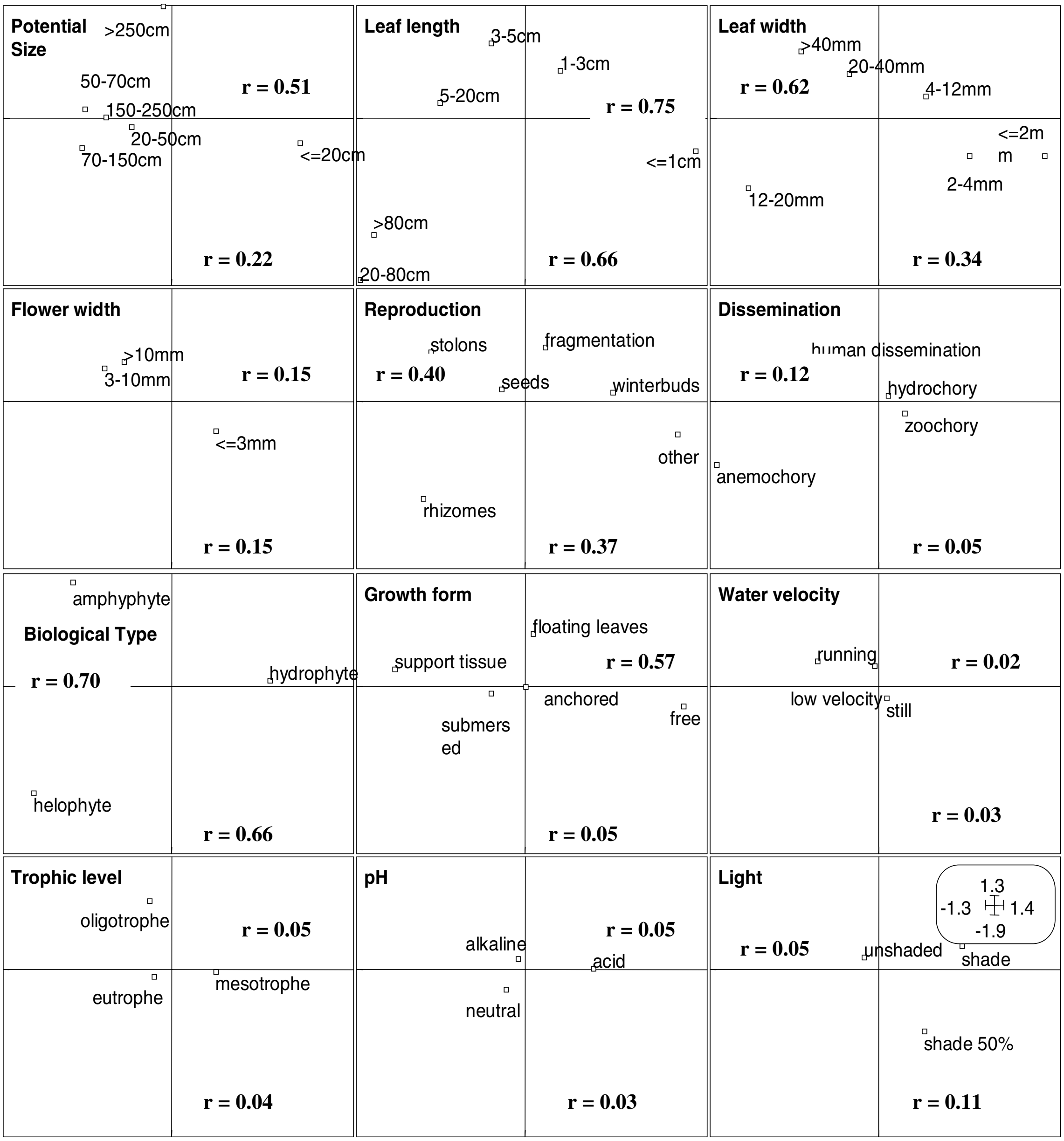

*Figure 1.* MCA analysis for traits of species in North America and in France. Ordination of species traits on the F1 × F2 factorial planes by MCA analysis. The distribution of modalities is indicated by small squares. Each modality is positioned at the weighted average of species representing that modality. Correlation ratios for each species traits are indicated on the axes.

country, but others are known only from a few occurrences (*Azolla caroliniana Willd., Callitriche stagnalis* Scop., *Glyceria maxima* (Hartman) Holmberg, *Hydrocharis morsus-ranae* L., *Iris pseudacorus* L., *M. quadrifolia, Nymphoides peltata* O. Kuntze, *Rorippa amphibia* (L.) Besser). Some species may not be viewed as particularly threatening in some areas; however they can cause serious problems elsewhere. In all cases where they are hardy, such species should be viewed as potentially invasive: e.g. *G. maxima* and *R. amphibia*, widespread in Canada and restricted in USA.

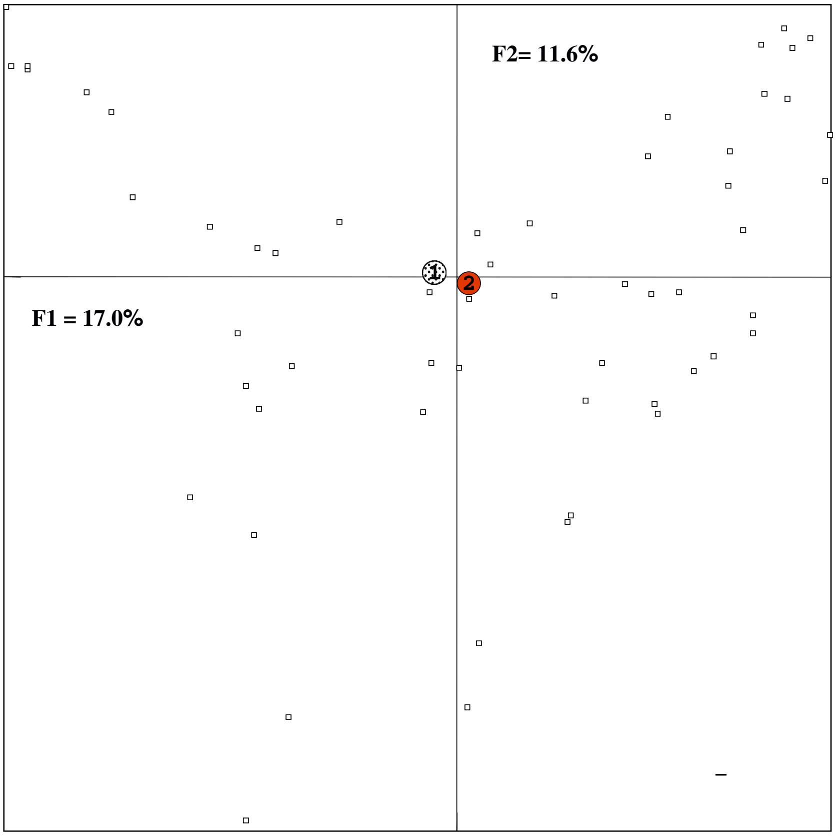

*Figure 2.* MCA analysis for species in North America (number 1 in circle) and in France (number 2 in circle) on the F1 × F2 plane. Small squares represent the species. Each circle is positioned at the weighted average of species found in each geographical area.

## Discussion

### *The characters of successful invaders*

Although this study showed that the invasiveness of non-indigenous species are related to biological traits, there is no general tendency for species to be different in their introduced ranges.

The mode of propagation may influence the spread of invasive species by affecting evolutionary potential and dispersal ability. Many aquatic species (e.g. *Elodea* spp., *E. densa*, *Myriophyllum* spp.) and several other plants used in aquaria can multiply by fragmentation – vegetative buds or cuttings – which is an efficient way of dispersing into new areas, especially for submerged or floating plants, on the condition that they can survive the winters. In several cases, introduced plants are seldom flowering (e.g. *Elodea nuttallii* (Planchon) H. St. John) or dioecious plants miss one sex as introduced (e.g. *E. canadensis, Acorus calamus* L.) or are sterile triploids. Many of the non-indigenous species have tubers or rhizomes (e.g. *P. crispus* L.) or suckers which help them re-juvenate, thus getting an advantage over other species by having an early start in growth. Many, but not all, non-indigenous species persist as competitive species according to the definition of Grime (2001). The majority of non-indigenous species share some or all the following characteristics: short life cycle, rapid growth rate, high level of energy allocated to reproduction, efficient dispersal mechanisms, high population growth rate, wide distribution, a high phenotypic plasticity, and flexible use of environmental resources. Probably a C–R strategy seems to be more

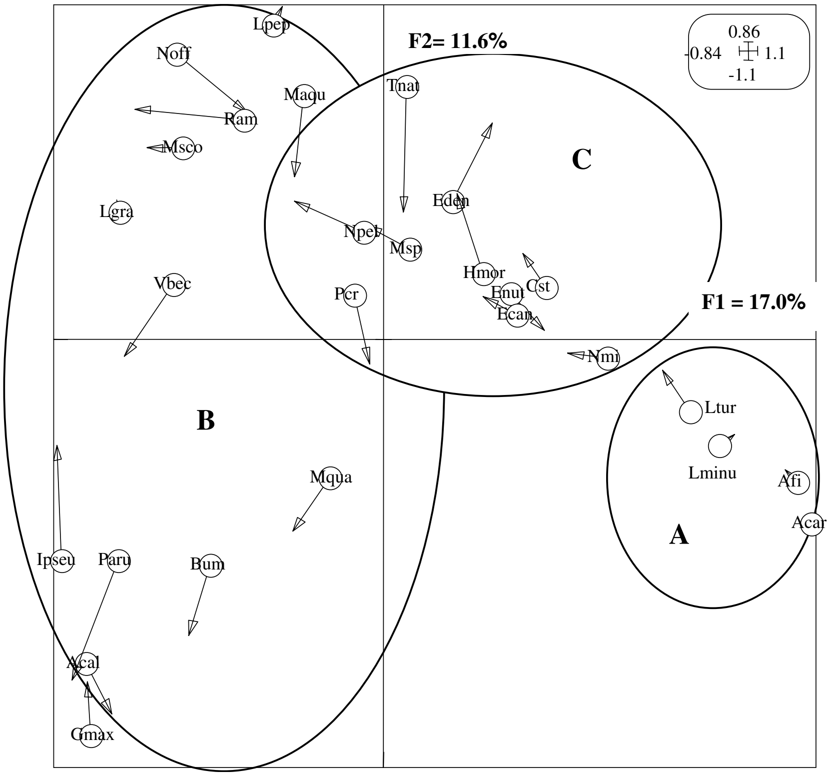

*Figure 3.* Comparison of species position on the two F1 × F2 planes by MCA analysis. Each species is defined by an arrow and a code (see Table 1 for species code and text for grouping A–C). Arrows in the circle mark the position of the species in North America (end) and its position in France (point).

adequate to describe the ecological strategy of a spreading aquatic macrophyte, as it was established for the native aquatic species *Ranunculus peltatus* Schrank. According to its morphological characteristics, *R. peltatus* tended indeed to adopt a K-strategy in nutrient-rich undisturbed sites and an *r*-strategy in disturbed sites (Garbey et al. 2004).

By knowing the general life history traits of native and non-indigenous plants, we may better understand the significance of species-specific deviation from this norm. This could lead to a better understanding of the traits that determine which species will be invasive, how invasive will these species be, which habitats they might invade, and how the species can be controlled (Sutherland 2004). Current studies on the ecological requirements (e.g. light, water velocity, water trophic level) of aquatic macrophytes will provide further elements necessary to generate a model. Fulfilment of these objectives should be the first step towards the creation of a general model based on assembly or response rules.

### *Invasiveness and invasibility*

Most of the 27 non-indigenous species found in freshwater habitats are widespread. However, some species are widespread in some area and restricted in others; for instance, *A. calamus* L. spread throughout northeast and central United States, while scattered populations occur elsewhere. The invasiveness of a species depends also on the number of occurrences and on the habitat invasibility. Stress could also affect invasibility. At least three types of environmental stress have been hypothesized to affect invasibility: low resource availability (Thiébaut 2005), presence of toxins, and extremes of temperature that limit metabolism or resource acquisition. In many

*Table 5.* Non-indigenous plants classification according to their invasiveness in North America and in France.

| | | | Invasive restricted | Potentially invasive | Widespread & invasive |
|---|---|---|---|---|---|
| Group I | *A. caroliniana Willd.* | Acar | x | | |
| | *A. filiculoïdes Lam.* | Afil | | x | |
| | *E. nuttallii* (Planchon) H. St. John | Enut | | | x |
| | *E. canadensis* Michaux | Ecan | | | x |
| | *L. minuta* H.B.K. | Lminu | | | x |
| | *L. turionifera Landolt* | Ltur | | x | |
| Group II | *A. calamus* L. | Acal | x (USA) | | x (NE, Central USA)) |
| | *B. umbellatus* L. | Bumb | | x (Connecticut) | x (Eastern region USA, Canada) |
| | *C. stagnalis* Scop. | Csta | x (Canada, USA) | x (Connecticut) | |
| | *G. maxima* (Hartman) Holmberg | Gmax | x (Eastern region USA) | | |
| | *H. morus-ranae* L. | Hmor | x (Eastern region USA) | | x (Canada) |
| | *I. pseudacorus* L. | Ipseu | x | | |
| | *M. quadrifolia* | Mqua | x (Eastern region USA) | x (Connecticut) | |
| | *M. spicatum* L. | Mspi | | | x |
| | *M. scorpioïdes* L. | Msco | | x (Connecticut) | x (Canada) |
| | *N. officinale* R.Brown | Noff | | x (Eastern region USA) | x |
| | *N. minor All.* | Nmin | | x (Eastern region USA) | |
| | *N. peltata* O. Kuntze | Npel | x | x (Eastern region USA) | |
| | *P. arundinacea* L. | Paru | | x | |
| | *P. crispus* L. | Pcri | | x | |
| | *R. amphibia* (L.) Besser | Ramp | x (Eastern region USA) | | x (Canada) |
| | *T. natans* L. | Tnat | | x | x (Eastern region USA) |
| | *V. beccabunga* L. | Vbec | | x | |
| Group III | *E. densa*[a] Planchon | Eden | x (Connecticut)) | x (Eastern region USA, France) | |
| | *L. peploides*[a] (Kunth) P.H. Raven | Lpep | | | x (France) |
| | *L. hexapetala*[a] (Hook And Arn) E.M. Zardini, H.Y. Gu et P.H. Raven | Lhex | | x (France) | |
| | *M. aquaticum*[a] (Velloso) Verdcourt | Maqu | x (Eastern region USA) | x (Connecticut) | x (France) |

[a] Native from South America.

cases, the colder climate in the north is the reason that non-indigenous tropical–subtropical species have not survived (e.g. *M. aquaticum* is widespread in the southern United States and in the south of France but scattered in the northeast of USA). However, alternative survival strategies (e.g. viability of seeds not affected by ice) may apply depending on the climate (Wallentinus 2002).

A number of alternative explanations has been invoked to account for the high proportion of widely distributed taxa among the aquatic plants. They include:

(1) Uniformity of the aquatic environment (Sculthorpe 1967), which is assumed to result in the broad dominance of best-fitted, single-purpose genotypes;

(2) High phenotypic plasticity, a result of general purpose genotypes (Barret et al. 1993). North America is being colonized by two distinct forms of *B. umbellatus* that differ strongly in they reproductive strategy as well as the vectors and pathways of invasion (Lui et al. 2005).

(3) Widespread clonality, which can contribute to the broad distribution of aquatic plants by reducing both the risk of genotype mortality and the genetic differentiation of spatially, separated populations (Barrett et al. 1993). Genetic evidence suggests that polyploids have become widespread and are more aggressive than diploids or triploids.

*Management applications*

Invasive plants have been found to exert worldwide a negative impact on ecosystem structure and function by reducing native species richness. North American plant managers reported most problems for *M. spicatum* and *P. crispus*. Because these species do not show the general tendency to be taller in their introduced than in their native ranges, doubts are raised on the efficacy of the biological control strategy of introducing sequences of phytophages. None of them delivers a knockout blow to a weed against the expectation that each successive phytophage will force the plant to devote more resources to defence and fewer to traits such as an increased size that make it more competitive (Thebaud and Simberloff 2001).

Müller-Schärer et al. (2004) argued that evolutionary changes during invasion will also affect plant–antagonist interactions, thereby having important implications for biological control programs targeted to invasive plants. *M. spicatum* has been shown to develop polyphenols, which retard the growth of some harmful cyanobacteria by inactivating some of their extracellular enzymes, for instance. However, its efficacy in practice should be verified.

Getting rid of one weed, however, may not solve the problem, since often it can be replaced by other introduced weeds. There are examples in France that a second introduced species has successfully competed with a previous weed. *E. nuttallii* and *E. densa* replaced *E. canadensis* in some parts of France (Thiébaut et al. 1997; Barrat-Segretain 2001) and in southern Europe (Wallentinus 2002), respectively. This seems to be an even more common phenomenon in other continents, where series of introductions have followed each other with different dominant species. Further studies are obviously required to predict the habitat invasibility and the invasiveness of aquatic and semi-aquatic species.

## Acknowledgements

Jean-Nicolas Beisel (LBFE, University of Metz) is gratefully acknowledged for helpful assistance in statistical analysis. I thank two anonymous referees for their constructive comments on a early draft of this manuscript.

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