

Range Extensions of Aquatic Vascular Plant Species¹

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ABSTRACT

The worldwide distribution of 198 aquatic vascular plant species is reviewed. Twenty six species are widespread or disjunct, but the native and alien areas are unknown or disputed. The remaining 172 species are presented in a table indicating the native and introduced range of each. The means of dispersal are discussed. It is noted that relatively few introduced plants have become "fully integrated" into the flora of their new area and that many have become weeds. It is concluded that the establishment of an introduced plant is more dependant on the nature of man's disturbance of the environment than on the mobility of the plant itself.

Key words: phytogeography, migration, distribution, weeds, native, exotic.

INTRODUCTION

It is widely believed that the uniformity of the aquatic environment allows aquatic plant species to occupy very large ranges. In an analysis of the aquatic plants endemic to Europe and the Mediterranean (Cook, 1983), it was indeed found that few species occupied very small ranges; examples being *Isoetes heldreichii* and *Oenanthe lisae*, most other taxa with restricted local distribution were found to be taxonomically disputed or recognized at ranks below the level of species. In contrast to most aquatics, the Podostemaceae (ca. 46 genera, ca. 260 species), could be considered habitat specialists, they are confined to rapids and waterfalls. In spite of being pantropical, most species in this family are local endemics, often confined to a single cataract. Perhaps the statement about uniformity of the habitat has some truth when considering the distribution of aquatics.

It is not disputed that many aquatics occupy large ranges and also that many of them have recently extended their range and become serious pests in newly occupied regions. The documentation on the range and spread of aquatics is, with few exceptions, unsatisfactory. The purpose of this paper is to present information on the migration of as many aquatic plant species as possible.

MATERIAL AND METHODS

Aquatics are defined in this work as vascular plants that grow (photosynthesize) under water for at least part of their life history, or are bound to the air-water interface.

For this evaluation the world is divided into 16 regions (Figure 1). These regions represent reasonably distinct phytogeographic elements. The numerals chosen are taken

from the system used at the Royal Botanic Gardens, Kew, UK, and are thus compatible with the numbers used in the Kew Record of Taxonomic Literature and the Kew Current Awareness Lists. The subdivisions, indicated by letters, are my own system.

The distributional data has been collected over the years, mostly from literature, but some from herbarium studies. A provisional list was circulated in the Newsletter of the International Association of Aquatic Vascular Plant Biologist (No. 15 pages 13-18, September 1983). From comments received, this list has been enlarged and improved. The following symbols are used: "1", for introduced-only those plants that have become established outside cultivation are included; "2", for native; "3", for native and introduced within the same area-for example, *Stratiotes aloides* is native in Central Europe, but introduced and established in Western Europe; "4", denotes that the plant is present but questionably native; "5", denotes that the plant is present but questionably introduced; "6", denotes a doubtful record-its occurrence is not certain.

RESULTS

It is surprisingly difficult to get recent and accurate distributional information on aquatics and even more difficult to discover where a particular species is native or introduced. The plant list in Table 1 contains species that are widely distributed or show disjunctions in their distribution. They are unlikely to be native throughout their range, but it is not possible today to determine where they are native and where they are introduced.

The extensive list in Table 2 gives the known range extensions of aquatic vascular plants. The geographical codes in Table 2 are located on Figure 1.

MEANS OF TRANSPORT

Aquatic plants tend to lack very light wind-carried diaspores and also large seawater resistant ones like the coconut, and are thus ill-equipped for long-distance dispersal. The plants of unknown native status listed in Table 1 have probably spread more or less naturally or, at least, before botanists were keeping records. The majority of aquatics have become mobile as man has become mobile.

Rice, the most important cereal worldwide, is an aquatic plant. The cultivation of rice and the transportation of its seed, particularly when poorly cleaned, is responsible for the spread of a great number of aquatic plant species. However, it is often forgotten how old world-wide communications are, for example, there was a regular galleon route between Acapulco (Mexico) and Manila (Philippines) by 1570 which was responsible for the transport of many plant species across the Pacific (Merrill, 1954). Rice was being cultivated in northern Italy by 1475 with seed being im-

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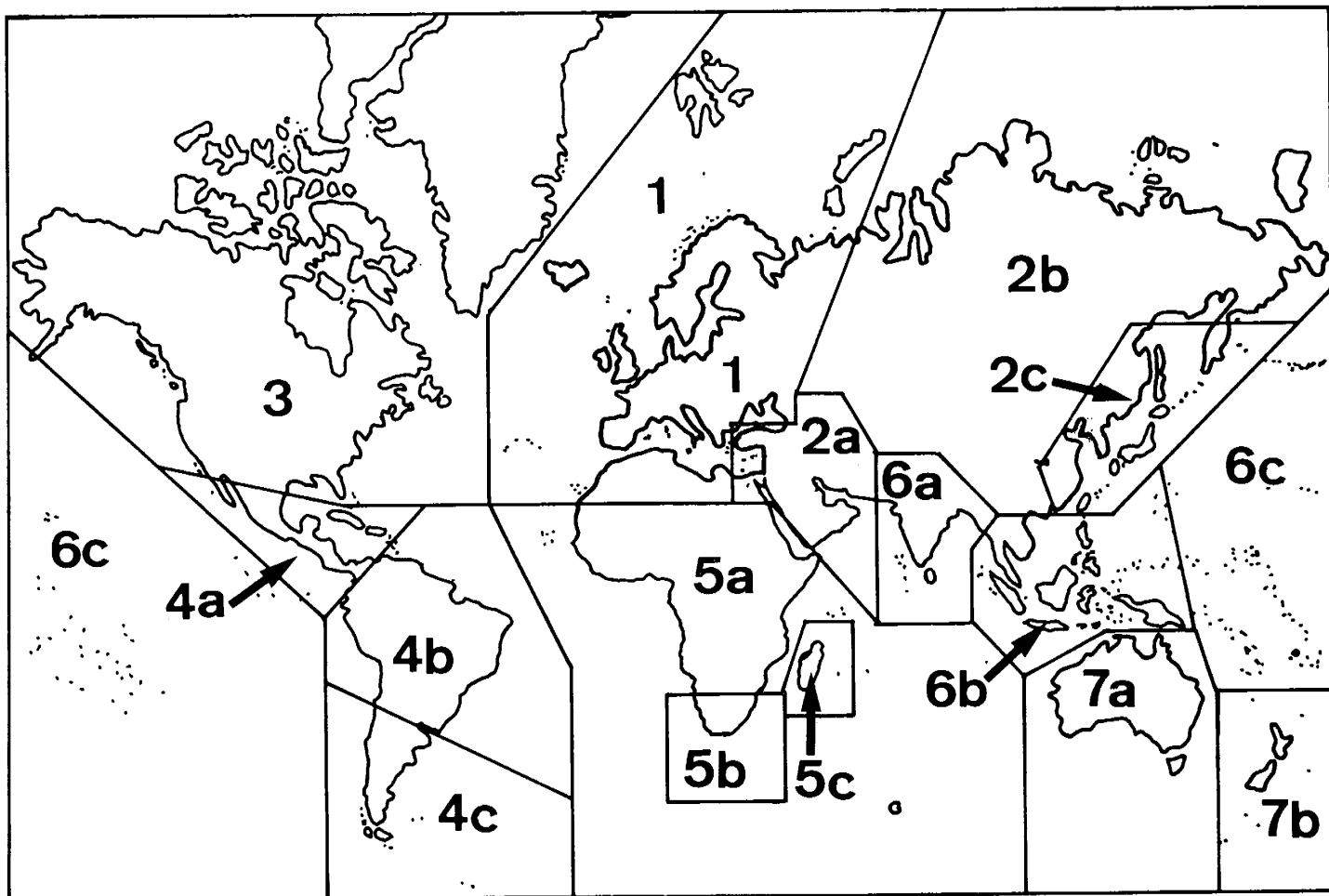


Figure 1. Sixteen phytogeographic regions of the world as taken from the system used at the Royal Botanical Gardens. The additional lettering designations are the authors sub-divisions. Figure legend or geographical codes are 1 = Europe and N. Africa, 2a = Asia Minor, 2b = Central Asia, 2c = East Asia, 3 = N. America, 4a = Central America, 4b = Tropical South America, 4c = Temperate South America, 5a = Tropical Africa, 5b = Southern Africa, 5c = Madagascar, 6a = India, 6b = Southeast Asia, 6c = Oceania, 7a = Australia, 7b = New Zealand.

ported from Asia. Today the weeds of ricefields are rapidly becoming internationally "standardized" as the most successful ones from each continent are mixed and then re-transported.

Among the aquatics there are other useful crop plants which have also been transported around the world, for example, *Trapa* (water chestnut), *Eleocharis dulcis* ("Chinese" water chestnut), *Nelumbo* (lotus), *Ipomoea aquatica*,

Acorus calamus, *Colocasia esculenta*, *Arundo donax* (for canes and woodwind reeds) and *Rorippa nasturtium-aquaticum* (water cress).

Other aquatics have horticultural value, an aesthetic enrichment of our lives. Some have attractive flowers, for example, *Eichhornia crassipes*, *Butomus umbellatus*, *Hydrocleis nymphoides*, *Nymphaea* spp. and *Aponogeton distachyos*. Others have attractive foliage and are planted in aquaria, for example, *Cabomba*, *Egeria*, *Elodea*, *Hydrilla* and *Vallisneria*. Others are botanically interesting and have been transported for study or teaching purposes, example are: *Azolla*, *Salvinia*, *Lagarosiphon* and *Lilaeopsis*. Most others have probably been inadvertently introduced either with other plant material, wool or ballast.

The journey a particular plant makes often does not follow the most direct route. For example, *Rotala ramosior*, a native of America, first spread to the Philippines where it became a successful weed of ricefields, and then it traveled from the Philippines to Europe (Cook, 1979). Also, *Salvinia molesta* almost certainly arrived in Asia from South America via European botanic gardens (Cook, 1971).

TABLE I. LIST OF AQUATIC SPECIES THAT ARE WIDELY DISTRIBUTED IN THE WORLD AND WHOSE NATIVE RANGES ARE UNKNOWN.

<i>Aldrovanda vesiculosa</i>	<i>Nymphoides indica</i>
<i>Bacopa monneri</i>	<i>Oryza rufipogon</i>
<i>Bergia capensis</i>	<i>Phragmites australis</i>
<i>Ceratophyllum demersum</i>	<i>Pistia stratiotes</i>
<i>Ceratophyllum submersum</i>	<i>Potamogeton pectinatus</i>
<i>Cladium mariscus</i>	<i>Ranunculus trichophyllus</i>
<i>Echinochloa crus-galli</i>	<i>Rotala hexandra</i>
<i>Eclipta prostrata</i>	<i>Rotala mexicana</i>
<i>Eleocharis acicularis</i>	<i>Rotala occultifolia</i>
<i>Eleocharis dulcis</i>	<i>Schoenplectus (Scirpus) triqueter</i>
<i>Eleogiton (Scirpus) fluitans</i>	<i>Scirpus maritimus</i>
<i>Ipomoea aquatica</i>	<i>Vallisneria</i> spp.
<i>Marsilea minuta</i>	<i>Zanichellia palustris</i>

TABLE 2. KNOWN RANGE AND EXTENSIONS OF AQUATIC VASCULAR PLANTS. GEOGRAPHICAL CODES ARE FOUND ON FIGURE 1. ABBREVIATIONS ARE: 1 = INTRODUCED, 2 = NATIVE, 3 = NATIVE AND INTRODUCED WITHIN AN AREA, 4 = QUESTIONABLY NATIVE, 5 = QUESTIONABLY INTRODUCED, 6 = UNCONFIRMED OR DOUBTFUL.

Taxon	Geographical code															
	1	2a	2b	2c	3	4a	4b	4c	5a	5b	5c	6a	6b	6c	7a	7b
PTERIDOPHYTA																
<i>Azolla caroliniana</i>	1	-	-	-	2	2	4	-	-	-	-	-	-	-	-	-
<i>A. filiculoides</i> ¹	1	-	-	-	3	2	2	-	-	1	-	-	-	5	2	2
<i>A. pinnata</i>	1	-	-	4	-	-	-	-	4	4	4	2	2	-	2	1
<i>Ceratopteris pteridoides</i>	-	-	-	-	4	4	2	-	-	-	-	1	1	-	4	-
<i>Salvinia minima</i> (= <i>rotundifolia</i>)	1	-	-	-	1	4	2	2	1	-	-	-	-	-	-	-
<i>S. molesta</i>	-	-	-	-	-	-	2	-	1	1	1	1	1	-	1	1
SPERMATOPHYTA																
<i>Acanthaceae</i>																
<i>Hygrophila polysperma</i>	-	-	-	-	1	-	-	-	-	-	-	2	2	-	-	-
<i>Alismataceae</i>																
<i>Alisma lanceolatum</i>	2	2	2	-	1	-	-	1	-	6	-	-	-	-	1	1
<i>A. plantago-aquatica</i>	2	2	2	2	1	-	-	1	2	-	-	-	1	-	1	1
<i>Sagittaria calycina</i>	-	-	-	-	2	2	-	-	-	-	-	-	-	-	1	-
<i>S. engelmanniana</i>	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-
<i>S. graminea</i>	1	-	-	-	6	2	4	-	-	-	-	-	1	-	1	-
<i>S. latifolia</i>	1	-	-	-	2	2	2	-	-	-	-	-	-	1	-	-
<i>S. montevidensis</i>	-	-	-	-	1	-	5	2	1	-	-	1	1	-	1	-
<i>S. platyphylla</i>	1	-	-	-	6	2	5	-	-	-	-	-	1	-	-	-
<i>S. rigida</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>S. subulata</i>	1	-	-	-	2	6	2	-	-	-	-	-	1	-	-	-
<i>S. wetherbiana</i>	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-
<i>Amaranthaceae</i>																
<i>Alternanthera philoxeroides</i>	1	-	-	-	1	-	4	2	-	-	-	1	1	-	1	1
<i>Apiaceae</i>																
<i>Apium nodiflorum</i>	2	2	2	-	1	6	6	1	-	-	-	-	-	-	-	1
<i>Hydrocotyle bonariensis</i>	-	-	-	-	2	2	2	2	5	-	-	-	-	-	1	-
<i>Lilaeopsis attenuata</i>	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
<i>Sium latifolium</i>	2	2	-	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Aponogetonaceae</i>																
<i>Aponogeton distachyos</i>	1	-	-	-	-	-	-	1	-	2	-	-	-	-	1	1
<i>Araceae</i>																
<i>Acorus calamus</i>	1	-	2	2	2	-	-	6	-	-	-	3	2	-	-	-
<i>Colocasia esculenta</i>	-	1	-	1	1	1	1	-	1	-	-	2	4	1	-	-
<i>Cyrtosperma chamissonis</i>	-	-	-	1	-	-	-	-	-	-	-	-	2	1	-	-
<i>Asteraceae</i>																
<i>Cotula coronopifolia</i>	1	-	-	-	1	-	4	4	-	2	-	-	-	-	5	4
<i>Brassicaceae</i>																
<i>Rorippa microphylla</i>	2	-	6	5	1	-	-	-	-	-	-	-	-	-	1	1
<i>R. nasturtium-aquaticum</i>	2	2	4	5	1	-	-	-	-	-	-	-	1	-	1	1
<i>Butomaceae</i>																
<i>Butomus umbellatus</i>	2	2	2	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Cabombaceae</i>																
<i>Cabomba aquatica</i>	-	-	-	-	-	2	2	-	-	-	-	1	-	-	-	-
<i>C. caroliniana</i>	1	-	-	-	3	-	-	-	-	-	-	1	-	-	-	-
<i>Callitricheae</i>																
<i>Callitriche deflexa</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>C. hamulata</i>	2	-	-	-	6	-	-	-	-	-	-	-	-	-	1	1
<i>C. heterophylla</i>	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1
<i>C. palustris</i>	2	2	2	-	2	-	-	-	-	-	-	-	4	-	5	-
<i>C. stagnina</i>	2	-	-	-	5	-	-	-	6	-	-	-	4	-	5	1
<i>Commelinaceae</i>																
<i>Murdannia keisak</i>	1	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-
<i>Crassulaceae</i>																
<i>Crassula bonariensis</i>	1	-	-	-	-	-	6	2	-	-	-	-	-	-	-	-
<i>C. helmsii</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
<i>Cyperaceae</i>																
<i>Carex acutiformis</i>	2	3	2	2	1	-	-	-	-	1	-	-	-	-	-	-
<i>Cyperus difformis</i>	1	-	-	-	5	5	-	2	2	-	-	2	2	5	5	-
<i>C. eragrostis</i>	1	-	-	-	1	-	4	2	-	-	-	-	-	-	1	1
<i>C. fuscus</i>	2	2	2	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>C. involucrus</i> (= <i>alternifolius</i>)	-	-	-	-	1	-	-	-	2	2	-	2	2	-	1	-
<i>C. papyrus</i>	1	-	-	-	1	-	-	-	2	2	2	-	-	-	1	-
<i>C. squarrosus</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>Eleocharis obtusa</i>	1	-	-	-	2	2	-	-	-	-	-	-	-	-	2	-
<i>E. olivacea</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>E. striatula</i>	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
<i>Isolepis setacea</i>	2	2	2	-	1	-	-	-	-	5	-	-	-	-	1	1
<i>Mariscus strigosus</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>Schoenoplectus mucronatus</i>	2	2	2	2	1	-	-	-	2	-	-	2	2	-	2	-
<i>S. prolifer</i>	1	-	-	-	-	-	-	-	2	-	-	-	-	-	4	2
<i>S. pungens</i> (= <i>americanus</i>)	1	-	-	-	2	-	-	-	-	-	-	-	-	-	1	4
<i>S. triquetter</i>	2	2	2	-	1	-	-	-	2	2	-	-	-	-	-	-

TABLE 2. (CONTINUED)

Taxon	Geographical code															
	1	2a	2b	2c	3	4a	4b	4c	5a	5b	5c	6a	6b	6c	7a	7b
<i>Elatinaceae</i>																
<i>Elatine ambigua</i>	1	-	-	4	1	-	-	-	-	-	-	2	2	-	-	-
<i>Eriocaulaceae</i>																
<i>Eriocaulon cinereum</i>	1	-	-	4	4	-	-	-	2	-	-	-	2	2	-	-
<i>Haloragaceae</i>																
<i>Myriophyllum aquaticum</i>	1	-	-	1	1	-	2	-	6	1	-	6	1	-	1	1
<i>M. heterophyllum</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>M. spicatum</i>	2	6	6	-	1	-	-	-	-	-	-	-	6	-	1	-
<i>M. verrucosum</i>	1	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
<i>Hydrocharitaceae</i>																
<i>Blyxa aubertii</i> s. stricto	-	-	-	2	1	-	-	-	1	-	1	2	2	-	4	-
<i>B. japonica</i> s. stricto	1	-	-	2	-	-	-	-	-	-	-	2	2	-	-	-
<i>Egeria densa</i>	1	-	-	1	1	-	2	2	1	1	-	-	-	-	1	1
<i>Elodea canadensis</i>	1	-	1	1	2	-	-	-	-	1	-	-	-	-	1	1
<i>E. callitrichoides</i>	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-
<i>E. nuttallii</i>	1	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-
<i>Halophila stipulacea</i>	1	2	-	-	-	-	-	-	2	-	2	-	-	-	-	-
<i>Hydrilla verticillata</i>	4	4	2	2	1	1	1	-	5	5	-	2	2	-	4	1
<i>Hydrocharis morsus-ranae</i>	2	2	2	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Lagarosiphon major</i>	1	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1
<i>Limnobium laevigatum</i>	-	-	-	-	-	2	2	3	-	-	-	-	-	-	-	-
<i>Nechamandra alternifolia</i>	-	-	-	-	-	-	-	-	1	-	-	2	1	-	-	-
<i>Ottelia alismoides</i>	1	-	-	2	1	-	-	-	1	-	-	2	2	2	2	-
<i>O. ovalifolia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1
<i>Stratiotes aloides</i>	3	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Juncaceae</i>																
<i>Juncus acutus</i>	2	2	-	-	-	-	4	-	-	4	-	-	-	-	1	-
<i>J. articulatus</i>	2	2	2	2	4	-	-	-	-	-	-	-	-	-	1	1
<i>Lamiaceae</i>																
<i>Lycopus asper</i>	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
<i>L. europaeus</i>	2	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Lemnaceae</i>																
<i>Lemna aquinoctialis</i>	1	-	-	2	2	2	2	2	2	-	2	2	2	2	2	-
<i>L. gibba</i>	2	2	-	1	2	2	2	2	2	2	-	2	-	-	-	-
<i>L. minor</i>	2	2	-	-	2	-	-	-	2	2	-	2	-	-	5	5
<i>L. minuscula</i>	1	-	-	-	1	2	2	2	2	2	-	1	-	-	-	-
<i>Spirodela punctata</i>	1	1	-	2	1	-	2	2	1	4	-	2	2	2	2	1
<i>Wolffiella hyalina</i>	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-
<i>Lilaeaceae</i>																
<i>Lilaea scilloides</i>	1	-	-	-	2	2	2	2	-	-	-	-	-	-	1	-
<i>Limnocharitaceae</i>																
<i>Hydrocleis nymphoides</i>	-	-	-	1	2	2	2	-	-	-	-	-	-	-	1	1
<i>Limnocharis flava</i>	-	-	-	-	2	-	2	-	-	-	-	1	1	-	-	-
<i>Lythraceae</i>																
<i>Ammannia auriculata</i>	1	-	-	-	5	-	-	-	2	-	-	2	2	-	-	-
<i>A. baccifera</i>	1	-	-	-	-	-	-	-	2	-	-	2	2	-	2	-
<i>A. coccinea</i>	1	-	-	-	2	2	2	-	-	-	-	-	-	-	-	-
<i>A. verticillata</i>	1	-	-	-	-	-	-	-	-	-	-	2	2	-	-	-
<i>Rotala densiflora</i>	1	-	-	-	-	-	-	-	-	-	-	2	2	2	2	-
<i>R. filiformis</i>	1	-	-	-	-	-	-	-	2	2	2	-	-	-	-	-
<i>R. indica</i>	1	5	-	2	1	-	-	-	1	-	-	2	2	2	-	-
<i>R. ramosior</i>	1	-	-	-	2	2	2	-	-	-	-	-	1	-	-	-
<i>Marantaceae</i>																
<i>Thalia dealbata</i>	-	-	-	-	2	2	2	-	-	-	-	-	-	5	1	-
<i>Menyanthaceae</i>																
<i>Nymphoides peltata</i>	3	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Najadaceae</i>																
<i>Najas gracillima</i>	1	-	6	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>N. graminea</i>	2	2	2	2	1	-	1	-	6	-	-	2	2	-	2	-
<i>N. minor</i>	2	2	2	2	1	-	-	-	-	-	-	2	2	-	-	-
<i>Nelumbonaceae</i>																
<i>Nelumbo nucifera</i>	1	2	2	2	1	-	-	-	-	-	-	2	2	-	2	-
<i>Nymphaeaceae</i>																
<i>Nymphaea alba</i>	2	2	2	-	1	-	-	-	-	-	-	4	-	-	-	1
<i>N. ampla</i>	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-
<i>N. blanda</i>	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-
<i>N. caerulea</i>	1	2	-	-	-	-	-	-	2	-	-	-	-	-	-	-
<i>N. capensis</i>	-	-	-	-	1	-	-	-	-	2	2	-	-	-	1	-
<i>N. jamesoniana</i>	-	-	-	-	1	-	2	-	-	-	-	-	-	-	-	-
<i>N. lotus</i> (incl. pubescens)	1	-	-	-	-	-	-	-	2	-	-	2	2	-	-	-
<i>N. mexicana</i> (incl. flava)	1	-	-	-	3	2	-	-	-	-	-	-	-	-	1	1
<i>N. odorata</i>	1	-	-	-	2	2	-	-	-	-	-	-	-	-	-	-
<i>N. tuberosa</i>	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-
<i>Nuphar lutea</i>	2	2	2	2	4	-	-	-	-	-	-	-	-	-	1	1

TABLE 2. (CONTINUED)

Taxon	Geographical code															
	1	2a	2b	2c	3	4a	4b	4c	5a	5b	5c	6a	6b	6c	7a	7b
<i>Onagraceae</i>																
<i>Ludwigia affinis</i>	--	--	--	--	--	2	2	--	1	--	--	--	--	--	--	--
<i>L. decurrens</i>	--	--	--	1	2	2	2	2	1	--	1	--	--	--	--	--
<i>L. erecta</i>	--	--	--	--	2	2	2	--	1	--	1	--	--	--	--	--
<i>L. palustris</i>	2	2	2	--	2	2	2	--	2	4	--	--	--	1	1	1
<i>L. peploides s. stricto</i>	--	--	--	--	4	2	2	--	--	--	--	--	--	1	--	--
<i>L. peploides ssp. montevidensis</i>	--	--	--	--	--	--	--	2	--	--	--	--	--	--	1	1
<i>L. peruviana</i>	--	--	--	--	1	2	4	2	--	--	--	1	1	--	1	--
<i>L. uruguayensis</i>	1	--	--	--	2	2	2	2	--	--	--	--	--	--	--	1
<i>Poaceae</i>																
<i>Alopecurus geniculatus</i>	2	2	2	5	1	--	--	--	--	--	--	--	--	--	1	1
<i>Arundo donax</i>	2	2	--	--	1	--	--	1	--	1	--	--	--	--	1	--
<i>Brachiaria mutica</i>	--	--	--	--	--	2	2	--	2	--	--	1	1	1	1	--
<i>Coleanthus subtilis</i>	2	6	2	--	5	--	--	--	--	--	--	--	--	--	--	--
<i>Echinochloa crus-gavonis</i>	1	--	--	--	2	2	2	2	--	--	--	--	--	--	--	--
<i>E. frumentacea</i>	2	2	2	6	1	6	6	6	2	--	--	--	--	--	--	--
<i>E. oryzoides</i>	2	2	2	--	--	--	--	1	--	--	--	--	--	--	1	1
<i>E. phyllopogon</i>	1	--	--	2	1	--	--	--	--	--	--	--	--	--	--	--
<i>Glyceria declinata</i>	2	2	--	--	2	--	--	--	--	--	--	--	--	--	1	1
<i>G. frutans</i>	2	2	2	6	4	--	--	1	--	--	--	--	--	--	1	1
<i>G. maxima</i>	2	2	2	--	1	--	--	--	--	--	--	--	--	--	1	1
<i>G. striata</i>	1	--	--	--	2	2	2	--	--	--	--	--	--	--	--	--
<i>Leersia oryzoides</i>	2	2	2	2	2	2	2	--	--	--	--	2	--	--	1	--
<i>Oryza australiensis</i>	--	--	--	--	--	--	--	--	--	--	--	1	--	--	2	--
<i>O. barthii</i>	--	--	--	--	1	5	1	--	2	--	--	1	--	--	--	--
<i>O. brachyantha</i>	--	--	--	--	--	--	--	--	2	--	--	1	--	--	--	--
<i>O. eichingeri</i>	--	--	--	--	--	--	--	--	2	--	--	1	--	--	--	--
<i>O. glaberrima</i>	--	--	--	--	--	--	--	--	2	--	--	1	--	--	--	--
<i>O. grandiglumis</i>	--	--	--	--	--	--	2	--	--	--	--	1	--	--	--	--
<i>O. latifolia</i>	--	--	--	--	--	2	2	--	--	--	--	1	--	--	1	--
<i>Panicum repens</i>	--	--	--	--	1	1	1	--	4	2	--	--	--	--	--	--
<i>Paspalum dilatatum</i>	1	1	1	1	4	4	2	2	1	1	1	1	1	1	1	--
<i>P. paspaloides</i>	1	--	--	2	1	--	--	--	--	--	--	--	--	--	2	1
<i>Phalaris arundinacea</i>	2	2	2	2	2	1	6	1	--	--	--	1	--	--	1	1
<i>Polypogon monspeliensis</i>	2	2	2	2	1	1	1	1	--	2	--	1	--	1	1	--
<i>Scolochloa festucacea</i>	2	2	--	--	5	--	--	--	--	--	--	--	--	--	--	1
<i>Zizania aquatica</i>	--	--	--	1	2	--	--	--	--	--	--	--	1	--	--	1
<i>Pontederiaceae</i>																
<i>Eichhornia crassipes</i>	1	1	--	1	1	4	2	5	1	1	1	1	1	1	1	1
<i>Heteranthera limosa/rotundifolia</i>	1	--	--	--	2	6	2	--	--	--	--	--	--	--	--	--
<i>H. reniformis</i>	1	--	--	--	2	2	2	2	--	--	--	--	--	--	--	--
<i>Monochoria vaginalis</i>	--	--	--	2	1	--	--	--	--	--	--	--	2	2	2	--
<i>Pontederia cordata</i>	1	--	--	--	2	2	2	2	--	--	--	--	--	--	1	--
<i>Potamogetonaceae</i>																
<i>Potamogeton crispus</i>	2	2	2	2	1	--	--	--	6	2	--	--	--	--	4	1
<i>P. epihydrus</i>	1	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--
<i>Ranunculaceae</i>																
<i>Ranunculus hederaceus</i>	2	--	--	--	1	--	--	--	--	--	--	--	--	--	--	--
<i>R. rionii</i>	1	2	2	--	--	--	--	--	--	1	--	--	--	--	--	--
<i>R. sceleratus</i>	2	2	2	4	1	--	--	--	--	--	--	4	--	--	1	1
<i>Scrophulariaceae</i>																
<i>Bacopa erecta</i>	--	--	2	--	--	--	--	--	1	--	--	--	--	--	--	--
<i>Dopatrium junceum</i>	--	--	--	--	1	--	--	--	--	6	6	2	2	--	2	--
<i>Limnophila indica</i>	--	2	2	--	1	--	--	--	2	--	--	2	2	--	--	--
<i>L. sessiliflora</i>	--	--	--	2	1	--	--	--	--	--	--	--	--	--	--	--
<i>Lindernia dubia</i>	1	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--
<i>L. anagallidea</i>	1	--	--	--	2	--	--	--	--	--	--	--	--	--	--	--
<i>Veronica anagallis-aquatica</i>	2	2	2	--	1	--	--	6	2	--	--	--	--	--	1	1
<i>V. catenata</i>	2	2	2	--	4	--	--	--	2	--	--	--	--	--	1	1
<i>Sphenocleaceae</i>																
<i>Sphenoclea zeylandica</i>	--	--	--	--	1	--	--	--	2	--	2	2	--	--	--	--
<i>Trapaceae</i>																
<i>Trapa natans s. lato</i>	3	2	2	6	1	--	--	--	2	2	--	2	2	--	--	--
<i>Typhaceae</i>																
<i>Typha latifolia</i>	2	2	2	2	2	--	--	--	--	--	--	--	--	--	1	--

†Introduced in East North America.

DISCUSSION

While searching through literature for information on aquatic plants it is surprising to discover that some relatively large genera which are widely cultivated and traded have not become established outside their native range; good examples are: *Echinodorus* (Alismataceae) native in America, ca. 47 species—particularly surprising as the ecologically similar and patristically related genera *Alisma* and *Sagittaria* have spread; *Cryptocoryne* (Araceae) native to Asia, ca. 60 species; *Aponogeton* (Aponogetonaceae) native in Australia, Asia and Africa, ca. 45 species only one of which (*A. distachyos*) has become established outside its native range.

A total of 172 species are listed in Table 2. One has migrated within America, 52 (30.2%) are common to the Old and New World 56 (32.6%) are exclusively native to the Old World and have become established in the New World while 66 (38.4%) have made the journey from the New to the Old World. The migration of aquatic plant species between east and west is fairly well balanced.

From the point of view of aquatic plant species, India is floristically very rich, probably as a result of its migration from the southern to the northern hemisphere during the Upper Cretaceous. Thirty two species native to India have become established elsewhere, while 21 species have been introduced in recent times. Such "give and receive" calculations are rarely so well balanced. The most extreme unbalanced case is probably that found in New Zealand. It has "received" no less than 42 species but has "given" no more than one (*Crassula helmsii*) which might have reached Europe from Australia where it is also native. The reason for this imbalance is probably due to the extraordinarily poor native aquatic flora which obviously left many ecological niches unfilled.

A marked imbalance also exists in the migration of species between North America and Europe (exclusively North American to Europe: 14 species, exclusively European to North America: 1 species). One reason for this imbalance is that Europe is not a phytogeographically distinct region as it is continuous with Asia and Africa. If one considers Eurasia as one region (a much larger area than North America), then 36 species have migrated to North America.

In a review of the aquatic species endemic to Europe and the Mediterranean (Cook, 1983), 61 taxa were considered to be endemic and of these 46 were considered to be neo-endemics which originated during or after the Pleistocene. The only European endemic that has established itself in North America is *Ranunculus hederaceus*, one of the few palaeoendemics. It was first recorded in 1821 and is believed to have come with ships' ballast. It has remained near its original sites of introduction along the Atlantic coast.

It is unlikely that all the remaining 60 European endemic aquatics have been denied transport to other regions.

The problems of establishment in new lands are obviously great, and it is perhaps rather naive to say that the aquatic environment is uniform and allows plants a wide geographical range without further qualification. Some aquatics such as *Brasenia* and *Dulichium* became extinct before or during the ice age in Europe, but persisted in North America. These plants have not become re-established in Europe in spite of the fact that they are in cultivation in Europe. This observation also lends weight to the argument that ecological niches in the aquatic environment are rather more complex than we commonly accept today.

The North American species that have become established in Europe represent a heterogeneous mixture. The first to cause comment was *Elodea canadensis* which became a serious pest at the turn of the century but has now become "integrated" into the native flora. However, it is apparently now being gradually replaced by *Elodea nuttallii*. Another group of invaders have become weeds of ricefields (*Cyperus squarrosus*, *Eleocharis olivacea*, *Lindernia anagal-lidea*, *L. dubia* and *Najas gracillima*). These species have not spread and remain in ricefields. The third group are escapes from cultivation such as, *Cabomba caroliniana*, *Nymphaea tuberosa* and *Sagittaria rigida* which have locally become established, but show no signs of spreading or becoming "integrated" into the native flora.

One must not combine the terms "introduced aquatic" and "weed". It is true that a great many weeds (undesirable plants) are introduced, but, almost by definition, weeds flourish in sites disturbed by man. Usually it is the nature of the disturbance that is more important for the establishment of the weed than its mobility. It is today almost universally accepted that as soon as a weed is "brought under control" it will be followed by another and probably worse one.

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