Environmental influences on aquatic plants in freshwater ecosystems

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Abstract: Aquatic plants are important components of many freshwater ecosystems. In this review we examine natural and anthropogenic influences on the distribution and abundance of aquatic plants, and develop a conceptual model of those diverse interactions. Species of aquatic plants vary greatly in their anatomy, physiology, life-history traits, and ability to tolerate inorganic and biological stressors. Key examples of inorganic stressors are extreme regimes of flow velocity, irradiance, salinity, ice cover, temperature, nutrients, and pollutants. Stressors associated with competition, herbivory, and disease may also limit the ability of species to utilize otherwise suitable habitats. Some aquatic plants have a cosmopolitan distribution and display high levels of polymorphism and phenotypic plasticity in response to variations of environmental factors; these qualities allow them to occur over a wide range of conditions. Other species, however, have narrower tolerances and are potentially useful indicators of environmental conditions, in terms of either their presence or relative abundance within communities. In this review, we examine key environmental influences affecting aquatic plants, and their potential use as indicators at local, watershed, and regional scales.

Key words: aquatic plants (aquatic macrophytes), environmental factors, environmental indicators, environmental stressors.

Résumé : Les plantes aquatiques occupent une place importante dans différents écosystèmes d'eau douce. Les auteurs passent en revue les influences naturelles et anthropogènes qui affectent la distribution et l'abondance des plantes aquatiques, et développent un modèle conceptuel pour ces diverses interactions. Les espèces de plantes aquatiques varient beaucoup selon leur anatomie, leur physiologie, les propriétés de leur cycle vital, et leur capacité à tolérer les agents stressants biologiques ou inorganiques. Les régimes extrêmes de vélocité du flux, d'irradiance, de salinité, de couvert glaçé, de température, de nutriments et de polluants, sont des exemples clés d'agents stressants inorganiques. Les agents stressants associés à la compétition, à l'herbivorie et aux maladies, peuvent également limiter la capacité des espèces à utiliser des habitats, par ailleurs convenables. Certaines plantes aquatiques ont une distribution cosmopolite et montrent de hauts degrés de polymorphisme et de plasticité, en réaction aux variations des facteurs environnementaux; ces qualités leur permettent de vivre sous une large gamme de conditions. D'autres espèces ont cependant des tolérances plus étroites et sont potentiellement utiles comme indicatrices des conditions du milieu, en termes soit de leur présence ou soit de leur abondance relative dans les communautés. Dans cette revue, les auteurs examinent les influences environnementales déterminantes qui affectent les plantes aquatiques ainsi que leur utilisation potentielle comme indicatrices, aux échelles locales, des bassins versants ou des régions.

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Mots clés : plantes aquatiques (macrophytes aquatiques), facteurs environnementaux, indicateurs environnementaux, agents stressants environnementaux.

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1. Introduction

Aquatic plants (or aquatic macrophytes) live in wet habitats. "True" aquatics, or hydrophytes, occur in permanently wet places, but others known as helophytes are more amphibious and may tolerate seasonal drying. As is true of all organisms, the distribution and abundance of aquatic plants are influenced by variations of environmental factors. This fact can be used to identify species and communities that are reliable indicators of important changes in their ecosystem, including ones that may serve as gauges of ecological integrity (Fennessy et al. 1998; Mack et al. 2000; Aznar et al. 2002). The usefulness of indicators is related to their sensitivity to both longer- and shorter-term changes in environmental factors, including those that act individually, or in a synergetic manner, to cause changes that may be interpreted as being beneficial or damaging. Aquatic plants can be successfully used for these useful purposes, alone or in association with the monitoring of other kinds of organisms (Seddon 1972; Carbiener et al. 1990; Seele et al. 2000; Thiebaut et al. 2002; Schneider and Melzer 2003; Stelzer et al. 2005).

Aquatic plants integrate temporal, spatial, chemical, physical, and biological qualities of their ecosystem. Studies in various climatic regions have demonstrated the influence of interacting environmental factors on the distribution and abundance of plants in both lotic (i.e., streams and rivers) and lentic (i.e., lakes and ponds) waters (Suren and Ormerod 1998; Heegaard et al. 2001; Barendregt and Bio 2003; Bernez et al. 2004). In general, the relative importance of particular environmental factors varies with spatial and temporal scales (French and Chambers 1996; Suren and Ormerod 1998; Lacoul and Freedman 2006*a*).

Hutchinson (1975) highlighted the usefulness of comparative studies of aquatic plants among water bodies differing in limnological characteristics; such research is valuable in understanding the effects of environmental factors on species and communities. Various studies have emphasized the key importance to aquatic plants of factors affecting the availability of light, including turbidity, dissolved organic carbon (particularly humic substances), chlorophyll (related to phytoplankton biomass), and depth (Canfield et al. 1985; Chambers and Kalff 1985; Stewart and Freedman 1989; Skubinna et al. 1995; Middelboe and Markager 1997; Vestergaard and Sand-Jensen 2000; Lacoul and Freedman 2006*a*). Also cited as important factors are sediment characteristics (Pearsall 1920; Barko and Smart 1986; Xie et al. 2005); trophic status as related to nutrient chemistry (Hutchinson 1975; Srivastava et al. 1995; Toivonen and Huttunen 1995; Jeppesen et al. 2000); physical factors such as slope, wind and wave action, and hydrologic variations (Duarte and Kalff 1986; Strand and Weisner 1996; Madson et al. 2001; van Geest et al. 2003; Schutten et al. 2004); and biological influences such as competition, allelopathy, grazing, and shading by periphyton (Sand-Jensen and Borum 1991; Gopal and Goel 1993; Lauridsen et al. 1993; Weisner et al. 1997). Various forms of multivariate analysis have been used to evaluate suites of physical–chemical environmental factors and to characterize the apparent influences of abiotic factors on macrophytes (Seddon 1972; Toivonen and Huttunen 1995; Heegaard et al. 2001; Mackay et al. 2003; Murphy et al. 2003; Mäkelä et al. 2004; Lacoul and Freedman 2006*a*).

In this contribution, we review studies of the influence of environmental factors on the distribution and abundance of aquatic plants in freshwater ecosystems, with the aim of suggesting practical indicators of ecological change. Insights from this review are useful in terms of conserving macrophyte species and communities, and in planning for managing entire watersheds to conserve natural resources and biodiversity, as is being encouraged by the European Community (European Commission 2000) and other authorities. This approach involves the comparative and integrated study of biodiversity and other ecological values among types of waterbodies within regions (Williams et al. 2003). Ultimately, the

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approach is intended to improve understanding of the effects of anthropogenic environmental change on ecological values and resources.

2. Aquatic plants

Aquatic plants occur in permanently or seasonally wet environments. As considered here, they include a diverse group of macrophytic, aquatic plants, including angiosperms, ferns, mosses, and liverworts, and some freshwater macroalgae. However, to limit the size and scope of this review, our focus is on non-arborecent angiosperms. Within this context, aquatic plants may be aggregated into four functional groups (Sculthorpe 1967; Cronk and Fennessy 2001; for a more detailed classification see Cook 1990, 1996):

- **emergent species** are rooted in bottom substrate but the plant extends above the water surface; they mostly occur in shallow water and include species of sedges and bulrush (Cyperaceae), rushes (Junceae), grasses (Poaceae), cattails (Typhaceae), and others.
- **floating-leaved hydrophytes** are rooted in sediment but have leaves that float on the water surface; they may occur at moderate depths and may be prominent in low-visibility water, and include species of lotus (Nelumbonaceae) and water lily (Nymphaeaceae).
- **submerged hydrophytes** are usually rooted in bottom substrate, but may be free-floating, and their foliage is normally underwater; they occur at various depths and include species of water-starwort (Callitrichaceae), water-milfoil (Haloragaceae), pondweed (Potamogetonaceae), and elodea, wild celery, and frogbit (Hydrocharitaceae).
- **free-floating hydrophytes** float on the water surface but do not have roots embedded in sediment; they freely move with wind and water currents, and include species of water-lettuce (Araceae), mosquito-fern (Azollaceae), water hyacinth (Pontederiaceae), and duckweed and watermeal (Lemnaceae).

About 7.5% of dicotyledonous plants are aquatic, and 11% of monocotyledonous ones (Les and Schneider 1995). If woody and emergent species are excluded, then 2–3% of angiosperms are hydrophytes, or 4700–7500 species (Cook 1990; Philbrick and Les 1996). Of course, if a broader definition of aquatic plants is used, such as any plants routinely occurring in wet places, a much larger number of species might be considered aquatic. According to Reed (1997), for example, there are about 7500 wetland species in the United States alone. Studies of the floras of Britain, Denmark, and India suggest that 10–15% of their vascular species occur in wetlands (Moeslund et al. 1990; Cook 1996; Gopal 1997; Preston and Croft 1997). However, the percentage is less in mountainous and Neotropical countries (6% in Nepal, <1% in Ecuador and Peru; Young and León 1993; Jørgensen and León 1999; Lacoul 2004).

3. Biogeography and dispersal

3.1. Large-scale biogeography

Unlike terrestrial plants, aquatic macrophytes are more species rich in temperate regions than in tropical ones (Crow 1993). However, endemism of aquatic plants may be rich in some tropical and subtropical regions (Sculthorpe 1967). For example, southern Africa (Botswana, Lesotho, Namibia, Swaziland, and Republic of South Africa) supports about 600 species of wetland plants, including 114 endemic taxa (Cook 2004). This includes two endemic monospecies families, the Prioniaceae (*Prionium serratum*) and Wardiaceae (*Wardia hygometrica*). Similarly, Uruguay supports 232 macrophytes, of which 13% are endemic to the country and 81% to subtropical South America, while only 6% are cosmopolitan (Pazl and Bessagodal 1999). However, endemic aquatic plants are also rich in some temperate regions, such as New Zealand (38 species; Coffey and Clayton 1988). Macrophyte endemism

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can, however, be sparse in temperate lakes, even ones that are ancient. The extremely large, old, and isolated Lake Baikal (Russia) has no endemics among its hydrophyte flora of 45 species (Kozhova and Izmestéva 1998), and Lake Biwa (Japan) has only two endemic hydrophytes (*Vallisneria biwaensis* and *Potamogeton biwaensis*; Nakajima 1994).

It is interesting to note that the rich endemism of the terrestrial flora of low-latitude counties is not paralleled by that of aquatic plants. For example, the Indian subcontinent supports about 5000 endemic vascular plants, but only 41 of them are aquatic species (Lavania et al. 1990). Many of the aquatic endemics (20 species of Podostemaceae) occur only in local specialized habitats associated with waterfalls and rivers with rocky beds (Gopal 1997). Similarly, terrestrial habitats ranging from tropical through alpine in Nepal support 312 endemic vascular plants, but only three of them are aquatics (Shrestha and Joshi 1996; Shrestha 1999).

Overall, Sculthorpe (1967) reported that about 40% of species of aquatic plants occur on only one continent. The other transcontinental 60% can be classified into three floristic groups: Arcto-tertiary (north-temperate and boreal), pantropical, and cosmopolitan (occurring widely in temperate and tropical habitats).

The floristic groups may also be reflected in local biogeography. In the Himalayas, where it is possible to study steep altitudinal and climatic gradients over a short latitudinal distance, the high-altitude lakes are dominated by Arcto-tertiary macrophytes, and low-altitude waterbodies by cosmopolitan and pantropical ones (Lacoul and Freedman 2006*a*). Prominent among the widely distributed Arcto-tertiary species are *Ranunculus trichophyllus, Callitriche palustris*, and *Festuca ovina*, along with the Himalayan endemic *Juncus allioides*. The pantropical and cosmopolitan species of lower (warmer) Himalayan altitudes include *Azolla imbricata, Ceratophyllum demersum, Eichhornia crassipes*, *Hydrilla verticillata*, *Nymphoides indica*, *Potamogeton crispus*, *Salvinia molesta*, and *Spirodela polyrhiza*, along with graminoids of the warm Indian subcontinent.

3.2. Dispersal and connectivity

Species of aquatic plants vary in their ability to disperse propagules to new habitats, and in the vectors by which this is accomplished (Sculthorpe 1967; Cook 1990). Communities of aquatic plants consist of those species that were able to disperse to local habitats and then survive there (Johansson and Nilsson 1993; Henry et al. 1996).

The three major dispersal vectors are water, wind, and animals. Dispersal by water (or hydrochory) is a common attribute that relies on hydrological connectivity. Examples of water-dispersed species include *Potamogeton crispus* (floating seeds), *Ludwigia peploides* (easily detached, floating stems), and *Eichhornia crassipes* (free-floating plants). Examples of wind-dispersed (or anemophilous) species include *Typha latifolia* and *Phragmites communis*, which have aerodynamic seeds. Species dispersed by animals (or zoochory) include *Nelumbo lutea* (hard-coated seeds that may survive passage through the gut of a herbivore), *Bidens frondosa* (tick-like fruits that snag on fur), *Lemna minor* and *Wolffia punctata* (tiny plants that are readily carried on fur or feathers). Humans are also important dispersal vectors for some species, and are responsible for the deliberate or accidental introduction of invasive species beyond their natural range (see section 5.1.).

The distribution of species of aquatic plants is associated with their large-scale ability to disperse sexual or vegetative propagules, as well as their ecological tolerance (Hutchinson 1975). Key attributes of wide-ranging species include easily dislodged propagules that can establish in novel but appropriate habitats, clonal growth, broad ecological tolerance, and long-distance dispersal vectors (Darwin 1859; Sculthorpe 1967; Grace 1993; Charalambidou and Santamaría 2002; Les et al. 2003).

The long-distance dispersal of aquatic plants by migrating birds has attracted some attention. Sculthorpe (1967) discussed the idea in the context of intra-continental dispersal, and it was extended by Hutchinson (1975) to the possibility of an inter-continental scale. However, Clausen et al. (2002) resisted aspects of that notion, noting the rapid flow-through of food through the gut of waterfowl.

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During typical migratory flight this would be equivalent to a distance of no more than about 300 km, which would limit the likelihood of inter-continental dispersal. However, Les et al. (2003) used DNA-molecular techniques to estimate the divergence time of 71 species of aquatic angiosperms (32 genera in 15 families, from five continents), and concluded that their average divergence time was 3 million years. This suggests that the extremely long time-scales of continental drift could not account for the wide geographical ranges of some aquatic plants, leading Les et al. (2003) to suggest that avian dispersal was the likely vector.

Not surprisingly, the proximity of other waterbodies has an influence on the local species richness and composition of macrophyte communities (Van den Brink et al. 1991; Bornette et al. 1998; Coops et al. 1999; but see van Geest et al. 2003 for an exception among floodplain lakes in the Netherlands). For instance, Linton and Goulder (2000) found that the richness of aquatic plants in British ponds was positively correlated with that in neighboring waterbodies. Their regression model suggests that ponds contain a baseline richness of long-distance migrants, plus additional species that had colonized from nearby waterbodies. Hydrological connectivity may be important in this respect, as was shown by Aznar et al. (2002) for the dispersal of invasive *Ludwigia peploides* among marshes in France.

Studies of the richness of aquatic plants in lotic systems have been helpful in extending the river continuum concept (RCC; Vannote et al. 1980) to biological variables. The RCC was originally formulated to better understand directional flows of water and continuous gradients of physical conditions and flows of organic matter in connected hydrological systems. In general, the RCC predicts larger volumes and higher concentrations in lower-altitude reaches. In addition, the RCC predicts that species richness should be greatest in intermediate-sized streams with a relatively large amount of physical heterogeneity, an intermediate level of disturbance, and a ratio of photosynthesis to respiration greater than one (Vannote et al. 1980). Studies of bryophytes in Himalayan streams have shown greater species richness in mid-elevation streams — upper reaches were restricted by nutrient limitation and snow cover, while lower reaches had excessive turbidity and sedimentation (Suren and Ormerod 1998). In comparison, a study of 208 Danish streams found that the richness of submerged plants was less in smaller streams at higher elevation, compared with larger and lower streams; however, there were no differences for other kinds of aquatic plants (Riis et al. 2001).

The facilitation of dispersal by hydrologic connectivity may result in relatively uniform and species-poor communities of aquatic plants in lotic habitats compared with lentic ones (Bornette et al. 1998). However, microhabitat heterogeneity associated with the flow regime (itself related to topography), substrate quality, and local anthropogenic influences may affect this observation (Ormerod et al. 1994; Suren and Ormerod 1998). For instance, lowland rivers and streams in western Europe may be richer in aquatic plants than nearby lentic habitats (Bornette et al. 1998; Williams et al. 2003). Nevertheless, the relatively high habitat variability of lentic bodies, at a regional level, has the potential to increase gamma diversity. Still, lentic bodies in flood plains or others connected to lotic systems are more likely to support water-dispersed aquatic plants and to be less dominated by air-dispersed ones, whereas isolated ponds and lakes are likely to be dominated by those dispersed by animals or air (Williams et al. 2003). Lacoul (2004) examined aquatic plants in isolated lakes at high altitude in the Himalayas (to 4780 m above sea level) and found them to be dominated by bird-dispersed species.

4. Factors affecting aquatic plants

Variations in environmental factors affect the distribution and abundance of aquatic plants, as is true of all organisms. Aquatic plants are primarily influenced by factors inherent in the limnology of water bodies, including those related to such physical attributes as geomorphology (geology and topography), sediment, climate, and hydrology. These factors are influenced by in situ qualities of waterbodies, and also by terrestrial components of their watershed. In addition, aquatic plants are affected by biological interactions, such as competition, predation, and disease.

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4.1. Climatic factors

The key climatic influences on aquatic plants are ambient temperature, ice cover, and hydrology. Synoptic variations of these factors are influenced by gradients of latitude and altitude.

4.1.1. Temperature

Ambient temperature (of water and sediment) influences the distribution of aquatic plants by affecting their physiology, including the germination of seeds, initiation and rate of seasonal growth, and onset of dormancy (Hutchinson 1975; Barko et al. 1982, 1986; Duarte and Kalff 1987; Rooney and Kalff 2000; Spencer et al. 2000). According to Welch (1952), "no other factor has so much profound direct and indirect influence on physico-chemical, biological, metabolic and physiological behaviour of aquatic ecosystems than temperature". The influence of water temperature on aquatic plants and their communities is well known (Barko and Smart 1981; Pip 1989; Scheffer et al. 1992; Madsen and Brix 1997; Rooney and Kalff 2000; Heino 2002; Lacoul and Freedman 2006*a*). Only a few species of macrophytes can survive unless ambient temperature during the growing season reaches at least 10 °C, and most species are killed or rendered dormant by temperatures cooler than 3 °C and warmer than 45 °C (Sculthorpe 1967; Christy and Sharitz 1980; Best and Boyd 2003).

The sprouting of propagules is regulated in part by temperature (Haller et al. 1976; van Wijk and Trompenaars 1985; Madsen and Adams 1988; Spencer and Ksander 1992). Many submerged hydrophytes have a wide temperature tolerance for the germination of propagules, e.g., *Vallisneria americana* 7–20 °C (Korschgen and Green 1988), *Potamogeton pectinatus* 3–15 °C (Spencer and Ksander 1992), and *P. nodusus* 10–20 °C (Flint and Madsen 1995). In nature, this is more closely related to sediment temperature than to that of water (Spencer et al. 2000).

In *Hydrilla verticillata*, the more northerly monoecious biotype has a lower threshold of 8 °C for sprouting of its overwintering turions, an upper tolerance of 16 °C, and an accumulated-heat requirement of 777 degree-days for 50% sprouting, while the parameters for the more southerly dioecious biotype are 12 °C, 21 °C, and 1295 degree-days, respectively (Steward and Van 1987; Spencer et al. 2000). These temperature-related traits may explain the dominance of monoecious *H. verticillata* in northern parts of its North American range (McFarland and Barko 1987; Spencer et al. 2000). Moreover, vegetative propagation by fragmentation of the monoecious biotype is favoured by higher temperatures, which may explain its persistence in southern parts of its range (McFarland and Barko 1999).

Ambient temperature and accumulated degree-days vary with latitude and altitude. In Fennoscandia, 74% of the variance associated with decreasing species richness of aquatic plants with increasing latitude was related to mean July temperature (Heino 2002). Similarly, in central North America the species richness of aquatic-plant communities is most strongly related to maximum annual water temperature (Pip 1989). Along a Himalayan altitudinal gradient extending from tropical to alpine, water temperature had the strongest statistical influence on the distribution of species (Lacoul and Freedman 2006*a*). The highest reported hydrophytes in the Himalayas are at 4780 m (*Ranunculus trichophyllus*; Lacoul and Freedman 2006*b*), but there is paleo-limnological evidence of them above 5000 m during an earlier warm period (Lami et al. 1998).

Submerged hydrophytes may show remarkable sensitivity to interannual variations of temperature. Rooney and Kalff (2000) studied boreal lakes in Quebec and found that aquatic plants occurred 25–170% deeper and produced 45–1160% more biomass in a relatively warm year than a cooler one (compared with 1997, 1998 was 6 °C warmer in May and 1 °C warmer during June through August). In a general sense, this observation is consistent with the enhanced productivity of aquatic plants near warm-water discharges of power plants (Grace and Tilley 1976; Haag 1983).

Community structure is also affected by variations of ambient temperature. Callaway and King (1996) found that *Typha latifolia* and *Myosotis laxa* could co-exist at relatively cool temperatures (11–12 °C) but not at warmer ones (24–25 °C) in which *Typha* was competitively dominant.

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4.1.2. Ice cover

Lake ice affects aquatic plants by casting shade and preventing access to the atmosphere, and by scouring littoral habitats when ice-rafts occur after break-up (Wilcox and Meeker 1991; Ormerod et al. 1994; Suren and Ormerod 1998; Lacoul and Freedman 2006*b*). Dieffenbacher-Krall and Jacobson (2001) found palynological evidence that suggested the species of aquatic plants quickly colonized North American lakes when they became seasonally ice-free following deglaciation ca. 12 000 years ago, including species of *Isoetes*, *Myriophyllum*, *Nuphar*, *Potamogeton*, *Sagittaria*, and *Typha*. An increasing length of the ice-free season, likely a response to regional warming, appears to be important in the recent colonization of high-altitude lakes in the Himalayas by *Ranunculus trichophyllus* (Lacoul and Freedman 2006 *b*).

4.1.3. Wind

Wind and wind-generated hydrodynamics affect aquatic plants through pollination, the dispersal of propagules, nutrient cycling, and uprooting and scouring. The exposure of plants in the littoral zone is related to wave height and direction, which are affected by fetch and wind speed and duration (Andersson 2001; Madson et al. 2001; Havens et al. 2004). H åkanson (1982) formulated a "dynamic ratio" to assess wind effects on lakes (calculated as the square root of surface area divided by mean depth). Lakes with a larger dynamic ratio are relatively susceptible to the effects of wind, resulting in more physical stress on aquatic plants (Havens et al. 2004).

Depending on their intensity and frequency, wind and waves may have negative or positive effects on aquatic plants. Also, the orientation and flexibility of macrophytes play important roles in resisting hydrological forces (Dawson and Robinson 1984). Habitats with intense exposure to wind and waves are suboptimal for aquatic plants because seedlings may be uprooted, mature plants damaged, and fine sediment and litter eroded (Wilson and Keddy 1986). For example, increasing wave heights from 0.1 m to 0.3 m enhances damages to *Myriophyllum spicatum*, although that may not cause mortal injury (Stewart et al.1997). However, a moderate intensity of wind and waves may enhance nutrient supply and reduce the loading of shading periphyton on foliar surfaces (Duarte and Kalff 1988; Strand and Weisner 1996; Madson et al. 2001). According to Keddy (1983), the species richness of littoral plant communities is greater at intermediate levels of exposure to wind and waves.

4.1.4. Precipitation

Precipitation volumes and seasonality are important to aquatic plants through their influence on hydrologic conditions, mediated by watershed factors such as evapotranspiration, geomorphology, and vegetation cover. In a few cases, a direct impact of local rainfall on morphological variation has been reported, such as *Sagittaria guayanensis* (Matias and Irgang 2005). The influences of hydrological variations on aquatic plants are discussed in section 4.2.

4.1.5. Latitude

High-latitude habitats have relatively extreme climatic conditions (e.g., cold winters, ice-scouring, and a brief growing season), and these factors limit the species richness of aquatic plants (Linkola 1933; Keddy 2000; Virola et al. 2001). The demonstrated effects of latitude on communities are greatest in studies examining wide gradients, but they may be insignificant over shorter ones. For example, Nõges et al. (2003) examined 86 lakes along a latitudinal gradient extending from southern Spain to northern Sweden and found greater richness and overall abundance in southern waterbodies. In contrast, Rørslett (1991) examined a much shorter latitudinal gradient among 641 lakes in Scandinavia and found little effect on richness.

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4.1.6. Altitude

In general, species richness decreases with increasing elevation, a change that can be attributed to climatic deterioration. An altitudinal decline in richness occurs in both temperate and tropical latitudes (Rørslett 1991; Heegaard et al. 2001; Jones et al. 2003; Lacoul and Freedman 2006*a*). A study of macrophytes in 316 lakes and ponds varying from 2 to 837 m in Cumbria, United Kingdom, suggested that altitude was the strongest predictor of species richness among the environmental factors examined (Jones et al. 2003). Similarly, a study of 28 lakes ranging over 77 to 4980 m in the Himalayas found that water temperature (which is strongly and linearly correlated with altitude) was the strongest predictor of macrophyte richness, followed by transparency, pH, alkalinity, and conductivity (Lacoul and Freedman 2006*a*).

Aquatic ecosystems at high altitude are extreme environments in which physical stressors associated with ice and snow (winter cover, scouring, and avalanche) and severe climate are limiting factors for the distribution of aquatic plants (Suren and Ormerod 1998; Lacoul and Freedman 2006*b*). The phenology of high-altitude plants is tightly coupled to that of the melting of snow or surface ice and other key seasonal events that initiate or end the brief growing season (Pangtey et al. 1990; Lacoul and Freedman 2006*b*). The dispersal of macrophytes among high-altitude lakes is limited by their isolation and infrequent visitation by animal vectors (Suren and Ormerod 1998; Lacoul 2004).

4.2. Hydrology

Hydrology has a great influence on the environmental characteristics of lentic and lotic ecosystems. The associated stressor regime (particularly disturbance and drought) affects the species composition, relative abundance, distribution, and successional dynamics of communities of aquatic macrophytes (van der Valk 1987; Keddy 2000; Mitsch and Gosselink 2000; Paal and Trei 2004). The hydrologic regime is related to temporal and spatial variations of water depth, sediment characteristics, water clarity and chemistry, and (in lotic systems) currents and scouring (Barko and Smart 1978, 1983; Neill 1990; Gafny and Gasith 1999). Aquatic habitats may be affected by water inputs associated with streams or rivers, as well as groundwater springs inflowing below the surface.

If hydrological conditions and water level are relatively stable, communities of aquatic plants in the littoral zone (i.e., in shallow water and the adjacent shoreline) tend to stabilize at a low level of species richness (Keddy and Reznicek 1986; van der Valk et al. 1994; Shay et al. 1999). In comparison, habitats with water levels that naturally fluctuate during the growing season may support richer littoral vegetation. This occurs because large seasonal variations of water level render the littoral habitat unsuitable for species that are highly competitive under more stable conditions, while providing opportunities for others tolerant of hydrologically stressful environments (Keddy and Reznicek 1986; Keddy 2000; Andersson 2001). Lake-edge species tolerant of these conditions are typically amphibious, ruderal (i.e., short-lived and r-strategist) helophytes, whose seeds require drawn-down water levels and oxygenated conditions to germinate and grow in low-competition habitats (Hutchinson 1975; Andersson 2001). Other longer-lived species, with broader environmental tolerances, may have phenotypically plastic responses to variations of water level and associated environmental conditions (Hutchinson 1975; Sand-Jensen and Frost-Christensen 1999).

Inflow waters of lentic systems are commonly enriched with nutrients, compared with the ambient water. Consequently, communities of aquatic plants growing in the vicinity of inflowing streams and groundwater springs may be relatively productive and species rich (Grootjans et al. 1998).

In lotic systems, large seasonal variations of hydrology are equivalent to scouring disturbances associated with intense flow, erosion, and turbidity, often followed by siltation (Riis et al. 2001; Mackay et al. 2003). In habitats where high-flow dominates the growing season, few or no macrophytes can establish and grow. Particularly intense hydrological disturbance may be associated with extreme precipitation events or outbursts from a glacial lake or failed reservoir. These severe disturbances can destroy macrophyte communities by scouring, perhaps followed by recovery through primary succession (Keddy 2000; Mitsch and Gosselink 2000).

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Riverine flooding events can greatly increase the area of fringing wetlands. For example, flooding of the Hassayampa River in Arizona increased the area of fringing marshes by five-fold; these wetlands were dominated by flood-tolerant cattail (*Typha domingensis*), bulrush (*Scirpus americanus*), and rush (*Juncus articulatus*) (Stromberg et al. 1997).

Large anthropogenic influences on hydrology are associated with the construction of dams, reservoirs, and diversions for hydroelectricity and agricultural purposes. The hydrologic variations caused by these structures are markedly different from the original natural ones, and often the littoral habitats become hostile and are poorly or non-vegetated by macrophytes (Carpenter et al. 1992; Keddy 2000). However, moderate anthropogenic influences on hydrology may result in a local enrichment of macrophyte productivity through the deposition of fertile sediment and enhanced availability of dissolved nutrients (Barko and Smart 1986).

In general, water velocities of 0.3–0.4 $m \cdot s^{-1}$ may be associated with a relatively large biomass and richness of macrophytes; these decline at higher velocities, and >1.0 $m \cdot s^{-1}$ is inhospitable (Nilsson 1987; Chambers et al. 1991; Riis and Biggs 2003). Some studies have found that critical hydraulic thresholds for survival and productivity vary among lotic ecosystems, depending on their geomorphology (Westlake 1967; Madsen and Søndergård 1983; Passauer et al. 2002; Riis and Biggs 2001*b*, 2003). In general, however, macrophyte communities in lotic habitats are best developed in a moderate flow regime with tolerable physical stress and enhanced nutrient supply.

The timing and frequency of extreme hydrologic events are important (Haslam 1978). According to Riis and Biggs (2003), aquatic plants are absent from streams with more than 13 annual flooding events of more than 7-times median flow. Of course, some species are relatively tolerant of higher-flow habitats (Butcher 1933; Haslam 1978; Riis and Biggs 2003). In general, streams with frequent flooding events are dominated by well-rooted species with high rates of propagule production (Riis and Biggs 2001*a*; Riis and Biggs 2003). Species of aquatic plants vary in their ability to survive high-flow conditions; for example, *Elodea canadensis*, *Myriophyllum exalbescens*, *M. triphyllum*, *Potamogeton cheesemanii, P. gramineus, Rorippa nasturtium-aquatica*, and *Veronica anagalis-aquatica* survive to 4.0 $m \cdot s^{-1}$ and *Ranunculus aquatilis* and *R. trichophyllus* at even higher water velocities (Haslam 1978; French and Chambers 1996; Riis and Biggs 2003).

4.3. Geomorphology

Geomorphology integrates the topography and geological qualities of an area. Major geomorphological settings include wetlands (marshes, swamps, bogs, fens), lotic systems (streams and rivers), and lentic ones (lakes and ponds). Geomorphology influences key habitat factors for aquatic plants, including hydrology, habitat area, shoreline development, depth gradients, and water chemistry (Canfield et al. 1985; Chambers and Kalff 1985; Chambers et al. 1991; Fernández-Aláez and Fernández-Aláez 1994; Ferreira 1994; Keddy 2000; Mitsch and Gosselink 2000; Passauer et al. 2002; Bernez et al. 2004).

4.3.1. Habitat area

In general, the number of species present increases with the area of suitable habitat (Arrhenius 1921; Connor and McCoy 1979; Weiher and Boylen 1994) and decreases with the isolation of habitat "islands" (MacArthur and Wilson 1967; Linton and Goulder 2000). The Arrhenius equation is a simple descriptor of the relationship of species richness and habitat area.

$$S = cA^z \quad [1]$$

where S is the number of species, c is a constant, A is habitat area, and z is the slope of a log/log relationship of S and A (Williamson 1988; Rosenzweig 1995).

The surface area of a waterbody may influence the richness of aquatic plants by affecting both the diversity and area of habitats (Rørslett 1991; Mäkelä 2004). However, there is a complex relationship

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between lake area and habitat heterogeneity (including non-habitable areas), depending on such factors as climate, depth, littoral slope, light availability, sediment types, wave exposure, and seasonal hydrology (Spence 1982; Duarte and Kalff 1986; Gasith and Hoyer 1998; Vestergaard and Sand-Jensen 2000).

Weiher and Boylen (1994) reported an Arrhenius slope of 0.23 in a study of 38 Adirondack lakes ($r^2 = 0.72$), while Møller and Rørdam (1985) found 0.29 for 16 Danish ponds ($r^2 = 0.80$), and Lacoul (2004) reported 0.37 ($r^2 = 0.79$) among 12 tropical lakes in Nepal. In contrast, a study of 316 lentic water bodies in Cumbria, United Kingdom, found a weak relationship (Arrhenius slope 0.17 adjusted $r^2 = 0.45$; Jones et al. 2003) and studies of 16 (Friday 1987) and 50 (Jeffries 1998) English ponds did not find a significant species–area relationship, nor did Rørslett (1991) in a study of 305 Norwegian lakes (only 25% of the variation in species richness was related to lake area).

While it appears that relationships between species richness and whole-lake area are not always significant, stronger interactions may be found in cases where only the actual vegetated area is used as a predictor (Vestergaard and Sand-Jensen 2000). In a review of world-wide data for 139 lakes, Duarte et al. (1986) found that the cover of hydrophytes is relatively smaller in larger waterbodies, rather than being a constant proportion of the lake area. However, they suggested that emergent macrophytes typically colonize a relatively constant proportion (7%) of the lake area, regardless of the absolute size of the waterbody. In general, models of area:richness are stronger if the datasets are restricted to lakes in similar shaped basins; shallow floodplain lakes yield results different from those in deeper basins (van Geest et al. 2003). Moreover, it appears that the Arrhenius relationship is stronger within relatively homogenous landscapes than in heterogeneous ones (Lacoul 2004).

In a wide-ranging review of species–area relationships across various kinds of organisms, Rosenzweig (1995) concluded that the form of the curve varies with spatial scale. If species are limited by their dispersal ability, then the local richness will differ from that found by randomly sampling of the metacommunity (i.e., at the level of gamma diversity). While all species are dispersal limited at some spatial scale, this effect becomes increasingly important at larger scales (Hubbell 2001).

Few studies have been made of stream size and the richness of aquatic plants, although Riis et al. (2000) did find that larger streams supported more macrophyte communities and greater overall species richness.

4.3.2. Light availability

Light is a critical factor in photosynthesis and in limiting the distribution of aquatic plants. This key influence has been studied in both the field (Chambers 1987; Madsen and Maberly 1991; Kirk 1996; Squires et al. 2002) and laboratory (Barko and Smart 1981; Madsen and Sand-Jensen 1994; Tavechio and Thomaz 2003). Shade tolerance and light-related morphological variations of some species (i.e., phenotypic plasticity) may provide a competitive advantage in light-constrained situations, thereby influencing community structure (Barko and Smart 1981; Middelboe and Markeger 1997).

Light availability at a higher intensity than the compensation point for net production is a primary factor affecting the local abundance of aquatic plants (Middelboe and Markeger 1997; Tavechio and Thomaz 2003). The depth of the euphotic zone is affected by various factors, including water colour (associated with dissolved organic compounds as well as the chlorophyll of phytoplankton), inorganic turbidity, and shading by riparian vegetation, periphyton, and aquatic plants (Pearsall 1920; Phillips et al. 1978; Barko and Smart 1983; Chambers and Kalff 1985; Day et al. 1988; Sand-Jensen and Borum 1991; Strand and Weisner 1996; Sheldon and Boylen 1997; Kalff 2001). Light availability in aquatic habitats may be studied quantitatively with photometers as fluxes of Joules, or as relative transparency using a Secchi disc or a spectrophotometric index.

In larger-scale studies of lentic ecosystems, gradients of turbidity and (or) transparency are important predictors of the distribution and abundance of aquatic plants (Squires et al. 2002; Boedeltje et al. 2001; Murphy et al. 2003; Lacoul and Freedman 2006*a*), while in lotic ecosystems shading by a riparian canopy may also be important (Mackay et al. 2003). Within these contexts, the influence of water depth

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on submerged hydrophytes is related to two interacting factors (*a*) light availability as directly affected by water colour and turbidity (Canfield et al. 1985; Chambers and Kalff 1985; Squires et al. 2002) and (*b*) the exponential attenuation of irradiance with depth (Hutchinson 1975; Duarte et al. 1986; Stewart and Freedman 1989; Sand-Jensen and Borum 1991; Middelboe and Markager 1997). Therefore, as clarity decreases or depth increases, the amount of light available to support photosynthesis diminishes. In addition, the relative amount of longer-wavelength visible light, particularly in the red part of the spectrum, diminishes more quickly than blue wavelengths. This spectral change has implications for the arrays of photosynthetic pigments present in hydrophytes growing at various depths (Hutchinson 1975; Moss 1998).

The ability of aquatic plants to survive under various conditions of light availability is partly related to their growth form. In general, low-light conditions in the shallow littoral zone promote dominance by helophytes (i.e., emergent species), while deeper water tends to support free-floating and floating-leaf species, rather than submerged ones (Canfield et al. 1985; Day et al. 1988; Stewart and Freedman 1989; Skubinna et al. 1995; Toivonen and Huttunen 1995; Bini et al. 1999; Vestergaard and Sand-Jensen 2000; Squires et al. 2002; Nurminen 2003).

Once established as mature plants, floating-leaf macrophytes such as *Nelumbo*, *Nymphaea*, and *Trapa* may grow well in low-transparency waters, although seasonal clarity of the water may be important in the establishment of new seedlings (Gopal and Sharma 1990). In general, emergent or floating-leaved aquatic plants seldom grow in water deeper than 3 m (Canfield and Hoyer 1992), although in tropical regions the floating-leaved *Trapa bispinosa* may be rooted as deeply as 5 m (Lacoul 2004). Some species of submerged macrophytes are highly intolerant of shading, such as *Chara* spp. and *Potamogeton alpinus*, while others may grow in gaps beneath a well-established canopy, such as *Ceratophyllum demersum*, *Hydrilla verticillata*, *Myriophyllum spicatum*, *Potamogeton crispus*, *P. pectinatus*, and *Urtricularia vulgaris* (Chambers and Kalff 1985; Minc 1997; Lougheed et al. 2001).

In general, submerged hydrophytes will grow as deeply as 2–3 times the Secchi depth (Canfield et al. 1985; Chambers and Kalff 1985). According to Dennison et al. (1993), submerged plants require 4–29% of surface-ambient light (depending on species), although Middelboe and Markager (1997) suggest a range of 2–15%. The germination of *Vallisneria* seeds is not sensitive to light but the survival of seedlings is lower at 2–5% surface irridance than at 9–25% (Kimber et al. 1995).

Seemingly live *Chara*, a macrophytic alga, has been found as deep as 100 m in extremely clear lakes (Middelboe and Markager 1997). Typically, aquatic bryophytes can survive much lower irradiances than can vascular hydrophytes (Middelboe and Markager 1997). In general, however, living vascular hydrophytes rarely occur deeper than 12–17 m in even extremely clear lakes (Chambers and Kalff 1985). The maximum colonization depth (Zc) is mostly related to light attenuation and the compensation point of species (Canfield et al. 1985; Chambers and Kalff 1985; Blindow 1992), but other key factors include the intensity of surface irradiance, hydrostatic pressure, temperature, grazing, and benthic substrate (Hutchinson 1975; Sand-Jensen and Søndergaard 1981; Duarte and Kalff 1987; Chambers and Prepas 1988; Sand-Jensen 1989).

4.3.3. Substrate characteristics

Sediment acts as an anchoring substrate and a source of nutrients for rooted plants (Pearsall 1920; Anderson and Kalff 1988; Duarte and Kalff 1990; Barko et al. 1991; Weisner 1991; Ferreira 1994; Suren and Ormerod 1998; Boedeltje et al. 2001). However, some bottom types are inhospitable. For instance, bedrock is impenetrable by roots, while coarse-textured cobble and fine clay may also provide few rooting microsites, sand is nutrient poor, excessively soft and flocculent substrates do not provide anchorage, and high-organic substrates may be anaerobic and rich in toxic sulphides, iron and manganese ions, and organic compounds (Hutchinson 1975; Barko and Smart 1983; Day et al. 1988; Keddy 2000). In general, relatively favourable benthic substrates are composed of a mixture of inorganic particulates and are rich in humified organic matter.

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The local balance of inorganic and organic components of sediment is affected by various factors, particularly geomorphology, land use, hydrology, and vegetation cover, both locally and over the watershed (Haslam 1978; Ferreira 1994; Crosbie and Chow-Fraser 1999; Mitsch and Gosselink 2000; Andersson 2001; Lougheed et al. 2001). Sediment texture, organic matter content, and siltation interact with each other and with bottom slope, basin depth, and watershed characteristics. Moreover, these factors may be greatly altered by anthropogenic influences. For instance, the disturbance of watersheds by agriculture, timber harvesting, construction, or other activities may greatly increase erosion and cause excessive sedimentation of aquatic habitats. Alternatively, alterations of flow regime by hydroelectric development may cause an aggressive scouring of bottom substrates if the flow is increased, or it may increase sedimentation if it is reduced. In the lower Great Lakes region, for example, shallow-water habitats receiving agricultural runoff tend to have a high proportion of fine, inorganic silts and clays in their sediment, while areas in mainly forested areas have typically organic muck and often gravel in their substrate (Minc 1997).

Over time, lake basins may infill because of the sedimentation of materials eroded from the watershed, along with the accumulation of endogenous organic matter (Keddy 2000; Mitsch and Gosselink 2000). This change increases the relative prominence of the littoral zone and may create low-slope, silty, shallow-water habitats that support a large biomass of aquatic plants (Pearsall 1920; Duarte and Kalff 1986). Infilling can be greatly accelerated by anthropogenic disturbance of the watershed.

Species of aquatic plants vary in their preference for sediment quality. For example, aquatic mosses such as *Fontinalis dalecarlica* and *Hygrohypnum ocraceum* may dominate mountain streams with abundant large boulders (boulder stability during floods favours the slow growing bryophytes; Cattaneo and Fortin 2000). In other situations, *Myriophyllum triphyllum*, *Potamogeton cheesemanii*, and *Ranunculus trichophyllus* usually grow in sandy substrate, while *Potamogeton pectinatus* and *Myriophyllum spicatum* are associated with clay, *Nymphaea* and *Nelumbo* occur in organic-rich clay, and *Sphagnum* species and *Brasenia schreberi* prefer organic substrates (Haslam 1978; Barko et al. 1991; Cattaneo and Fortin 2000; Riis and Biggs 2003; Lacoul and Freedman 2006*a*).

4.3.4. Nutrients and trophic status

Depending on their growth strategy, aquatic plants may obtain dissolved nutrients from either or both of the sediment and water column (Barko et al. 1986; Chambers 1987; Schneider and Melzer 2003; Xie et al. 2005). Rooted species can typically obtain nitrogen, phosphorus, calcium, and other key nutrients from sediment, even while absorbing inorganic carbon from the water column. In contrast, non-rooted submerged hydrophytes absorb all of their nutrients from water, while emergent and floating species also have access to atmospheric sources of some nutrients, particularly carbon dioxide.

Various factors related to nutrients and acidity and alkalinity have important influences on aquatic plants and their communities (Catling et al. 1986; Toinvonen and Huttunen 1995; Bini et al. 1999; Magee et al. 1999). In general, productivity is limited by the supplies of phosphate and nitrogen (as nitrate and (or) ammonium), but other nutrients may also be important (e.g., inorganic carbon, calcium, and potassium) (Barko et al. 1986; Toivonen and Huttunen 1995; Khedr and El-Demerdash 1997; Heegaard et al. 2001; Serag and Khedr 2001; Thiebaut et al. 2002).

In marshes, the productivity of aquatic plants is generally nitrogen limited when the N:P ratio is <14, and phosphorus limited when N:P is >16 (Koerselman and Meuleman 1996; Verhoeven et al. 1996). However, generalizations based on N:P ratios cannot yet be made for aquatic plants and their productivity in wetlands or in lentic ecosystems (Bedford et al. 1999; Mores et al. 2004).

In less fertile lentic habitats, the productivity of aquatic plants is most likely to be limited by the availability of phosphate and (or) inorganic nitrogen (as nitrate or ammonium, depending mostly on acidity). This is also generally the case in more productive situations, although for submerged hydrophytes the supply of inorganic carbon may also be limiting to photosynthesis (Barko et al. 1986). In general, dissolved CO_2 is the preferred source of inorganic carbon, but its concentration is generally

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low in water, particularly in situations with pH > 5.4 (Hough and Fornwall 1988). Most species of non-acidic habitats can utilize bicarbonate-C, but this is inefficient under low-light conditions because of the energy requirement for active transport of bicarbonate (Hough and Fornwall 1988).

Various studies have examined the potential use of species of aquatic plants or their communities as indicators of the trophic status of their habitat (Uotila 1971; Arts et al. 1990; Tracy et al. 2003). Studies of this sort have been made in

- lakes (e.g., Seddon 1972; Jens én 1979; Srivastava et al. 1995; Toivonen and Huttunen 1995; Jeppesen et al. 2000)
- rivers and streams (Carbiener et al. 1990; Robach et al. 1996; Ali et al. 1999; Thiebaut et al. 2002; Schneider and Melzer 2003)
- marshes (Lougheed et al. 2001; Murphy et al. 2003; Bayley and Mewhort 2004)

In Europe, species of aquatic plants have been aggregated into categories according to the trophic condition of their typical habitat, ranging from low- (oligotrophent) to high-nutrient (eutraphent) indicators (Linkola 1933; Seddon 1972; Wiegleb 1981; Pietsch 1980; Mäkirinta 1989; Kovács 1992; Jensén 1994; Toivonen and Huttunen 1995; Heegaard et al. 2001; Schneider and Melzer 2003). These analyses show that many species have a broad ecological range, occurring over a wide array of trophic conditions. Some species, however, have a narrower distribution and are useful indicators of trophic conditions and of limitation by specific nutrients, for example:

- oligotrophents: *Chara hispida*, *C. intermedia*, *Juncus subnodulosus, Najas flaxilis*, *Nitellopsis obtusa*, *Pontederia cordata, Potamogeton coloratus*, *P. polygonifolius, P. richardsonii, Subularia aquatica, Sparganium angustifolium, Utricularia minor*; note that some of these also occur in mesotrophic habitats
- eutrophents: *Chara fragilis, C. vulgaris*, *Ceratophyllum demersum*, *Elodea nuttalli*, *Hydrocharis dubia*, *Lemna trisulca, Myriophyllum spicatum, Nitella mucronata*, *Oenanthe aquatica*, *Potamogeton malaianus*, *Potamogeton nodusus*, *Ranunculus fluitans*; *Sagittaria sagittifolia*; again, some may occur in mesotrophic habitats
- generalists: *Cabomba caroliniana*, *Callitriche humulata*, *Elodea canadensis*, *Mentha aquatica*, *Nuphar lutea*, *N. alba*, *Potamogeton natans*, *P. pectinatus*, *P. perfoliatus*, *Sparganium emerson, Zannichella palustris*.

A few macrophytes are indicators of the availability of particular nutrients. For instance, *Callitriche stagnalis*, *Ceratophyllum demersum, C. submersum, Potamogeton polygonifolius, P. praelongus*, and *Urtricularia* spp. are useful indicators of high nitrogen conditions (Goulder and Boatman 1971; Best 1980; Kovács 1992; Heegaard et al. 2001; Tracy et al. 2003). In general, high ammonium conditions are not tolerated by submerged macrophytes or by *Potamogeton coloratus* and *Chara hispidata* (Wiegleb 1984; Carbiener et al. 1990; Onaindia et al. 1996; Boedeltje et al. 2001), but they may support pollution tolerant emergent species such as *Polygonum mite* and non-rooting *Lemna*, *Spirodela*, and *Ceratophyllum* (Rodwell et al. 1995; Boedeltje et al. 2001; Samecka-Cymerman and Kempers 2002). Carnivorous macrophytes (Droseraceae) of acidic dystrophic waters, such as *Aldrovanda vesiculosa*, use ammonium as their source of nitrogen (Adamec 1995, 2000).

Littorella uniflora is restricted to low phosphorus habitats, while *Lemna minor*, *Spirodela polyrhiza* and *Zanichellia palustris* require medium to high phosphorus concentrations (Heegaard et al. 2001, Trei and Pall 2004). However, the distributions of *Isoetes lacustris*, *Lemna minor*, *Lobelia dortmanna*, *Myriophyllum alterniflorum*, *Sparganium angustifolium*, and *S. erectum* are influenced by integrated gradients of nitrogen, phosphorus, and sometimes other nutrients (Heegaard et al. 2001; Rubio et al.

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2003; Paal and Trei 2004). Lentic habitats with organic, nutrient-rich bottom substrates are supportive of floating-leaved species, such as *Trapa japonica* and *Nelumbo nucifera* (Kunii 1991; Kadono 1982; Lacoul 2004).

Some species show a nutrient response to base cations, especially calcium, and this is reflected in an affinity for calcareous habitats. Examples of such species include *Berula erecta*, *Littorella uniflora*, *Myriophyllum spicatum*, *Ranunculus aquatilis*, *R. fluitans*, and *R. trichophyllus* (Dale and Miller 1978; Carbiener et al. 1990; Heegaard et al. 2001; Bernez et al. 2004; Lacoul and Freedman 2006*b*). Likewise, *Potamogeton obtusifolius* and *P. pusillus* have a strong affinity for magnesium and occur in watersheds with dolomitic rocks (Heegaard et al. 2001). Some species may be limited by micronutrients, as may be the case of *Elodea canadensis*, which requires high-available iron and may also be negatively sensitive to copper (Spicer and Catling 1988; Mal et al. 2002). An emergent species, *Stratiotes aloides*, is negatively sensitive to sulphate (Smolders et al. 2003).

Sediment quality may interact with trophic affinities. For instance, *Hydrilla verticillata* and *Nymphoides indica* inhabit mesotrophic to eutrophic habitats with silty sediment (Singhal and Singh 1978; Papastergiadou and Babalonas 1992; Lacoul and Freedman 2006*a*). In comparison, *Potamogeton crispus* prefers low-silt habitat of similar trophic status (Uotila 1971; Sahai and Sinha 1976; Gopal and Sharma 1990), while *P. pectinatus* often prevails in clay-rich conditions (Harvey 1984; Barko and Smart 1985, 1986; Gafny and Gasith 1999).

It appears, however, that relatively small numbers of aquatic plants are reliable indicators of trophic conditions and of limitation by specific nutrients — most species have a broad autecological amplitude with respect to these factors. This is due to their inherent phenotypic plasticity as well as the ecological complexity of shallow-water environments, particularly physical–chemical variations associated with sediment and water, as well as the seasonality of inundation (Barko and Smart 1986; Day et al. 1988; Barko et al. 1991; Jackson et al. 1994; Barko and James 1998).

The species richness and relative abundance of aquatic plants in their communities may be useful indicators of trophic status (Carbiener et al. 1990; Barendregt and Bio 2003; Schneider and Melzer 2003; Paal and Trie 2004). In general, species richness is higher in habitats ranging from mesotrophic to eutrophic, and lower in nutrient-poor oligotrophic and dystrophic and nutrient-rich hypereutrophic waterbodies (Rørslett 1991; Weiher and Boylen 1994; Toivonen and Huttunen 1995; Toivonen 2000; Murphy 2002). In fact, hypereutrophic lakes heavily shaded by phytoplankton may lack submerged vegetation and even have little in the littoral zone (Phillips et al. 1978; Blindow 1992; Riis and Sand-Jensen 1998; Morris et al. 2003; Rodríguez-Gallego et al. 2004).

4.3.5. Alkalinity, pH, and associated chemical factors

Aquatic plants can be organized into the following major groups with respect to their preference for conditions associated with alkalinity, pH, and associated factors:

- softwater habitats (<0.2 mequiv./L HCO_3^-), with low concentrations of dissolved ions, including nutrients, and clear water; there are two types (*i*) circumneutral, with pH ca. 6.0–7.5 and low alkalinity and (*ii*) acidic, with pH < 5.5 and zero alkalinity

- hardwater habitats (> 0.4 mequiv./L HCO_3^-), with high concentrations of carbonates and pH > 7

- brownwater habitats, with high concentrations of dissolved humic substances (or dissolved organic carbon; DOC), poor visibility, zero alkalinity, and pH < 5.5

- saline waterbodies, with high concentrations of sodium, chloride, and sometimes other ions, and with extremely high alkalinity and pH

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Softwater habitats are associated with watersheds having siliceous bedrock and thin soil with low carbonate and nutrient content; these predominantly oligotrophic waterbodies are vulnerable to becoming acidified by anthropogenic influences, such as the deposition of acidifying substances from the atmosphere (Freedman 1995; Brouwer et al. 2002). A distinguishing attribute of aquatic plants occurring in acidic versus non-acidic softwaters is their ability to use particular forms of dissolved inorganic carbon. Non-acidic softwaters are dominated by bicarbonate, and aquatic plants generally need HCO_3^- > 0.2 mequiv./L to sustain a positive net production (Madsen and Sand-Jensen 1994; Madsen et al. 1996). In contrast, acidic habitats with pH < 5.0 lack bicarbonate and plants must be able to utilize CO_2 as their source of inorganic carbon (Murphy 2002). Brownwater lakes often have bog or poor-fen covering part of their watershed; drainage from these acidic wetlands is the source of the large amounts of DOC that causes these brown-coloured habitats to have a low visibility.

Hardwater habitats are associated with watersheds rich in carbonate minerals such as limestone and dolomite, and they have high concentrations of alkalinity (>0.4 mequiv./L HCO_3^-). Saline habitats are associated with watersheds having a high water deficit (potential evapotranspiration exceeds precipitation), so that salts accumulate to extremely high concentrations, sometimes exceeding the tolerance of aquatic plants. Saline habitats are also associated with estuaries and some coastal ponds. In high-conductivity saline waters with pH > 12.5, the dominant form of inorganic carbon is the carbonate ion (CO_3^{-2}).

Studies in lentic, lotic, and wetland habitats have found that pH and related factors (such as alkalinity) have an important influence on aquatic plants and their communities (Iversen 1929; Fassett 1930; Moyle 1945; Catling et al. 1986; Pip 1987; Jackson and Charles 1988; Duarte and Kalff 1990; Robach et al. 1996; Brandrud and Mjelde 1997; Vestergaard and Sand-Jensen 2000; Riis et al. 2000; Arts 2002). In general, species richness is higher in hardwater lakes with pH > 7, particularly of elodeids and charophytes, than in more acidic and dilute waters (Brandrud and Mjelde 1997; Vestergaard and Sand-Jensen 2000). Surveys have established floristic gradients extending from low-alkalinity–acidic lakes to high-alkalinity and even saline ones. In general, species richness is relatively low in boreal-to-temperate acidic waterbodies (pH 4.0–5.9), which may be dominated by acidophilic *Sphagnum* spp., *Nardia compressa*, and *Juncus bulbosus* (Heitto 1990; Pietsch 1996; Arts 2002; Brandrud 2002). Submerged *Sphagnum* species occur within a pH range of about 3.5 to 5.9 (Halvorsen 1977; Arts 1990; Pietsch 1996; Brouwer et al. 2002). In extremely acidic conditions (pH 2–3) associated with mine spoils the most tolerant species include *Juncus bulbosus* (as low as pH 2.5), followed by *Sphagnum* (to pH 4) (Pietsch 1996; Nixdorf et al. 2001). Aquatic species of *Sphagnum* vary in their tolerance of acidity; in northwestern Europe, *Sphagnum cuspidatum* occurs in more acidic and more dilute waters than *S. denticulatum* (Arts 2002).

Broadly similar observations have been made of the influences of pH and related factors on aquatic plants in wetlands, for example, in boreal North America (Vitt and Chee 1990; Jeglum and He 1995). It should be noted, however, that these effects are only marked when examining relatively large gradients of pH and related factors (i.e., alkalinity, bicarbonate, and calcium); if less expansive gradients are examined, significant influences may not be detected (Seddon 1972; Srivastava et al. 1995; Jeffries 1998; Lacoul and Freedman 2006*a*).

In general, hardwater lakes are dominated by elodeids and charophytes (Brandrud and Mjelde 1997). Species of submerged hydrophytes that reach their greatest abundance in hardwater habitats include *Ceratophyllum demersum*, *Elodea canadensis*, *E. nuttallii*, *Hydrilla verticillata*, *Hydrocharis dubia*, *Myriophyllum alterniflorum*, *M. spicatum*, *Potamogeton compressus*, *P. crispus*, *P. filiformis*, *P. friesii*, *P. lucens*, *P. nillii*, *P. nodosus, P. obtusifolius*, *P. pectinatus*, *P. vaginatus*, *Ruppia martima*, *R. occidentalis*, *Utricularia vulgaris*, and *Zanichellia palustris* (Hellquist 1980; Kadono 1982; Pip 1987; Kantrud 1990; Brandrud and Mjelde 1997; Murphy 2002). Additional floating-leaved species of hardwater lakes in tropical to subtropical regions include *Euryale ferox, Nelumbo nucifera*, and *Trapa quadrispinosa* (Lacoul and Freedman 2006*a*).

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In general, the submerged macrophytes of softwater lakes are mostly isoetids, while brownwater habitats have few or no submerged species (Fassett 1930; Moyle 1945; Spence 1964; Seddon 1972; Moeller 1985; Arts 2002; Murphy 2002). Indicator species of oligotrophic, clear softwaters in northwestern Europe include *Apium inundatum, Callitriche humulata, Hypericum elodes*, *Isoetes lacustris*, *Juncus bulbosus*, *Lobelia dortmanna*, *Luronium natans*, *Myriophyllum alterniflorum*, *Potamogeton confervoides, P. diversifolius, P. globulifera*, *P. gramineus*, *Sparganium angustifolium*, *Subularia aquatica*, and *Scripus fluitans*, along with the bryophytes *Fontinalis* and *Sphagnum* (Heitto 1990; Arts 2002; Brandrud 2002; Brouwer et al. 2002; Murphy 2002). In northeastern North America, comparable species include *Eleocharis acicularis, Eriocaulon septangulare, Isoetes* spp., *Juncus bulbosus*, *Litorella uniflora*, *Lobelia dortmanna*, *Potamogeton confervoides, P. diversifolius, Urticularia purpurea*, and *U. vulgaris*, along with *Fontinalis* and *Sphagnum* (Hellquist 1980; Catling et al. 1986; Stewart and Freedman 1989; Arts 2002). These species may occur in both circumneutral and acidic softwaters; in general, changes in trophic conditions have a much stronger effect on the species composition and abundance of aquatic plants in clear softwaters than do changes in acidity. Although acidification affects the carbonate–bicarbonate equilibrium, so that CO_2 is dominant in acidic conditions, it appears that many species of clear softwaters can tolerate this change.

However, studies in northwestern Europe have suggested that the anthropogenic acidification (by atmospheric deposition of acidifying substances) of softwater oligotrophic lakes has resulted in expanding benthic mats of *Sphagnum subsecundum, Juncus bulbosus*, and *Drepanocladus* spp., which may competitively reduce the abundance of the hydrophytes *Lobelia dortmanna*, *Litorella uniflora*, and *Isoetes* species (Grahn et al. 1974; Hultberg and Grahn 1975; Grahn 1977, 1986; Satake et al. 1995; Riis and Sand-Jensen 1998; Arts 2002). *Juncus bulbosus* and *Urticularia purpurea* have also apparently increased in Europe and North America as a result of the acidification of softwater lakes (Moeller 1978; Nilssen 1980; Roberts et al. 1985; Roelofs et al. 1994; Lucassen et al. 1999; Arts 2002). It has even been suggested that expanding mats of *Sphagnum* may accelerate the process of acidification, through the efficient absorption of basic cations (especially Ca^{2+} and Mg^{2+}) in exchange for H^+. After the base cations are depleted from the ambient water, acidification becomes accelerated because of a lack of acid-neutralizing alkalinity, and the pH may then rapidly fall to $\leq$4.5 (Brouwer et al. 2002). According to Brandrud et al. (1999), more than 100 species of aquatic plants have declined or disappeared from acidified lakes and rivers in Norway. *Myriophyllum alterniflorum* is considered an acidification indicator in European softwaters, as it disappears at pH $<$ 5.0–5.7 (De Lyon and Roelofs 1986; Brandrud and Mjelde 1993). Of course, species of softwater habitats vary in their sensitivity to acidification in northwestern Europe, with *Lobelia dortmanna* and *Isoetes* spp. being less tolerant than *Littorela uniflora* and *Myriophyllum alterniflorum* (Vöge 1992, 1995; Arts 2002).

In addition, changes in the ratio of ammonium and nitrate occur as waters acidify — the relative amounts of ammonium increase tremendously, because bacterial nitrification to nitrate is halted in acidified waters. This change apparently favours *Juncus* and *Sphagnum* over many other species of aquatic plants (Roelofs et al. 1994).

To some degree, acidification can be mitigated by liming waterbodies back to a circumneutral condition (Clair and Hindar 2005). In Scandinavia, liming has resulted in the reestablishment of at least 15 acid-sensitive species in treated lakes, including *Fontinalis* spp., *Myriophyllum alterniflorum*, *Potamogeton* spp., *Sphagnum auriculatum*, *Subularia aquatica*, and *Utricularia vulgaris* (Lazarek 1986; Brandrud 2002). The acidification-sensitive species have a critical level of about pH 5.5, and are believed to require HCO_3^- for their inorganic-C nutrition. At the same time, acidophilic *Nardia compressa, Sphagnum auriculatum, S. capillifolium*, and *S. papillosum* may decline or be eradicated as a result of liming (Brettum and Hindar 1985; Clymo et al. 1992; Bragg and Clymo 1995; Brandrud 2002).

There are no consistent indicator species of acidic brownwaters. The key effect of organically coloured water is to restrict aquatic plants to shallow, littoral habitats because of the restricted availability of light. Floating-leaved and emergent species are the strongly dominant growth forms. For example,

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in boreal brownwater lakes in Finland, *Nuphar lutea* and *Nympahea tetragona* are prominent species (Mäkelä et al. 2004). In northeastern North America, *Nuphar variegatum* and *Nympahea odorata* are prominent (Stewart and Freedman 1989).

4.3.6. Salinity

Salinity is an important factor affecting aquatic plants in saline prairie wetlands and lakes, salt marshes, estuaries, and some coastal ponds and lakes (Adam 1990; Brewer and Grace 1990; Zedler et al. 1990; Howard and Mendelssohn 1999; Mitsch and Gosselink 2000; Deegan et al. 2005). Most aquatic plants cannot tolerate >10 g/L of dissolved salts (Reimold and Queen 1974; Ungar 1974; Deegan et al. 2005).

Tolerance thresholds vary among species, depending on the type of salt (usually Na^+ or Mg^{2+}), life stage, duration and intensity of exposure, and other factors (Llewellyn and Schaffer 1993; Flynn et al. 1995; Grace and Ford 1996; Howard and Mendlessohn 1999). The genus *Ruppia* tolerates a wider range of salinity than any other hydrophytes (Brock 1979). A literature review on wigeongrass (*Ruppia maritime*) found that its occurs over a range of 0.6–390 g/L in lakes where $MgSO_4$ is the principal salt (Kantrud 1991). In tropical coastal lakes, *R. maritime* dominates in waterbodies having 13–15 g/L during the warm season, but dominance may shift to *Chara* sp. when salinity decreases to 9–10 g/L (see Kantrud 1991 and literature therein). Salinity also influences the distribution of *Scirpus maritimus* and *S. robustus* in coastal and interior wetlands; *S. maritimus* occurs in water with salt concentrations of 0.2–308 g/L, while *S. robustus* does not occur above 30 g/L (Kantrud 1996).

Haller et al. (1974) studied the growth of 10 aquatic plants in various NaCl salinities. A concentration of 17 g/L was toxic to *Pistia stratiotes* and 25 g/L to *Eichhornia crassipes*. *Lemna minor* could tolerate up to 167 g/L. Other macrophytes examined were much more intolerant, including *Azolla caroliniana*, *Hydrilla verticillata*, *Myriophyllum spicatum*, *M. brasiliense*, *Naja guadalupensis*, *Salvinia rotundifolia*, and *Valisneria americana*. See Partridge and Wilson (1987) for a comprehensive list of the salt-tolerance of aquatic plants. Experiments by Mendelssohn and McKee (1992) suggest that a high cell sap concentration of the amino acid proline is an indicator of a recent exposure to salt stress. Laboratory studies of NaCl salinity on *Potamogeton pectinatus* showed that concentrations of 3 g/L restrict shoot productivity and seed germination, but turion formation and growth could occur to 6 g/L (Teeter 1963 1965; Kantrud 1990).

Seawater intrusions may result in short-term increases in salinity. For example, Chabreck and Palmisano (1973) found an increase in salinity from 0.9 to 3.6 g/L after the passage of a hurricane in the Mississippi River delta. This change caused *Panicum hemitomon* to disappear within 3 weeks and to remain absent for about a year, long after the salinity had returned to the pre-hurricane level. In comparison, *Eleocharis palustris*, *Sagittaria lancifolia*, and *Scripus americanus* were little affected by the salinity change. Howard and Mendelssohn (1999) found a similar rank-order of salinity tolerance in greenhouse experiments: *Panicum hemitomon* < *Sagittaria lancifolia* < *Eleocharis palustris* < *Scripus americanus*.

Extremely saline lakes, such as the Dead Sea, do not support any vascular hydrophytes, although some species of phytoplankton are present (Oren and Ben-Yosef 1997). However, moderately saline lakes may support a large biomass of submerged hydrophytes, while estuaries have euryhaline ones such as *Zostera marina*.

4.4. Biological interactions and macrophyte communities

The structure of plant communities is affected by the life-history characteristics of component species and their tolerance of environmental conditions associated with disturbance, stress, and competition. Grime (2001) captures this essence in his C-S-R model that suggests three primary life-history strategies of plants: competitor, stress-tolerator, and ruderal. The following lists assign representative aquatic plants

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according to Grime's tripartite life-history classification (after Barrat-Segretain 1996, 2001; Middleton 1999; Keddy 2000, 2001):

- ruderals establish soon after disturbance and are r-strategists with rapid and prolific propogation; examples include *Hippuris vulgaris*, *Luronium natans*, *Paspalum distichium, Polygonium punctatum, P. persicaria*, and *Sparganium emersum*

- stress-tolerant species may occur in infertile, acidic or alkaline, or saline habitats that are infrequently disturbed, and are long-lived species that grow and reproduce slowly, and often store energy in below-ground tissues such as rhizomes and turions; they include *Isoetes lacustris*, *Spartina alterniflora*, *Subularia aquatica*, and *Zostera marina*

- competitor species occur in fertile, infrequently disturbed habitats and have high productivity, often cast a dense shade, and may be invasive; they include *Eichhornia crassipes*, *Elodea canadensis, E. nuttallii, Hydrilla verticillata, Myriophyllum spicatum, Potamogetom crispus*, and *Typha latifolia*.

Numerous studies have been made of the propagule bank dynamics of aquatic plants. The germination of propagules tends to decrease with increasing burial depth within sediment (Spencer 1987; Bonis and Lepert 1994; Dugdale et al. 2001; Gleason et al. 2002), and this sets limits to the "ecologically active" portion of the bank of viable propagules (Haag 1983). For example, sediment-load experiments by Gleason et al. (2002) found that a burial depth of 5 cm caused a 92% reduction in seedling emergence in a marsh. A similar burial depth of 4–5 cm is believed to limit the active component of the propagule bank in lakes (Bonis and Lepart 1994; Dugdale et al. 2001). However, if deeper sediment is disturbed and mixed, viable propagules may be brought upward into the active pool.

4.4.1. Competition

Competition refers to interference occurring among individuals (intraspecific) and taxa (interspecific) that are seeking access to scarce resources, and it affects the relative abundance of species within communities. The underlying logic of competition theory is that productivity will increase until one or more resources become limiting; less-capable competitors then decline and may be eliminated from the community (Tilman 1982; Fargione and Tilman 2002). This interpretation of competition has been extended to communities of aquatic plants (Wilson and Keddy 1986; Gopal and Goel 1993; Keddy 2001). Interestingly, Keddy (2000) suggests that the relative importance of competition in structuring natural wetland communities is typically less than 5%, while hydrology accounts for about 50% and other environmental factors the remainder. However, the relative importance of competition is much greater than this if invasive aliens are present in the community (see below).

To a substantial degree, the intensity and outcome of competition is related to the relative biomass of the competitors, which is related to both plant size and density (Harper 1977; Wilson and Keddy 1986; Twolan-Strutt and Keddy 1996). The influence of standing crop on intraspecies competition is expressed as self-thinning and is described by the power law of –3/2, as reported in common reed, *Phragmites australis* (Harper 1977). It has also been used to examine interspecific competition between *Potamogeton pectinatus* and *Myriophyllum exalbescens* (Moen and Cohen 1989) and between *Lythrum salicaria* and *Carex crinita* (Twolan-Strutt and Keddy 1996).

Interspecific competition may result in the displacement of inferior species to marginal habitats (Barrat-Segretain 1996; Grace and Wetzel 1981, 1998; Van den Berg et al. 1998; Keddy 2001). For example, when the cattails *Typha angustifolia* and *T. latifolia* grow together, *T. angustifolia* is often relegated to deeper habitat (Grace and Wetzel 1981, 1998). This outcome is apparently mediated by the greater competitiveness of *T. latifolia* under nutrient-rich conditions, possibly because of its relatively larger allocation of biomass to rhizomes (Tanaka et al. 2004).

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Interspecific competition is particularly intense among taxa that are biologically and ecologically similar (Hofstra et al. 1999; Doyle et al. 2003). For instance, Hofstra et al. (1999) examined the relative competitive potential of *Hydrilla verticillata* against several other invasive hydrophytes: *Ceratophyllum demersum*, *Elodea canadenis*, *Egeria densa*, and *Lagarosiphon major*. The productivity of *H. verticillata* was least when challenged by *E. canadenis*, *E. densa*, and *L. major*, all of which are anatomically similar species in the Hydrocharitaceae, and greatest when grown with *C. demersum* (Ceratophyllaceae), which was the most different species anatomically.

Alien invasive macrophytes are strong competitors that may diminish or exclude native species from habitats (Gopal and Goel 1993; Nagasaka et al. 2002). Invasive aliens can do this because, in their novel habitats, they are relatively free of controlling diseases and herbivores. For instance, *Lythrum salicaria* is a prominent invader of wetlands in North America. In controlled experiments, Gaudet and Keddy (1988) found *L. salicaria* to be competitively superior to 44 other wetland species when grown in pairwise combinations. In another study, Weihe and Neely (1997) found that *L. salicaria* could out-compete *Typha latifolia* regardless of light regime. However, competitive outcomes cannot necessarily be predicted on the basis of controlled experiments. For example, experiments involving invasive *Myriophyllum spicatum* and native *M. sibiricum* found that the latter was competitively superior in biomass production (Valley and Newman 1998). In the field, however, *M. spicatum* is widely displacing *M. sibiricum* and other hydrophytes.

Various anatomical and physiological attributes may be important in the competitive ability of aquatic plants, particularly invasive species. For instance, the ability of *Elodea canadensis* and *Myriophyllum spicatum* to exclude other submerged hydrophytes from shallow habitats is largely attributed to their superior ability to appropriate light and space, particularly in relatively fertile habitats (Nichols and Shaw 1986; Madsen et al. 1991*a*, 1991*b*). Free-floating *Azolla pinnata, Eichhornia crassipes*, and *Salvinia molesta* are similarly effective at appropriating surface and in casting shade in subtropical and tropical habitats (Gopal 1990; Scheffer 1998; Rea and Storr 1999).

Other attributes of invasive species may also be important. Certain invasive species of Hydrocharitaceae are effective at appropriating nutrients as well as space, particularly bicarbonate under low-light conditions (e.g., *Elodea canadenis, E. nuttallii*, *Egeria densa*, *Hydrilla verticillata*, and *Lagarosiphon major*; Nagasaka et al. 2002). Moreover, *H. verticillata* has a facultative C4 ability that allows it to access inorganic carbon under extremely limiting conditions in eutrophic habitat (Bowes et al. 2002).

The invasive success of *Elodea nuttallii* in Japanese lakes has been partly attributed to its active growth at low temperatures, as well as its high dispersal and regeneration abilities (Kunii 1981 1984; Nagasaka et al. 2002). *Elodea nuttallii* is particularly successful in habitats with muddy sediment; in coarser-grained areas the invasives *Hydrilla verticillata* and *Vallisneria americana* are more prominent, possibly because of their well-developed rhizome systems (Hamabata 1991; Imamoto et al. 1998; Nagasaka et al. 2002). However, *Hydrilla verticillata* dominates *Vallisneria americana* in high-nutrient conditions, while the opposite occurs when nutrients are scarce (Van et al. 1999). Other factors affecting competitive outcomes include early initiation and vigour of growth in the springtime (Smart 1994; Van den Berg et al. 1998).

Allelopathy is another competitive interference that has been demonstrated in aquatic plants. Species thought to release allelopathic chemicals include *Aldrovanda vesiculosa*, *Chara aspera*, *C. globularis*, *Eleocharis acicularis, E. coloradoensis*, *Glyceria aquatica, Hydrilla verticillata, Hydrocotyle sibthorpioides, Ipomoea aquatica, Myriophyllum spicatum*, *Potamogeton amplifolius*, *Najas marina*, *Nelumbo nucifera*, *Nuphar lutea*, *Stratiotes aloides*, *Trapa bispinosa, Typha domingensis*, and *T. latifolia* (Agami and Waisel 1985; Alliotta et al. 1990; Lodge 1991; Gopal and Goel 1993; Elakovich and Wooten 1995; Albalat Domenéch et al. 1997; Gallardo et al. 1998; Berger and Schagerl 2003; Ervin and Wetzel 2003; Mulderij et al. 2005). Allelopathic polyphenols released by *M. spicatum* inhibit the growth of algae, improve water clarity, and repel herbivores (Lauridsen and Lodge 1996; Nakai et al. 1999, 2000; Gross et al. 2003; Lindén and Lehtiniemi 2005). There are also reports of allelochemical autotoxicity

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in several emergent macrophytes, including *Typha* (McNaughton 1968; Grace 1983; Ervin and Wetzel 2003), *Phragmites* (Gopal and Goel 1993), *Cyperus* (Elakovich and Wooten 1995), and *Juncus*(Ervin and Wetzel 2000).

Of course, competitive outcomes and community structure are also affected by changes in environmental conditions. For instance, as the water in Lake Veluwemeer in the Netherlands cleared because of decreased nutrient loading, the dominant hydrophyte changed from *Potamogeton pectinatus* to *Chara* spp. (Meijer 2000). Similar observations have been made elsewhere with respect to changes in fertility (Van et al. 1999; Nagasaka et al. 2002) and acidification (Lazarek 1986; Brandrud 2002). An explicit simulation model (known as "Charisma") has been developed to predict alternative equilibrium states of hydrophyte communities under various environmental conditions (van Nes et al. 2003).

4.4.2. Herbivory

Aquatic plants may be grazed by invertebrates, fish, turtles, waterfowl, and mammals, and this affects their abundance and the composition of communities (Kiørboe 1980; Lodge 1991; Van Donk et al. 1994; Mitchell and Perrow 1998; Van Donk 1998; Gross et al. 2001; Pìpalová 2002).

In some cases, herbivores have been used as a management tool to reduce the abundance of aquatic plants (Opuszynski and Shireman 1995; Hanlon et al. 2000). For example, grass carp (*Ctenopharyngodon idella*) feeds on more than 170 species of aquatic plants and has been widely used to reduce their biomass (Redding and Midlen 1992; Pìpalová 2002). This fish has been shown to reduce the abundances of *Ceratophyllum, Egeria, Hydrilla, Lemna, Limnophila, Myriophyllum, Najas, Nechamandra, Ottelia, Potamogeton, Spirodela, Trapa, Utricularia, Vallisneria*, and *Wolffia*, but it is ineffective in controlling the floating plants *Eichhornia, Pistia, Salvinia*, and *Nymphaea*. Other herbivorous fish used to reduce the abundance of hydrophytes include common carp (*Cyprinus carpio*; Schuytema 1977; Sidorkewicj et al. 1998), species of tilapia (e.g., *Tilapia zillii*; Saeed and Ziebell 1986) and rudd and roach (*Scardinius erythrophthalmus* and *Rutilus rutilus*, respectively; Prejs 1984; Prejs and Jackowska 1978; Lammens and Hoogenboezen 1991). In some cases, however, selective feeding by fishes may lead to an irruption of resistant aquatic plants, such as *Ranunculus* released by grass carp herbivory in a canal system in Turkmenistan (Charyev 1984). Moreover, there are many examples of introduced herbivorous fishes becoming seriously invasive in novel ranges, as has occurred with various species in North America (e.g., common carp, grass carp, bighead carp (*Hypophthalmichthys nobilis*), silver carp (*Hypophthalmichthys molitrix*), black carp (*Mylopharyngodon piceus*), and northern snakehead (*Channa argus*)). A comprehensive review of interactions between fish and aquatic plants in inland waters is provided by Petr (2000).

Species of Anatidae (ducks, geese, and swans) as well as non-anatids such as coots (*Fulica* spp.) are also voracious consumers of aquatic plants, particularly in relatively productive, shallow lakes and ponds. Intensive grazing by birds may have a large effect on communities of aquatic and wetland plants (Lauridsen et al. 1993; Van Donk and Otte 1996; Mitchell and Perrow 1998; Van Donk 1998). For example, large populations of snow goose (*Chen caerulescens*) have greatly reduced the abundance of rhizomatous grasses and sedges in subarctic and arctic salt-marshes, and have even created expanses of devegetated mud (Williams et al. 1993; Kerbes 1996). In Delta Marsh, Manitoba, waterfowl may consume as much as 40% of the standing crop of *Potamogeton pectinatus* (Anderson and Low 1976). In Loch Leven, Scotland, waterfowl eat about 30% of the potential biomass of *Potamogeton filiformis* — plants experimentally protected from grazing were up to 5.3 times larger than unprotected ones (Jupp and Spence 1977). In Tipper Grund, Denmark, waterfowl consumed about 50% of the biomass of submerged hydrophytes (Kiørboe 1980).

The abundance of herbivorous birds may itself be affected by changes of aquatic plants. In Currituck Sound, North Carolina, an irruption of invasive *Myriophyllum spicatum* supported increased populations of various dabbling ducks (*Anas acuta, A. americana, A. crecca, A. platyrhynchos, A. rubripes*), ring-necked duck (*Athya collaris*), and coot (*Fulica americana*) (Wicker and Endres 1995). Similarly,

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the population of coots (*Fulica atra*) increased on Lake Zwemlust, the Netherlands, when perennial hydrophytes became dominant after biomanipulation (Van Donk 1998). In contrast, when hydrophyte beds in Lake Ellesmere, New Zealand, suffered long-term damage from a windstorm, the population of black swan (*Cygnus atratus*) declined from 40 000–80 000 to only 4000 over 20 years (McKinnon and Mitchell 1994). As the abundance of hydrophytes increases in Florida lakes, herbivorous birds (such as ring-necked duck and coot) increase in abundance, while those preferring open-water habitats decline, although overall avian abundance and species richness may be relatively stable (Hoyer and Canfield 1994). Lush beds of aquatic plants also provide habitat for invertebrates, which if abundant are a key food source for waterfowl, particularly for raising their young (Nelson and Kadlec 1984; Lillie and Evrard 1994).

Herbivorous mammals may also affect aquatic plants and their communities. In Florida and Guyana, the manatee (*Trichechus manatus*) consumes at least 36 genera of aquatic plants, and in some cases can keep waterbodies relatively clear of invasive *Eichhornia crassipes*, *Hydrilla verticillata*, and other hydrophytes (Ronald et al. 1978; Etheridge et al. 1985; Hauxwell et al. 2004). Captive manatees may consume 5–15% of their body weight (wet) per day (they typically weigh about 1000 kg; Best 1981; Etheridge et al. 1985).

Nutria or coypu (*Myocaster coypus*) are also prodigious feeders on aquatic plants. They have been introduced from their native South America to Africa, Europe, the Middle East, and the southern United States as a furbearer and source of wild meat, but are now widely regarded as an invasive animal that can damage hydrophyte beds (Gibson 1973; Schuytema 1977; Harper et al. 1990). The muskrat (*Ondatra zibethicus*) of North America has been similarly introduced to Europe, where it depletes hydrophyte biomass and damages shoreline habitat by tunneling (Pelikan et al. 1971; Akkermann 1975).

Insects are also important herbivores of aquatic plants, although their effect is not yet well-studied. The purple loosestrife (*Lythrum salicaria*), an invasive plant of wetlands in North America, is being controlled in some regions by two herbivorous beetles (*Galerucella calmariensis* and *G. pusilla*) introduced from its native range (Stamm et al. 1999). In some regions of North America, declines of invasive Eurasian water-milfoil (*Myriophyllum spicatum*) may be due to herbivory by the native weevil *Euhrychiopsis lecontei* (whose usual host is the native *Myriophyllum sibiricum*; Creed 1998).

4.4.3. Diseases

Few studies have been made of the effects of disease outbreaks on aquatic plants. In the 1930s, there was a widespread dieback of eelgrass (*Zostera marina*) in temperate estuaries of eastern North America, apparently caused by a slime fungus, *Labyrinthula* (Muelstein et al. 1991; Barnegat Bay National Estuary Program 2001). The resulting habitat degradation caused the extinction of the eelgrass limpet (*Lottia alveus*) and a large population decline of the Atlantic brant (*Branta bernica*), a dependent goose. Similar diebacks have been noted for turtlegrass (*Thalassia testudinum*) in subtropical estuaries.

Several studies have been made of the potential for using pathogens as management tools to control invasive aquatic plants (Charudattan 1991; Shrearer 1998). A fungal pathogen, *Cercospora rodmanii*, was tested as a potential control agent against *Eichhornia crassipes* (Conway et al. 1979), and a strain of *Mycoleptodiscus terrestris* against *Hydrilla verticillata* (Shrearer 1998). Although screening tests have shown that some pathogens could potentially be used in this way, reliable ways of using them in field applications have not yet been developed (Charudattan 1991).

5. Anthropogenic influences

5.1. Invasive species

Because of the severe ecological damage they cause, alien invasive species are one of the most rapidly increasing and pressing environmental problems of recent times (Enserink 1999; Kolar and Lodge 2000; Pimentel et al. 2000; Palumbi 2001). The grave concern about invasive species has led to the development of national and international programmes, such as the Global Invasive Species Program

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of the World Conservation Union, which is mandated to combat these ecological pathogens and reduce the damage they cause to native species, natural ecosystems, and economic resources.

Invasive plants of aquatic and wetland ecosystems are alien species that produce large numbers of disseminules (seeds and (or) vegetative propagules), distribute them over long distances, and become rapidly abundant in novel habitats, where they may exclude native plants, degrade the habitat of animals, and cause economic damage to recreation, irrigation, and other human interests (Richardson et al. 2000; Kercher and Zedler 2004; see Table 1 for key examples). However, not all alien aquatic plants become abundant enough in wild habitats to be considered seriously invasive — in many cases, they have little influence on native species (Anderson 1995; Hager and McCoy 1998; Farnsworth and Ellis 2001; Houlahan and Findlay 2004). Globally, about 6–10% of alien aquatic plants are considered seriously invasive (Williamson 1996; Houlahan and Findlay 2004).

In general, the success of invasive aquatic plants depends on there being a relatively empty niche for them to exploit, or on their competitive superiority in appropriating resources and tolerating anthropogenic stressors, especially those associated with cultural eutrophication (Howard-Williams 1993; Uveges et al. 2002; Corbin and D'Antonio 2004). In addition, alien invaders typically have few or no natural herbivores or diseases to limit their productivity and abundance (Cronk and Fuller 1995; Mack et al. 2000). For example, *Lythrum salicaria* is a highly invasive competitor in wetlands in North America, although its success may be diminished if controlling herbivores are introduced from its native habitat (Smith and Smith 2001; Stiling 2002; Houlahan and Findlay 2004).

On islands, relatively species-poor communities of native aquatic plants may be especially vulnerable to disruption by invasive aliens. In New Zealand, for example, invasive species of Hydrocharitaceae (particularly *Elodea canadiansis, Egeria densa*, and *Lagarosiphon major*) plus *Ceratophyllum demersum* now dominate almost every lake they have reached, an effect attributed to a lack of native canopy-forming hydrophytes (Howard-Williams 1993).

Disturbance may play a role in enabling invasive species to penetrate relatively mature communities (Lugo 1994; Nagasaka et al. 2002). For example, measures taken to control invasive *Eichhornia crassipes* in Florida lakes resulted in irruptions of other aliens in the newly opened habitat, particularly *Alternanthera philoxeroides* and *Pistia stratiotes* (Schmitz et al. 1993; McCann et al. 1996). In some cases, the ability of invaders to tolerate specific environmental conditions has been important, for example, a tolerance of shading or of low levels of inorganic carbon or oxygen (Madsen and Maberly 1991; Middelboe and Markager 1997; James et al. 1999; Bowes et al. 2002).

Severe damage caused to aquatic and wetland habitats by invasive plants has been reported worldwide, and the problem is increasing in both extent and severity (Barko et al. 1994; Keddy 2000; Cronk and Fennessy 2001; Nagasaka 2002). Invasive aquatic plants can spread quickly when introduced to suitable habitats beyond their native range. For instance, the small duckweed (*Landoltia punctata* = *Spirodella oligorhiza*) spread 2000 km in North America in less than 70 years, while *Elodea canadensis* expanded 365 km in only 5 years in Britain (Les and Mehrhoff 1999; Les et al. 2003). Free-floating *Eichhornia crassipes* and *Salvinia molesta* have also spread remarkable quickly in tropical and subtropical regions (Gopal 1987; Talling and Lemoalle 1998). *Alternenthera philoxoides* spread over 13 million km^2 in only 4 decades in China (Wang and Wang 1988).

Of the noxious aquatic plants listed in Table 1, the World Conservation Union has designated 11 as being of global significance. The most problematic free-floating species are *Azolla pinnata, Eichhornia crassipes*, *Pistia stratioites*, and *Salvinia molesta*, whose noxious effects are widespread in tropical and sub-tropical regions. Other global-scale invasives are *Lythrum salicaria*, *Myriophyllum spicatum*, *Potamogeton crispus*, and *Trapa natans*. Some species are problematic only in certain regions, e.g., *Elodea canadensis* in Europe (Sculthorpe 1967; Simpson 1984; Cook and Urmi-König 1985), *Elodea nuttallii* in Japan (Kunii and Maeda 1982; Nagasaka et al. 2002), *Egeria densa* and *Hydrilla verticillata* in North America (Cook and Lüönd 1982; Cook and Urmi-König 1984; Langeland 1996), and *Lagarosiphon major* in New Zealand (Chapman et al. 1974; Howard-Williams and Davies 1988).

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Table 1. Selected examples of invasive aquatic plants and regions where they are causing serious ecological problems.

Name of species	Native range	North America	South America	Asia	Europe	Africa	Oceania
Alternanthera philoxeroides	Panama River, South America	•		•			•
Azolla pinnata[*]	Asia, Africa, Australia	•		•		•	•
Butomus umbellatus	Eurasia	•					
Cabomba caroliniana[*]	Sub-tropical & temperate Americas	•	•	•			•
Ceratophyllum demersum	North America	•		•	•	•	•
Crassula helmsii	Australia, New Zealand				•		
Egeria densa Planch.	Minas Geraes region of Brazil	•					•
Eichhornia crassipes[*]	Amazon basin	•	•	•		•	•
Elodea canadensis	Temperate North America				•	•	•
Elodea nuttallii	North America			•		•	•
Hydrilla verticilliata[*]	Asia, North Australia	•	•				•
Hydrocotyl ranunculoides	North America				•	•	
Hydrocharis morsus-ranae	Europe	•				•	
Hygrophila polysperma	India, Malaysia, Taiwan, East Indies	•					
Ipomoea fistulosa	South America			•			
Iris pseudacorus	Europe, North Africa, Mediterranean region	•					
Lagarosiphon major	Southern Africa						•
Limnophila sessiliflora	India, Sri Lanka, Philippines	•					
Lythrum salicaria[*]	Eurasia	•			•		•
Myriophyllum aquaticum[*]	South America (Amazon River)	•	•	•			•
Myriophyllum spicatum[*]	Eurasia, North Africa	•				•	
Naja minor	Europe	•			•	•	
Nasturtium officinale	Eurasia	•					
Nymphoides peltata[*]	Eurasia	•		•	•		
Panicum repens	Australia	•					
Pistia stratiotes[*]	South America	•	•	•			•
Potamogeton crispus[*]	Eurasia, Africa, Australia	•		•		•	•
Salvinia molesta	Pantropical	•		•		•	
Landoltia (Spirodella) pinctata	Australia, Southeast Asia	•				•	
Trapa natans[*]	Eurasia	•		•	•		•

[*]Indicates invasive species of global importance according to the Invasive Species Programme (GISP, IUCN).

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In some cases, initially irruptive populations of hydrophytes have subsequently relaxed to a lower level of abundance, as has occurred with *Elodea nutallii* in Japan (Nagasaka et al. 2002). Definite reasons for the decline of *E. nutallii* are not known, but they may be related to pathogens or decreased nutrient loading (Kadano et al. 1997; Nagasaka et al. 2002). Similar rationales have been offered for the declines of some invasive hydrophytes in Europe (Barko et al. 1994).

In some cases, the natural herbivores or pathogens of invasive species have been imported and used as biological controls. Attempts to control *Lythrum salicaria* in North America by a root-weevil (*Hylobius transversovittatus*) and leaf-beetles (*Galerucella calmariensis*, *G. pusilla*, and *Nanophyes marmoratus*) were previously noted (Stamm et al. 1999). In addition, *Eichhornia crassipes* has been bio-controlled by weevils (*Neochetina eichhorniae* and *N. bruchi, and Sameodes albiguttalis*) in parts of Africa, South Asia, and North America (Haag 1986; Gopal, B. 1987; Grodowitz 1998; Julien and Griffiths 1998). Similarly, *Salvinia molesta* has been controlled by a weevil (*Crytobgous salniniae*) in some subtropical and tropical countries (Julien 1992). Some invasions of *Hydrilla verticilliata* have been managed using a tuber-feeding weevil (*Bagous affinis*), a stem borer (*Bagous hydrillae*), an aquatic moth (*Parapoynx diminutalis*), leaf-mining flies (*Hydrellia balciunasi, H. bilobifera, H. pakistanae*), and the grass carp (*Ctenopharyngodon idella*) (Hoyer and Canfield 1997; Weeden et al. 1997; US Army Corps of Engineers 1999). Additional examples include: the control of *Myriophyllum aquaticum* by the beetle *Lysathia* in South Africa, *Myriophyllum spicatum* by the weevil *Euhrychiopsis lecontie* in North America, *Pistia stratiotes* by a leaf weevil (*Neohydronomus affinis*) and leaf moth (*Spodoptera pectinicornis*) in parts of Asia, and *Egeria densa* by grass carp in New Zealand (Tanner et al. 1990; Center 1994; Julien and Griffiths 1998). In many other cases, however, biological control has been ineffective or not attempted, and herbicide spraying, mechanical harvesting, and (or) hydrological methods have been used to try to reduce the abundance of invasive aquatic plants.

5.2. Disturbance and pollution

Aquatic plants are also affected by anthropogenic disturbance and pollution of their habitat, including changes in hydrology associated with reservoir development and canalization, and pollution by heat, nutrients, and toxic chemicals (Haslam 1987; Rørslett 1989; Nilsson and Keddy 1990; Rydlo 1996; Nilsson and Berggren 2000; Richardson et al. 2005).

Reservoir development is often characterized by the hydrologic conversion of a lotic system into a lentic one. Particularly in tropical and temperate regions, the relatively stabilized hydrologic conditions of reservoirs, often coupled with high nutrient availability, favours irruptions of alien aquatic weeds, including *Azolla filiculoides*, *Ceratophyllum demersum*, *Eichhornia crassipes*, *Myriophyllum aquaticum*, *Salvinia molesta*, and *Typha australis* (Petr 1978; Cogels et al. 1997; Nilsson and Berggren 2000; Rodríguez-Gallego et al. 2004). Such irruptions of aquatic plants are much less common in boreal or alpine reservoirs.

Sometimes irruptive populations of aquatic plants are harvested to reduce their abundance, a practice that must be repeated as the weeds regenerate (Nichols 1991; McCann et al. 1996). The harvested biomass may be put to a useful purpose, such as animal fodder, biogas generation, or the production of compost for agricultural use. Baattrup-Pedersen and Riis (2003) found macrophyte communities differed markedly between waterbodies in Demark that were being harvested and those that were not. In contrast, Paal and Trei (2004) reported little effect of harvesting on community composition in Finnish marshes. Smaller-scale disturbances may be associated with boat wakes, with floating-leaved and free-floating species being particularly vulnerable to suffering damage (Haslam 1987; Rydlo 1996).

In terms of pollution, the most frequent anthropogenic influence on aquatic plants is nutrient loading and the cultural eutrophication it induces (see also section 4.3.4.). In general, severe eutrophication of shallow lakes results in a large decline in aquatic plants, which is presumably caused by intense shading by phytoplankton and filamentous algae (Phillips et al. 1978; Blindow 1992; Morris et al. 2003). In a study of fertilized mesocosms, Morris et al. (2003) found that eutrophication resulted in a phytoplankton bloom that induced a large decline in *Vallisneria americana*.

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Emergent, free-floating, and floating-leaved plants are generally more tolerant to toxic pollutants than are submersed species (Merezhko 1973; Dickman 1988; Outridge and Noller 1991; Rodríguez-Gallego et al. 2004). For instance, in an Ontario river affected by dissolved metals, submersed *Ceratophyllum*, *Elodea*, and *Myriophyllum* were less tolerant than floating-leaved *Nuphar*, *Nymphaea*, and *Potamogeton*, which were themselves less tolerant than emergent *Phragmites* and *Typha* (Dickman et al. 1980, 1983; Dickman 1988). *Typha* can tolerate lead, copper, and chromium accumulations as high as 1% (dry-weight basis) in foliage and zinc to 2.5%, and dissolved petroleum hydrocarbons to 1 g/L in ambient water (Merezhko 1973; Mudroch and Capobianco 1979). *Veronica* spp. also have the capacity to accumulate and tolerate copper to high tissue concentrations (Sawidis et al. 1995). Free-floating *Lemna* appears to be particularly sensitive to dissolved cadmium, nickel, and lead (Huffman and Allaway 1973; Samardakiewicz and Woźny 2005).

Herbicides have been widely used to kill aquatic plants in situations where they are judged to be a nuisance (i.e., to be weeds). In most cases, however, the treatment must be repeated as the aquatic weeds may regenerate rapidly from the herbicide-caused disturbance. 2,4-D, a phenoxy herbicide, has been widely used for this purpose, and is effective at killing various hydrophytes (such as *Myriophyllum spicatum*) at an aqueous exposure to 2 mg/L or less; in this use the 2,4-D has a relatively short half-life of < 10 d (Green and Westerdahl 1988; Parsons et al. 2001). Atrazine, a triazine herbicide, is also used as an aqueous herbicide; an exposure to 1 mg/L caused a 50% decrease in biomass of *Ceratophyllum*, *Elodea*, and *Lemna* over a 30 d period in a prairie wetland (Johnson 1986), and *Potamogeton perfoliatus* may be affected by only 0.05 mg/L (Swanson et al. 1991). Glyphosate, an organophosphorus herbicide, is also used but must be applied directly to the foliage of emergent or floating-leaved species to be efficacious (Sheehan et al. 1987). In some cases following glyphosate use, submersed hydrophytes may be stimulated by decreased shading or phosphate fertilization (e.g., *Potamogeton pectinatus* in prairie ponds; Hartman and Martin 1985).

5.3. Climate change

It is widely acknowledged that anthropogenic activities, particularly the combustion of fossil fuels and deforestation, have resulted in large increases in the atmospheric concentrations of CO_2 and other greenhouse gases, with likely consequences in terms of climate change associated with warming of the lower atmosphere (IPCC 2001).

The major intersections of predicted climate change with aquatic plants are an extensive dewatering of waterbodies in regions subjected to increased drought (because of decreased precipitation and (or) increased evapotranspiration), decreased hydrological loading in riverine systems partly fed by glacial meltwaters (due to meltback and possible disappearance of the glaciers), changes in the annual thermal regime and in UV exposure, changes in runoff that alter the loading of nutrients and dissolved organic carbon to waterbodies, and duration of the ice-free and stratified seasons in high-latitude and high-altitude lakes (Schindler et al. 1990, 1996*a*, 1996*b*; Arnell et al. 1996; Magnuson et al. 2000; Poff et al. 2002). Scenarios of climate change in temperate and higher-latitude regions suggest that wetland, pond, and shallow-lake habitats are more likely to be severely affected than are larger, deeper lakes (Carpenter et al. 1992; Mulholland et al. 1997; Poff et al. 2002).

Some limnologists have suggested that a later freeze-up and earlier ice-thaw in northern lakes might result in ecological "benefits" because of a longer growing season, enhanced exchange of gases with the atmosphere, increased rates of nutrient cycling by wind-driven turnover, lessened risk of winter hypoxia, and other factors (Schindler et al. 1990, 1996*a*; Magnuson et al. 2000; Poff et al. 2002; Quayle et al. 2002). In one case, Lacoul and Freedman (2006*b*) attributed the recent colonization by *Ranunculus trichophyllus* of previously non-vegetated high-altitude lakes in the Himalayas to increases in length of the ice-free season. However, there are also potential risks, particularly due to extensive losses of wetland and lake habitat because of decreased precipitation and (or) increased evapotranspiration, and in some regions, the loss of hydrologic inputs from glacial meltwater, as well as nutrient-induced eutrophication

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and shifts to algal dominance (Schindler et al. 1990, 1996*a*; Carpenter et al. 1992; Mulholland et al. 1997; Poff et al. 2002).

Depending on their particular ecophysiology and dispersal ability, species of aquatic plants will likely respond in an individualistic manner to the predicted effects of climate change (Haag and Gorham 1977; Barko and Smart 1981; Pip 1989; Svensson and Wigren-Svensson 1992; Santamaria and Van Vierssen 1997; Rooney and Kalff 2000; Sala et al. 2000; Lacoul and Freedman 2006*b*; see also section 4.1). For instance, species of macrophytes differ markedly in the temperature cues that influence seed germination and the sprouting of overwintering propagules (Haller et al. 1976; Madsen and Adams 1988; Spencer and Ksander 1992). As previously noted, this may vary among geographic races or biotypes, as has been shown for *Hydrilla verticilliata* (Steward and Van 1987; Spencer et al. 2000).

Rooney and Kalff (2000) studied the relationship between climate and inter-annual variations of macrophyte communities, and found large increases in whole-lake biomass during years when the growing season was relatively warm and long. In a 2 year mesocosm study, however, McKee et al. (2002) found that experimental warming (to 3 °C above ambient) had no significant effect on the productivity of a temperate community of *Elodea nuttallii*, *Lagarosiphon major*, and *Potamogeton natans*, with or without nutrient addition and (or) herbivorous fish. The hydrophyte species did, however, vary in their responses with *L. major* showing a significant increase in productivity and relative abundance, while the other species did not. McKee et al. (2002) suggested that the relative thermophilic response of the non-native *L. major* might indicate that climate warming would increase its invasive potential, as has been independently proposed for this species in New Zealand (Howard-Williams and Davies 1988; Wells et al. 1997). Other warming experiments in boreal littoral habitats showed earlier emergence and higher productivity of aquatic plants, particularly of emergent species (Kankaala et al. 2000).

In general, post-glacial range expansions of aquatic plants have been interpreted as being individualistic responses to habitat availability and climate warming (Mulholland et al. 1997; Lami et al. 1998; Dieffenbacher-Krall and Jacobson 2001; Sawada et al. 2003). It has been suggested that aquatic plants will behave in a similar way in response to ongoing warming and related climatic and habitat changes (Dieffenbacher-Krall and Jacobson 2001; Lacoul and Freedman 2006*b*).

6. Conclusions

An interesting biogeographic observation about aquatic plants is that their frequency of endemism is less than that of terrestrial plants. Even in ancient tropical habitats, there are relatively few endemic species of aquatic plants (i.e., compared with terrestrial plants). Many species of aquatic plants are widespread, occurring on more than one continent as a result of extensive dispersal by natural vectors (and more recently, by humans). Nevertheless, all species have particular ranges of environmental tolerance.

Inhospitable environments for aquatic plants are characterized by some combination of dryness, a flow velocity >1 m/s, irradiance <2 % of that at the surface, high salinity >390 g/L, persistent ice cover >9 months (i.e., a short growing season), and growing-season temperature <3 °C at high latitude or altitude or >45 °C in thermal habitats. Although many aquatic plants can tolerate a wide range of conditions, others are narrower in their tolerance and are potentially useful as environmental indicators.

As was suggested in various sections of this review, it is possible to identify various species of macrophytes that are sensitive to specific thresholds of environmental conditions, and are therefore potentially useful indicators of change. However, these tolerances are idiosyncratic, in that species that are sensitive to one environmental factor are not necessarily highly responsive to other ones. As such, the use of aquatic plants as indicators must rest on a foundation of the known tolerances of species, within an ecoregional context. The greatest dearth of relevant understanding concerns interacting factors, such as complexes of factors (i.e., chemical, physical, and biological) and their effects on indvidual species and commuities.

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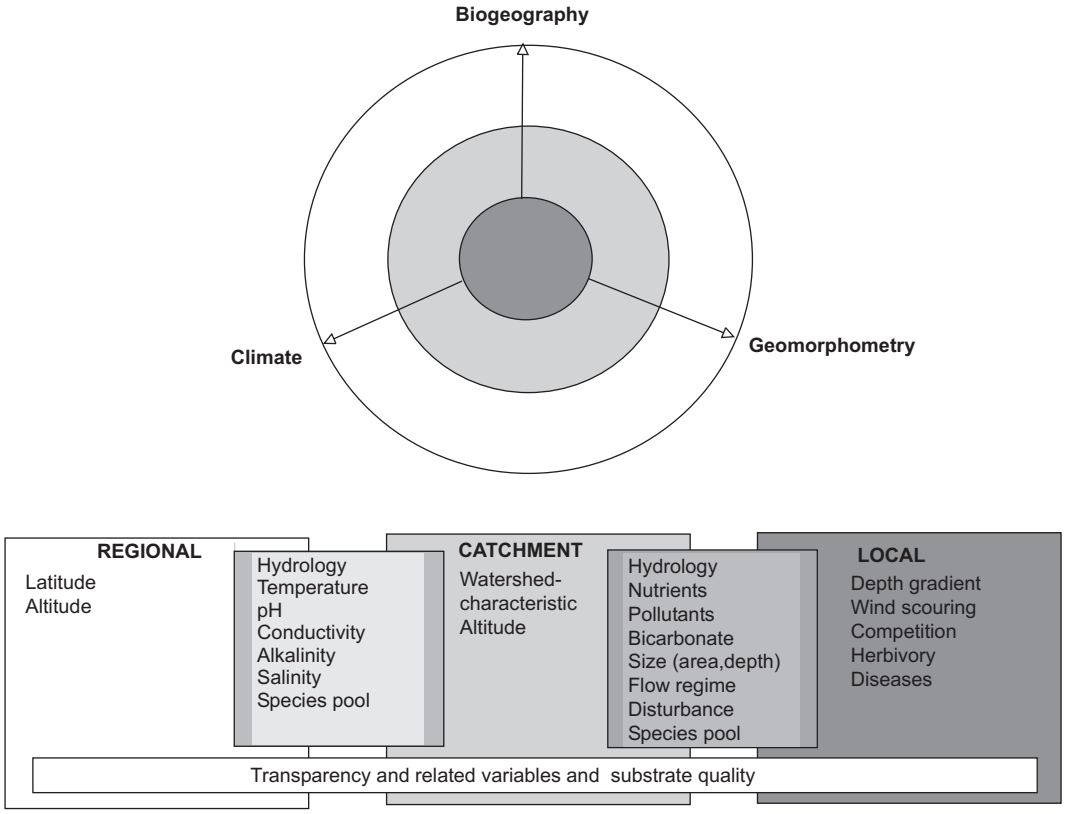
Fig. 1. A conceptual model of variables affecting the distribution and abundance of aquatic plants at different scales. In the diagram, the concentric circles represent regional, catchment, and local scales (from outer to inner, respectively). Key variables are grouped according to the scale at which they are most influential. The model suggests that aquatic plants and their communities are affected by three major complexes of environmental influences (biogeography, climate, and geomorphology) operating at three scales (regional, catchment, and local). The intermediate boxes imply overlap of spatial scale. See text for additional detail.



Factors affecting the distribution of aquatic plants can be considered at various spatial scales (Fig. 1). The **regional** level operates at a coarse-grain or synoptic scale of either geography (e.g., continental, or biome in terms of boreal, temperate, or tropical distributions) or environmental conditions (e.g., hard or soft water, acidic or alkaline, clear or coloured and (or) turbid, saline or fresh). A **catchment** or medium-grain filter relates to particular hydrologic ecosystems (e.g., a watershed or an entire waterbody) and the conditions occurring there (e.g., nutrients, pH, bicarbonate, colour). Finally, the **local** or fine-grain scale relates to particular habitats and communities and the factors operating at that level (e.g., competition, herbivory, sediment characteristics).

Environmental factors affecting the distribution and abundance of aquatic plants are varied and interacting, but they can be aggregated into three key vectors that operate at all scales: biogeography, climate, and geomorphology (Fig. 1).

- **Biogeography** refers to the latitudinal and altitudinal distribution of species. At large scales it relates to distributions across and within continents and regions. In local habitats and communities it influences the nature of biological interactions.

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- **Climate** relates to hydrology, temperature, length of the growing season, and related factors. These factors can vary at all scales, from large-regional to microhabitat.

- **Geomorphology** is relevant to physical dimensions related to geography, such as basin attributes and many chemical qualities. These factors are affected by large-scale influences on regional topography, bedrock, soil, and geological history (such as glaciation). They also vary on shorter-time and smaller-region scales, for example, according to local topography, rock, and soil qualities.

However, these various factors interact spatially and temporally to varying degrees: the concentration of phosphate, for example, is related to rock and sediment qualities as well as biological, climatic, and geochemical influences on nutrient cycling. Because of these kinds of complex interactions, environmental factors are not independent variables affecting the distribution and abundance of aquatic plants. Nevertheless, bivariate and multivariate analyses can help to sort out the relative predictive strengths of variables and their vectors in particular ecological contexts. If these relationships are known and mathematically robust, they can be used by managers of aquatic ecosystems and by ecologists to predict the environmental impacts of proposed human activities (i.e., those relevant to aquatic plants and their communities).

Moreover, many species of aquatic plants show a high level of polymorphism and phenotypic plasticity in their responses to variations of environmental factors, a quality that allows them to occur over a wide range of conditions. Because of this inherent biological variation, many macrophytes are poor indicators of specific habitat conditions. Nevertheless, some species have narrower tolerances, and are potentially useful indicators of environmental conditions, either in terms of their presence or their relative abundance within communities. Examples of potentially useful indicator species were noted throughout this review.

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