Why are most aquatic plants widely distributed?
Dispersal, clonal growth and small-scale heterogeneity in a stressful environment

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Abstract

Non-marine aquatic vascular plants generally show broad distributional ranges. Climatic factors seem to have limited effects on their distributions, besides the determination of major disjunctions (tropical–temperate–subarctic). Dispersal should have been frequent enough to assure the quick colonisation of extensive areas following glacial retreat, but dispersal limitation is still apparent in areas separated by geographic barriers. Aquatic vascular plants also show limited taxonomic differentiation and low within-species genetic variation. Variation within populations is particularly low, but variation among populations seems to be relatively high, mainly due to the persistence of long-lived clones. Ecotypic differentiation is often related to factors that constrain clonal reproduction (salinity and ephemeral inundation). Inland aquatic habitats are heterogeneous environments, but this heterogeneity largely occurs at relatively small scales (within waterbodies and among neighbouring ones). They also represent a stressful environment for plants, characterised by low carbon availability, shaded conditions, sediment anoxia, mechanical damage by currents and waves, significant restrictions to sexual reproduction, and sometimes also osmotic stress and limited nutrient supply. I propose that the generality of broad distributions and low differentiation among the inland aquatic flora is best explained by a combination of: (1) selection for stress-tolerant taxa with broad tolerance ranges. (2) The selective advantages provided by clonal growth and multiplication, which increases plant tolerance to stress, genet survivorship and population viability. (3) Long-distance dispersal of sexual propagules and high local dispersal of asexual clones. (4) The generality of broad plastic responses, promoted by the combination of clonal growth, high local dispersal, small-scale spatial heterogeneity and temporal variability.
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1. Introduction

Non-marine aquatic organisms, and among them aquatic plants, typically occur in island-like habitats. Despite the isolation of their habitats, aquatic plants tend to have broader distributions than their terrestrial counterparts. This discrepancy, particularly in combination with the limited life span of lakes and wetlands on geological and evolutionary time scales (Hutchinson, 1975; Wetzel, 1988), has often been used to conclude that dispersal means (chiefly bird-mediated dispersal) must be readily available (e.g., Barrett et al., 1993; Jacobs and Wilson, 1996).

However, broad distributional ranges require more than high dispersal rates. Geographic distribution of terrestrial plant species is often limited by climatic factors, by competition with species that perform better under their local environment (Woodward and Williams, 1987; Woodward, 1988) and by the reduced reproductive success of range-limit populations (García et al., 2000). A number of alternative explanations have been invoked to account for the high proportion of widely distributed taxa among the aquatic plants. They include:

(i) the uniformity of the aquatic environment (e.g., Sculthorpe, 1967; Cook, 1985; Les, 1988; Barrett et al., 1993), which is assumed to result in the broad dominance of best-fitted, single-purpose genotypes (sensu Barrett et al., 1993);

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(ii) widespread clonality, which can contribute to the broad distribution of aquatic plants by reducing both the risk of genotype mortality and the genetic differentiation of spatially separated populations (Barrett et al., 1993);

(iii) high phenotypic plasticity, a result of general-purpose genotypes (Barrett et al., 1993).

In this paper, I will first review data on the distribution of vascular aquatic plants, to evaluate the generally held assumption that aquatic plants are more often broadly distributed than terrestrial plants. I will then assess the extent to which existing distributions result from ecological (largely climatic) constraints as opposed to dispersal limitation, to the effect of geographic barriers and to historical factors. I will also review recent studies on taxonomic differentiation, genetic variation and ecotypic differentiation, evaluating the extent to which the generality of broad distributions among vascular aquatic plants is associated with low levels of (taxonomic, genetic or ecotypic) variability. After this, I will review the factors that could contribute to this broadly distributed, poorly differentiated character, with an emphasis on the constraints posed by habitat heterogeneity and the source of phenotypic variation displayed by the aquatic plants in response to it (plasticity vs. genetic variation).

Hereafter, I will use the term 'aquatic plants' in its broadest sense, with the specific aim of including all growth forms along the ecological and evolutionary continuum ranging from plants in flooded soils to submerged plants. In this I will follow Barrett et al. (1993), because I feel that paying attention to the differences among particular growth forms is crucial in understanding the differences between aquatic and terrestrial plants. Throughout the paper, however, I will focus more often on floating-leafed and submerged plants, since they represent the ecological and evolutionary extreme of the terrestrial–aquatic gradient (Duarte et al., 1994).

2. Distribution of vascular aquatic plants

2.1. Geographical ranges

Practically every researcher interested in aquatic plants has noted the wide geographical range they occupy (e.g., Sculthorpe, 1967; Hutchinson, 1975). Many species have broad world-wide or continental ranges (for example, *Ceratophyllum demersum* L., *Lemna minor* L., *Potamogeton pectinatus* L. and *Typha latifolia* L.; Stuckey, 1993) and the helophyte *Phragmites australis* is perhaps the most cosmopolitan angiosperm (Hutchinson, 1975). Sculthorpe (1967) identified 60% of recorded hydrophytes as having extensive world-wide ranges (i.e., occurring in more than one continent), while only 40% were confined to a single continent. Local endemisms are rare, although their abundance seems to increase in the tropics (Cook, 1983, 1985). Even rare and endemic species tend to have large geographic ranges: for

example, the rare Indian endemic *Wiesneria triandra* (Dalzell) Micheli occupies a geographic range of approximately 900 km (Camenish and Cook, 1996).

In contrast, terrestrial plants show a lower proportion of broadly distributed species and much higher indices of endemicity. Although aquatic plants only represent a very small proportion of vascular plants (1–2%; Cook, 1990), subcosmopolitan taxa identified by Thorne (1972) in his review on major disjunctions included a high proportion of aquatics (more than half of the genera and nearly all species). Similarly, in a study of the flora of southern Australia, Kloot (1984) noted that out of 98 native species considered to have disjunct natural distributions between Australia and other temperate regions of the world, 61 were aquatic. Species from aquatic, coastal and wet habitats are also over-represented among the herbaceous disjunct species from Tasmania and New Zealand (Jordan, 2001).

Even within a relatively small subcontinent, such as Europe, aquatic species tend to show larger ranges than closely related terrestrial species. An example is provided by the genus *Ranunculus*, which includes both aquatic and terrestrial species. A comparison of the European distribution of both groups of species using published distribution maps (Finnish Museum of Natural History, 1999) showed that terrestrial species have a much higher proportion of species with narrow distributions (Kolmogorof–Smirnoff test, $P < 0.001$; Fig. 1, upper panel) and occur within significantly smaller latitudinal ranges (Kolmogorof–Smirnoff test, $P < 0.001$; Fig. 1, lower panel).

2.2. Distribution patterns

Ecological factors, and climate in particular, are known to constrain the distribution of plant species, resulting for example in large vegetation zones (Walter, 1973). Aquatic plant distribution reflects to some extent this zonation, although it is strongly simplified and largely restricted to very broad climatic regions. A major disjunction between the temperate and tropical floras is indicated by the distribution of aquatic plant families (Crow, 1993). Some families have strong tropical affinities, with higher species diversity in tropical latitudes (e.g., Podostemaceae, Hydrocharitaceae, Limnochariataceae, Mayacaceae, Xyridaceae, Eriocaulaceae, Pondeteriaceae, Aponogetonaceae; Crow, 1993). Others are primarily temperate, with higher diversity in temperate latitudes (e.g., Potamogetonaceae, Juncaginaceae, Sparganiaceae, Haloragaceae, Elatinaceae, Callitrichaceae and Hippuridaceae; Crow, 1993). Practically none of these families is, however, restricted to a single climatic region (i.e., even typically tropical families such as the Podostemaceae and Xyridaceae have temperate representatives).

Several families with temperate affinities include genera with broad distributions, which represent the remnants of the Arcto-Tertiary flora that covered the northern hemisphere on both continents prior to the continental glaciation
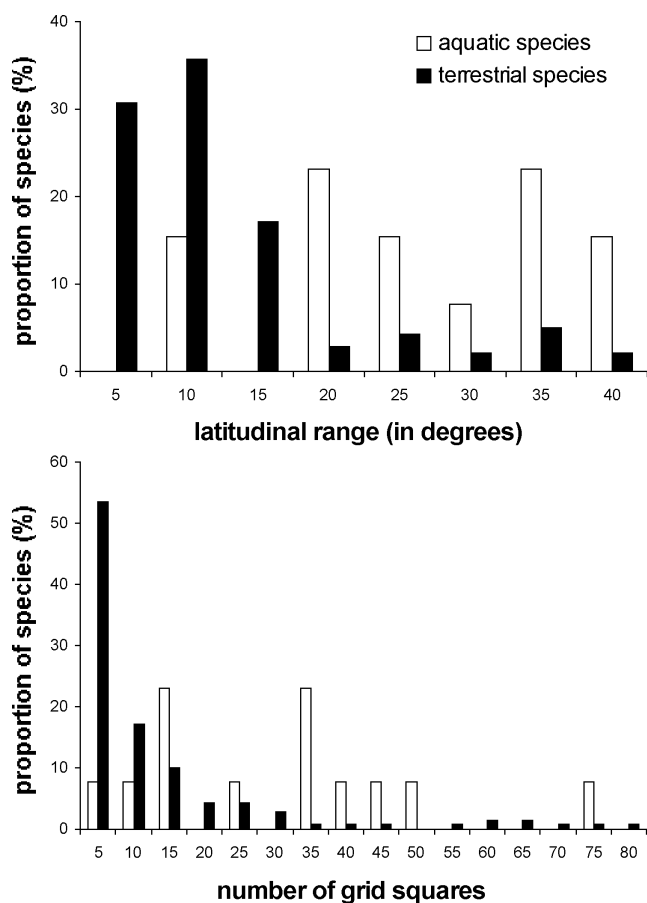
Fig. 1. A comparison of the geographic ranges of aquatic and terrestrial species of *Ranunculus* over Europe. The x-axis represents the latitudinal range (upper panel) and the number of grid squares (5° latitude × 6° longitude, lower panel) at which each species was present. The comparison includes taxa considered as species by Flora Europaea (Finnish Museum of Natural History, 1999). However, since lack of taxonomic resolution could bias the distribution of aquatic species towards larger species ranges, five taxonomically conflicting aquatic subspecies (*R. peltatus* sbspp. *peltatus*, *baudotii* and *fucoides*; and *R. trichophyllus* sbspp. *trichophyllus* and *eradicatus*) were given species status.
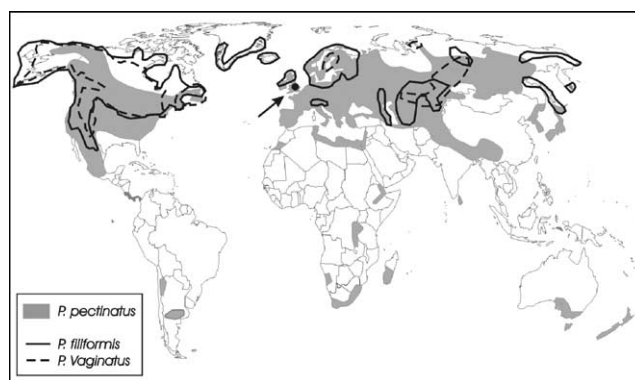

Fig. 2. Distribution of the three species of *Potamogeton* section *Coleogeton* (which include subcosmopolitan *P. pectinatus* and boreal *P. filiformis* and *P. vaginatus*). The arrow points to the locality (indicated by a dot) where two populations of *P.* x *suecicus* (= *P. pectinatus* × *P. filiformis*) situated Southern of the distribution range of one of its parents, *P. filiformis*. The figure is based on published data from Meusel et al. (1965), Hultén and Fries (1986), Naturhistoriska riksmuseet (1996), Preston (1995) and Preston et al. (1999), and unpublished observations by H.H. Halgelbroek, J.J. Pilon and L. Santamaría.

(Stuckey, 1993). This flora survived glaciation along the glacial ice margin or in isolated refugia, and extended northwards following the glacial retreat. Included in this group are boreal species that are restricted to colder climatic regions (northern latitudes and temperate mountain ranges, e.g., *Potamogeton alpinus* Balb. and *P. gramineus* L.; Preston, 1995). It is interesting to note that many of these boreal species have closely related species with broad, boreal-temperate distributions, suggesting ecological differentiation of sympatric species in their northern ranges (e.g., *Potamogeton* section *Coleogeton*, which include subcosmopolitan *P. pectinatus* and boreal *P. filiformis* Pers. and *P. vaginatus* Turcz., Fig. 2; or subcosmopolitan *Sagittaria sagittifolia* L. and boreal *S. natans* Pall.; Preston, 1995; Naturhistoriska riksmuseet, 1996).

Geographical barriers and patterns of long-distance dispersal are often referred to as contributors to the distribution of aquatic floras (Jordan, 2001). In their biogeographical analysis of the freshwater flora of Australasia, Jacobs and Wilson (1996) conclude that the existing distributional patterns are best explained by a combination of dispersal, vicariance and local speciation. They observed a major disjunction between the tropical and temperate aquatic floras, attributed to a climatic barrier and more clearly defined at the species and genus level than at the family level. In addition, geographically close areas within the tropical or temperate zones had more similar floras (particularly at the family level), indicating limited dispersal of species across large distances or through geographic barriers (Jacobs and Wilson, 1996). Local speciation was considered of occasional importance, at the species level, in aquatic genera that proliferated in certain regions following arrival via long-distance dispersal (Jacobs and Wilson, 1996). All in all, Jacobs and Wilson (1996) conclude that the biogeography of water plants shows the lasting imprint of waterbird migration, super-imposed on a major disjunction determined by climatic factors.

Historical factors may also affect plant distribution, as indicated by Stuckey (1993) in his analysis of the geographical distribution of the North American aquatic flora. After excluding a group of 21 widespread species, he found the distribution of the more restricted species to correlate well with continental physiographic regions (Stuckey, 1993). Furthermore, he related the present distribution of native hydrophytes to historical processes, which arose from a series of range contractions and expansions following major climatic changes and from the influence of geographic barriers upon those (e.g., the invasion of SW coastal plains from the Appalachian Upland region, the invasion of northern US and Canada following the retreat of the Wisconsin glacier and the invasion of the Great Plains semiarid region following the Cordilleran Uplift; Stuckey, 1993).

Climatic factors thus seem to have limited importance in determining the distribution of aquatic plants. Their influence is restricted to large climatic contrasts, such as tropical vs. temperate vs. boreal/subarctic, and to low taxonomic levels (species, genus). Dispersal events seem to have been frequent enough to ensure the quick recolonisation of extensive areas following glacial retreat. Dispersal limitation is still traceable, however, in isolated continents and in islands where the arrival of new species depends on less frequent, long-distance dispersal events (such as Australasia; Jacobs and Wilson, 1996) or in continental areas separated by geographic barriers (such as east and west North America; Stuckey, 1993).

3. Taxonomic and genetic differentiation

3.1. Taxonomic differentiation

Aquatic plants show relatively little taxonomic differentiation compared with terrestrial groups (Sculthorpe, 1967; Hutchinson, 1975; Les, 1988; Cook, 1990). Of the 33 strictly aquatic families, 30 include fewer than 10 genera, 17 contain only one genus and three consist of a single species (Sculthorpe, 1967; Barrett et al., 1993). Moreover, the amount of evolutionary diversification declines as one moves from amphibious and emergent groups to fully submerged, hydrophilous taxa (Barrett et al., 1993). The reduced taxonomic differentiation of the vascular aquatic plants is in sharp contrast with their large variation in morphology, life-history and reproductive biology. It is thus tempting to relate this lack of taxonomic differentiation to the abundance of species with broad distributions. The limited impact of allopatric speciation among populations occurring in separate geographic areas, and of adaptive radiation following long-distance dispersal events (driven by the ecological opportunity that exists in new geographical areas) seems to have contributed to the maintenance of few species with broad ranges.

Conclusions about the lack of taxonomic differentiation among aquatics should however be drawn with caution. Aquatic plants generally show a strong reduction in morphological traits and high intraspecific variation (often attributed to high levels of plasticity), which seriously constrain taxonomic resolution (an extreme example is provided by the genus *Wolffia*; Crawford and Landolt, 1995). On closer examination, particularly by the application of molecular tools, broadly distributed species might be shown to actually represent groups of cryptic, sibling species. Examples abound among aquatic organisms (particularly marine pelagic organisms, Knowlton, 2000; Norris, 2000; but also freshwater, King and Hanner, 1998; Martin and Bermingham, 2000; Witt and Herbert, 2000), although until now they are rare among freshwater plants (but see Crawford et al., 1996, 2001).

It is thus important to bear in mind that, on close examination, cosmopolitan species might be composed of groups of sibling species. An example is provided by *Zannichellia palustris* L., a species generally taken to represent a single taxon with cosmopolitan distribution (e.g., Naturhistoriska riksmuseet, 1996; BONAP, 1998; Finnish Museum of Natural History, 1999). A detailed examination of the taxonomic status of European *Zannichellia* based on morphometry, ecophysiological traits and chromosome numbers (Van Vierssen, 1982a, b) gave strong support to its subdivision into four species: *Zannichellia palustris* L., *Zannichellia pedunculata* Rchb., *Zannichellia major* Boenn. and *Zannichellia peltata* Bertol. The distribution of these species in Europe follows a latitudinal gradient, with *Z. major* being most abundant in the Baltic region, *Z. palustris* and *Z. pedunculata* in temperate central Europe and *Z. peltata* in southern Europe (Van Vierssen, 1982b, c). This gradient is correlated with an increase in salinity tolerance and a shift in emphasis from asexual perennation to sexual reproduction, allegedly related to the increase in temporary habitats from northern to southern Europe (Van Vierssen, 1982b, c). It is however worth noting that, even after subdividing the European *Zannichellia* into four species, these still show broad distributions: *Z. major* ranges from Scandinavia to the Netherlands, *Z. pedunculata* from Scandinavia to southern France and *Z. palustris* from Scandinavia to Greece (Van Vierssen, 1982b, c).

3.2. Genetic variation

The conservative macroevolutionary pattern found among the vascular aquatic plants seems to be associated with low genetic variability and weak population differentiation below the species level (Les, 1988; Barrett et al., 1993). In 1993, Barrett et al. (1993) reviewed the existing literature on allozyme variability in aquatic plants and concluded that widespread monomorphism and weak population differentiation was common among submerged (hydrophylous) species. While extensive monomorphism was also observed in some helophytes (*Typha*) and annual halophytes (*Salicornia*), short-lived emergent plants seemed to be an exception (Barrett et al., 1993).

Later studies have confirmed that hydrophytes (Triest, 1991a, b; Hettiarachchi and Triest, 1991; Hofstra et al., 1995; Hollingsworth et al., 1995; Gornall et al., 1998; Nakamura et al., 1998) and emergent species (Pellegrin and Hauber, 1999) show limited isozyme variation at least within populations. A few studies have suggested an association between distributional range and genetic variation, with broadly distributed species showing higher diversity than species with restricted distributions (Crawford et al., 1997). Endemic species, in particular, showed very low isozyme diversity within and between populations (e.g., the south-Indian endemic *Wiesneria triandra*, the Californian vernal-pool endemic *Howellia aquatilis* and the mountain

endemic *Glyceria nubigena*; Lesica et al., 1988; Godt and Hamrick, 1995; Camenish and Cook, 1996).

Variation within populations tends to be low, but strong differentiation among populations seems common (Djerbrouni, 1992; Laushman, 1993; Hofstra et al., 1995; Cole and Voskuil, 1996; Hollingsworth et al., 1996b; Akimoto et al., 1998; Gornall et al., 1998; Gao et al., 1999, Gao and Hong, 2000a, b). There are some exceptions to this, however. For example, emergent species *Sagittaria isoetiformis* and *S. teres* showed high overall and within-population genetic variation (Edwards and Sharitz, 2000). In some hydrophytes, high small-scale genetic diversity has been reported within populations (Lokker et al., 1994). In *Lemna minor*, loss of sexual reproduction due to generalised apomixis (i.e., seed production without fertilisation and/or meiosis) did not seem to limit genetic diversity (Vasseur et al., 1993). In *Lemna aequinoctialis*, no pattern of large-scale geographic variation was detected (i.e., distant populations contained the same alleles detected in the local populations; Crawford et al., 2001).

Owing to its higher discriminatory power, DNA-based markers usually detect higher polymorphism than isozyme methods (Fernando and Cass, 1996; Ge et al., 1999). Still, they seem to confirm isozyme results: moderate overall genetic diversity, low within-population variation and high among-population variation (Zeidler et al., 1994; Jordan et al., 1996; Koppitz, 1999). Other studies have detected, however, considerably larger genotypic variation than isozyme studies (Mader et al., 1998). It is noteworthy that for some emergent species, a decrease in clonal diversity from shore to water has been reported (e.g., *Phragmites australis*; Koppitz, 1999).

The low levels of within-population variation, and the high population differentiation are most likely related to widespread clonal multiplication. Clonal multiplication is likely to result in low genotypic diversity, but does not necessarily imply low genetic diversity at genet level. Indeed, reported genotypic diversity values were often similar to terrestrial vegetatively reproducing plants (Lokker et al., 1994; Cole and Voskuil, 1996; Hollingsworth et al., 1996b) and several authors have argued that population structure of emergent species reflects a primarily vegetative mode of reproduction and spread (Pellegrin and Hauber, 1999; Ivey and Richards, 2001). For example, a detailed analysis of the partitioning of genetic diversity among ramets and genets in *Cladium jamaicense* showed that clonal reproduction was responsible for the observed patterns of genetic differentiation among populations (Ivey and Richards, 2001). In contrast with ramet-level estimates (which reflect clonal structure), genet-based estimates indicated that no significant population differentiation occurred. The observed pattern of genetic differentiation was consistent with the persistence through long-lived clones of patterns established during colonisation (Ivey and Richards, 2001).

Variation among populations in the amount of genotypic diversity may also result from differences in sexual recruitment, i.e., from the co-existence of populations colonised from a single clone and populations where frequent seedling recruitment occurs (Piquot et al., 1996). A good example of geographic patterns that probably reflect spatial variation in sexual recruitment was provided by two separate analyses of the population structure in *Potamogeton pectinatus*, carried out over different geographic scales. At a continental scale, high levels of genetic divergence were found among northern range populations as compared with central European ones, allegedly due to the higher frequency of asexual reproduction and clonal divergence in northern than in central regions (Mader et al., 1998). At a local scale, high levels of within-population genotypic variation were found within a central European freshwater estuary (H. Hangelbroek et al., unpublished).

Population differentiation may also result from restricted gene flow (isolation by distance). Isozyme and DNA studies have indicated restricted gene flow among populations of aquatic species (Barrett et al., 1993), based on correlations between geographic and genetic distance that were in agreement with isolation by distance (i.e., with stepping-stone models of population structure; Hollingsworth et al., 1996b; Mader et al., 1998). The threshold distance above which populations showed restricted gene flow was however variable, e.g., 100 km for *Eichornia paniculata* (Barrett et al., 1993) and 1000 km for *Potamogeton pectinatus* (Hollingsworth et al., 1996b). Such variation in threshold geographic distance may reflect the effect of propagule transport by waterfowl, which operates at different scales in different geographic regions (R. Gornall and A. King, unpublished; Mader et al., 1998).

Finally, differences among populations may result from adaptive responses to local differences in selection pressure. Population differentiation in morphological and physiological traits was indeed reported for a number of aquatic species (Koch and Dawes, 1991a, b; Barrett et al., 1993; Idestam-Almquist and Kautsky, 1995; Koch and Seeliger, 1988,) and it was interpreted as adaptive in most instances. Examples include genetically based differences in the response to salinity (e.g., *Ruppia maritima*; Koch and Dawes, 1991a, b), salinity + habitat temporality (e.g., *Ruppia maritima*; Koch and Seeliger, 1988) and salinity + sediment type (e.g., *Ruppia occidentalis*; Barrett et al., 1993) of plants originating from different populations. Genetic differentiation within populations, but sometimes also among populations, has also been reported in response to variation in flooding and water level (e.g., in *Ranunculus flammula*, *Glaux maritima* and *Spartina* spp.; Cook and Johnson, 1968; Jerling and Elmgren, 1996; Lessmann et al., 1997). Such differentiation often results in small-scale spatial segregation of ecotypes along centre-periphery gradients in temporary ponds and vernal pools (Cook and Johnson, 1968) and along flooding gradients in salt marshes and river floodplains (Cook and Johnson, 1968; Lessmann et al.,

1997), suggesting that it is caused by selection pressures rather than by restricted dispersal (Barrett et al., 1993). In contrast, *Ruppia maritima* populations from Florida and North Carolina did not differ in their response to climatic factors such as temperature or photoperiod; instead, they seem to react to climatic differences by modifying their growing season in the field (Koch and Dawes, 1991b).

4. A review of the arguments that could explain the broad distributions, and low taxonomic and genetic differentiation of aquatic angiosperms

4.1. Uniformity of the aquatic environment

It is widely believed that the uniformity of the aquatic environment allows aquatic plant species to occupy very large ranges. Occasional statements concerning the alleged uniformity of the aquatic environment are common in the literature (Sculthorpe, 1967; Cook, 1985; Les, 1988; Barrett et al., 1993,), but they tend to be rather vague and rarely specify which environmental variables they refer to or what they mean by 'uniformity'. In general, this term is used to refer both to the alleged similarity of aquatic habitats over large geographic regions, or to the relative 'benign' character of this milieu where the extremes of terrestrial environments are moderated. Other authors have dissented from the view of the aquatic environment as 'benign', arguing instead that it poses a great number of limitations to plant growth and reproduction (Bowes, 1987). In the following paragraphs, I will argue that the alleged uniformity of the aquatic environment should not be taken for granted, and that it is particularly sensitive to the environmental variables considered and the spatio-temporal scale of observation. For this purpose, I will briefly review the scale of variation of key environmental variables, and their effect on the productivity and specific composition of the aquatic vegetation.

4.1.1. Light

The light environment experienced by emergent and floating plants is roughly comparable with that experienced in open terrestrial habitats, although canopy shading also occurs in forested lakeshores and riverbanks, for example. Submerged aquatic plants, on the other hand, are faced with a great diversity of light climates, which results from the different optical properties of the waters they inhabit (Jeffrey, 1981; Holmes and Klein, 1987; Duarte et al., 1994). Light attenuation through the water column largely depends on phytoplankton abundance, suspended solids concentration (often related to siltation) and the concentration of dissolved material (Holmes and Klein, 1987; Chambers and Prepas, 1988). Owing to differences in the trophic status (Jeppesen et al., 1990, 1994) and in the amount of wind-induced siltation (Blom et al., 1994), neighbouring lakes can show enormous differences in water transparency, which translate into large differences in light regime (irradiance

and spectral quality). The effect of this variation on submerged plant growth strongly depends on lake morphometry (depth and slope; Duarte et al., 1986; Canfield and Duarte, 1988). Large rivers tend also to show a strong decrease in water transparency from their upper to their lower courses (Dawson, 1988). In lakes with turbid waters, sharp shore-centre light gradients can be found (Duarte et al., 1986). In addition, submerged and amphibious plants growing in those lakes will encounter a vertical light gradient and have been reported to react with plastic responses such as canopy formation and photosynthetic acclimation (Bijl et al., 1989). In lakes inhabited by species with seasonal growth cycles, temporal differences in siltation and phytoplankton growth also result in large temporal variation in underwater light climate (Blom et al., 1994; Santamaría et al., 1996; Vermaat et al., 2000). As a consequence, latitudinal variation in irradiance, related to variation in solar elevation and winter ice cover, is less important than local (among lakes) and seasonal variation (Duarte et al., 1986; Canfield and Duarte, 1988).

In comparison with terrestrial, emergent and floating plants, almost all submerged plants are shade adapted: they show low light saturation and compensation points, and low photosynthetic rates (Bowes, 1987; Duarte et al., 1994). In many cases, carbon limitation seems to represent a stronger limitation than too little or too high irradiance (Bowes, 1987). Owing to large variation in plant morphology (and to a lesser degree in leaf mass ratio, leaf chlorophyll content and photosynthetic performance; Duarte et al., 1994; Hootsmans and Vermaat, 1994; Santamaría and van Vierssen, 1995), different species differ considerably in their capacity to grow under the strong shading that characterises eutrophic and otherwise turbid lakes (Barko et al., 1982; Chambers and Kalff, 1987; Fig. 3). This results in considerable variation in the cover and biomass yield (Duarte et al., 1986; Canfield and Duarte, 1988), species composition (Chambers, 1987; Vestergaard and Sand-Jensen, 2000a) and species richness (Vestergaard and Sand-Jensen, 2000b) of submerged plant communities among lakes of contrasting trophic status.

4.1.2. Temperature

Water buffers aquatic organisms against rapid fluctuations in air temperature, but seasonal extremes can be observed (from 0 to 40 °C, particularly in densely vegetated surface waters; Bowes, 1987). Vertical thermal gradients often develop in the water column of densely vegetated ponds and shallow lakes, creating considerable within-plant variation in thermal conditions. Floating, amphibious and emergent species are exposed in increasing degree to daily and seasonal temperature fluctuations. Damp soils probably show higher thermal conductivity than dry soils, exposing the root zone of wetland species to larger temperature fluctuations than would take place in neighbouring terrestrial habitats. In addition, aquatic species probably track water temperatures more closely than terrestrial plants do
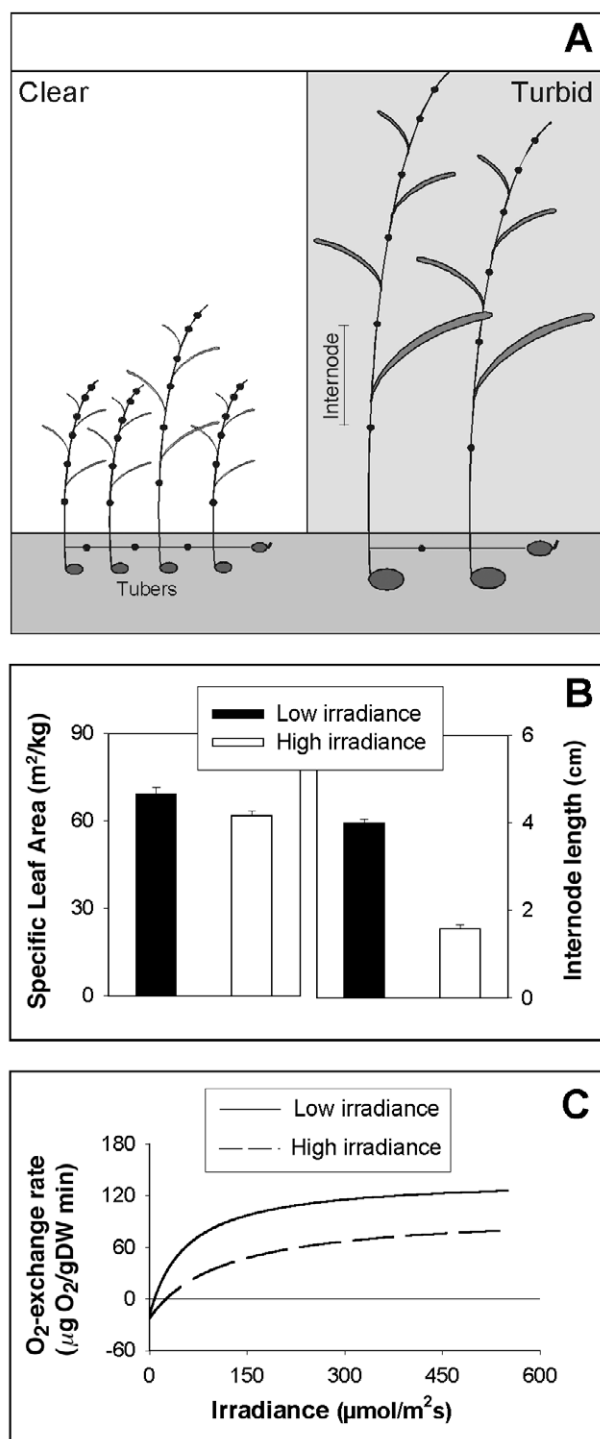
Fig. 3. Plastic responses of the submerged angiosperm *Potamogeton pectinatus* in response to changes in the light climate caused by increased water turbidity. A. Pictorial representation of responses to decreased irradiance, including changes in morphological traits (e.g., increased internode length and specific leaf area, shown in B; and decreased number of ramets) and their effect on physiological rates (e.g., increases in the rates of irradiance-saturated photosintesis and apparent quantum yield, shown in C). Acclimation responses may also take place across clonal generations, for example, through increased tuber size under shaded conditions (depicted in A). The figure is based on unpublished data from J.J. Pilon and L. Santamaría (morphological and physiological changes), and H. Huber and L. Santamaría (tuber size).

with air temperatures, due to the higher thermal conductivity of water and to the absence of insulating or heat-dissipating structures in the surface of submerged leaves and stems.

There seems to be an apparent contradiction between the reduction in seasonal temperature fluctuations and in frost damage risk, and the strong seasonality in plant growth shown by many temperate species. Should temperature be strongly buffered, one would expect extended growth seasons. Although tropical/subtropical species and some cold-water isoetids grow as perennial, most temperate submerged and floating plants overwinter by means of asexual propagules and show shorter growth seasons than many terrestrial grasses, for example. Daylength differences provide a proximate mechanism to explain the induction of perennation and senescence (Salisbury, 1981; Titus and Hoover, 1991; Van Vierssen and Hootsmans, 1994). However, they are unlikely to provide an ultimate explanation for reduced growth seasons, since experimental manipulations have shown a weak effect of short daylengths on growth and biomass yield (Koch and Dawes 1991b; Santamaría and van Vierssen, 1995).

Submerged plants also have high temperature optima (Santamaría and van Vierssen, 1997; Fig. 4). Although some perennial isoetids are able to maintain low rates of photosynthesis at low temperatures (Boylen and Sheldon, 1976), most species show optimal rates of photosynthesis and respiration at 20–35 °C (Bowes, 1987; Santamaría and van Vierssen, 1997) and a limited capacity for thermal acclimation (Santamaría and Hootsmans, 1998; Pilon and Santamaría, 2001, 2002). In temperate species, growth strongly decreases or becomes arrested at temperatures between 10 and 15 °C (Barko et al., 1982; Pilon and Santamaría, 2002). All this has been taken as an indication that the aquatic environment is well buffered against thermal fluctuations. Temperatures below 15 °C are however common during most of the year in temperate regions (Fig. 4). Submerged plants growing in different regions seem to adapt their phenology rather than their thermal response (Pilon and Santamaría, 2002) and specimens collected over broad latitudinal gradients show small intra- and interspecific differences in their optimal temperature for growth and photosynthesis (Santamaría and van Vierssen, 1997; Pilon and Santamaría, 2002; L. Santamaría and Aitink, unpublished; Fig. 4). In alpine and sub-alpine lakes of North America, aquatic angiosperms were confined to depths with temperatures greater than 10 °C (Dale, 1986). Instead of being optimally adapted to a thermally uniform environment, aquatic plants seem to be strongly constrained in their thermal response and respond to environmental heterogeneity by shifting their growth period. This constraint could stem from a general physiological limitation to avoid photorespiration at low temperatures, which probably relates to the low carbon availability of the aquatic environment (Bowes, 1987). Alternatively, high temperature optima may reflect modifications in the photosynthetic biochemis-

try necessary to enhance carbon uptake under water (Bowes and Salvucci, 1989).
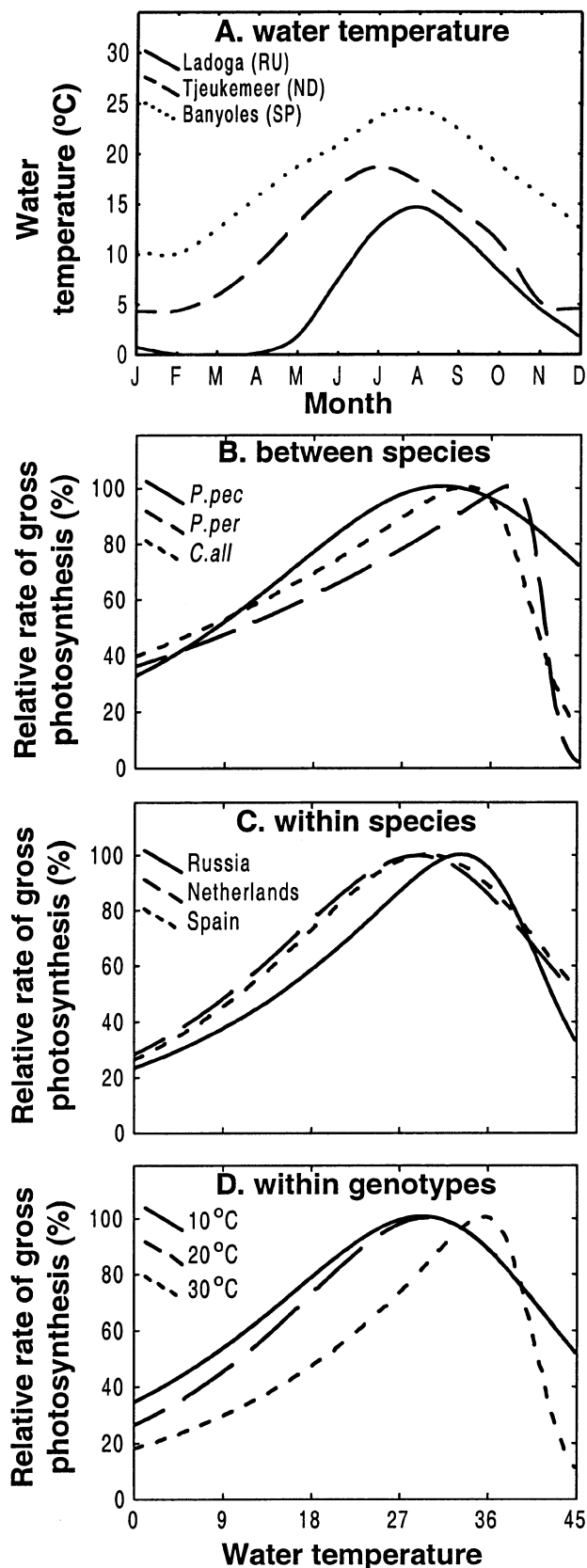

Fig. 4. Spatial and temporal variation in water temperature and the variation displayed by submerged angiosperms as a response to it. A. Monthly surface water temperature in lakes Ladoga (Russia), Tjeukemeer (the Netherlands) and Banyoles (Spain). Note that the lakes differ also in their size and average depth, from respectively $0.042 \, \text{km}^3$ and 2 m in Lake Tjeukemeer to $908 \, \text{km}^3$ and 58 m in Lake Ladoga. B. Temperature response curves of three submerged plant species collected in the Netherlands (May 1999), where they show largely different phenologies, from winter growth as an evergreen perennial in *Callitriche* sp. ('*Call*'), through late-spring growth in *Potamogeton pectinatus* ('*Pect*') to summer growth in *Potamogeton perfoliatus* ('*Pperf*'). C. Temperature response curves of three different clones of *Potamogeton pectinatus*, originally collected at broadly different latitudes and grown under standardized conditions at 20 °C. D. Temperature response curves of the same Spanish clone of *P. pectinatus* shown in panel C, following growth under standardized conditions at three different temperatures. Relative rates of photosynthesis shown in the temperature curves were obtained by dividing photosynthetic rates measured at each given temperature by the rate at the optimal temperature. Water temperature data are from the World Lakes Database of the International Lake Environment Committee (ILEC), available at http://www.ilec.or.jp/database/database.html. Temperature response curves are from Pilon and Santamaría (2001, 2002).

4.1.3. Carbon availability

Growing under water imposes a strong constraint to plant photosynthesis. The diffusion resistance of water and the low levels of dissolved inorganic carbon (DIC) in natural waters result in a strong limitation to photosynthetic carbon uptake (Bowes, 1987; Duarte et al., 1994). In addition, pH affects the equilibrium between the various forms of DIC: with increasing pH, the relative abundance of free CO_2 decreases and that of HCO_3^- increases, and at still higher pH values, HCO_3^- decreases and CO_3^{2-} becomes dominant. Photosynthetic activity becomes increasingly constrained with increasing pH: all submerged plants can use free CO_2, some of them (e.g., mosses, pteridophytes and the submerged forms of amphibious plants) tend to be poor users of HCO_3^- and it is generally agreed that CO_3^{2-} ions are not used directly for photosynthesis (Bowes, 1987). Since free CO_2 concentration decreases with temperature and photosynthetic activity increases the pH of the aqueous medium, the concentration and form of DIC often shows large seasonal and daily variation (Maberly and Spence, 1983; Santamaría et al., 1994, 1996). In shallow lakes with dense patches of submerged vegetation, considerable horizontal variation in carbon availability has also been reported (Spencer et al., 1994; Fig. 5).

Habitat differences in carbon availability related to water alkalinity and pH may thus result in large differences in their aquatic flora. Several authors have linked the distribution of some submerged vascular plants in hard and soft waters to their ability to utilise HCO_3^- (Allen and Spence, 1981; Maberly and Spence, 1983; Sand-Jensen, 1983, 1987; Vestergaard and Sand-Jensen, 2000a). The photosynthetic strategies used by aquatic plants to ameliorate the unfavourable low CO_2 and high O_2 conditions include C_4 acid utilisation (e.g., *Hydrilla verticillata*), bicarbonate utilisation (e.g., *Myriophyllum spicatum*), hydrosoil CO_2 utilisation (e.g., in isoetids) and aerial leaves (in amphibious
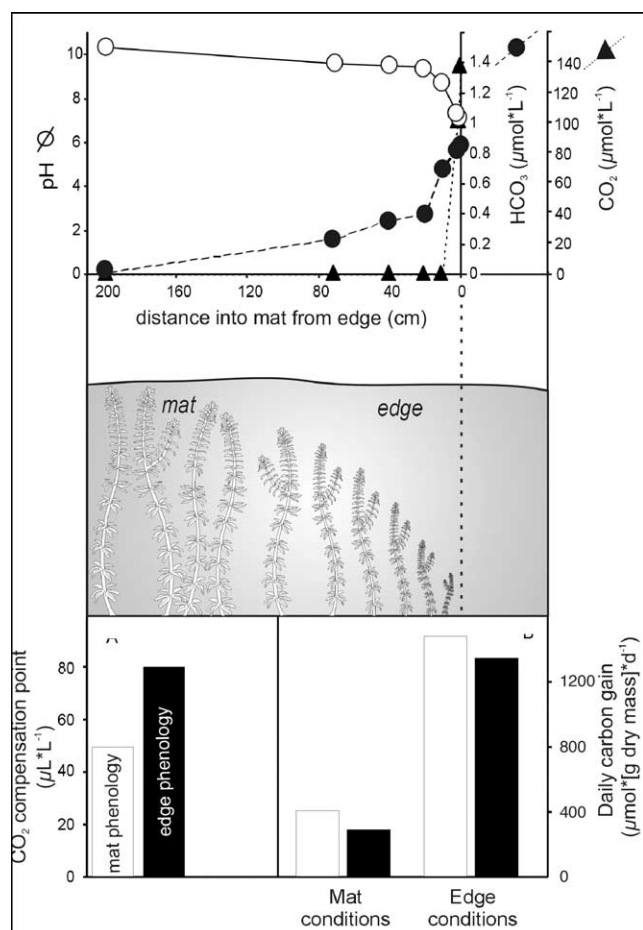
Fig. 5. Spatial and temporal variation in carbon availability and the phenotypic variation displayed by submerged angiosperm *Hydrilla verticillata* as a response to it. The upper graph shows spatial variation in mid-day values of dissolved CO_2 and HCO_3^-, and water pH, when moving from the edge to the center of a *Hydrilla verticillata* mat (depicted in the central pannel). The lower figure shows phenotypic specialisation in carbon uptake from the edge to the center of the mat (A), and the higher carbon gain efficiency of the 'mat phenotype' when incubated under both mat and edge conditions (B). Redrawn from Spencer et al. (1994), with permission of the Ecological Society of America.

plants) (Bowes, 1987). These strategies are likely to perform optimally in different environments (e.g., shallow waters for amphibious plants, cold waters with CO_2 rich sediments for isoetids, alkaline waters for bicarbonate users), although some species can resort to more than one of these strategies (Bowes, 1987). In addition, submerged and amphibious plants show considerable phenotypic plasticity in photosynthetic carbon metabolism (Maberly and Spence, 1983; Jones et al., 1993; Robe and Griffiths, 1998, 2000), which probably relate to the strong temporal variation in DIC availability that characterise shallow aquatic habitats (Spencer et al., 1994; Fig. 5).

4.1.4. Salinity and ephemeral inundation

Brackish and saline waters occur world-wide and include a great variety of chemical compositions and concentration ranges (Melack, 1988). The number of aquatic plants that

grow and reproduce in these habitats gradually decreases with increasing salinity and the halophytic submerged flora is reduced to a few, closely related families: Zannichelliaceae (*Zannichellia*, *Althenia* and *Lepilaena*), Potamogetonaceae (*Potamogeton*) and Ruppiaceae (*Ruppia*) (Melack, 1988). Halophytic species generally are stress-tolerant and show broad tolerance to osmotic stress and can be found growing at very different salinities (Verhoeven, 1979; Brock, 1982a; Santamaría et al., 1996). Adaptations to growth in brackish/saline waters involve the ability to osmoregulate, which in *Ruppia* species relates to the capacity to concentrate proline in the plant tissues (Brock, 1981).

On a regional scale, brackish and saline lakes are often in clusters—either in coastal regions or in endorheic lake complexes. On a broader geographic scale, however, the ubiquity of saline/brackish habitats results in a fairly regular intermingling of freshwater and saline/brackish lake clusters. Finally, owing to the strong temporal variation in salinity and inundation found in many brackish/saline lakes, they tend to develop centre-shore gradients, with drought-resistant or short-lived species and ecotypes at the periphery and halophytic species/ecotypes in the centre (Van Vierssen and Verhoeven, 1983; Grillas et al., 1993; Santamaría et al., 1996). Comparable zonation patterns can be found in non-saline, vernal pools, where they relate exclusively to the duration of the inundation period. It is noteworthy that most examples of ecotypic differentiation in aquatic plants come precisely from wetlands with contrasting salinity and/or inundation regimes, or along shore-centre zonations in temporary wetlands. Such ecotypic differentiation frequently involves reproductive characteristics finely tuned to the local habitat and differences in salinity tolerance (Brock, 1982a, b, 1991). It is also noteworthy that the diversification and abundance of aquatic annual species tends to be maximal in areas where temporary and/or saline wetlands abound (e.g., *Ruppia* in Australia, Brock 1982a, b, 1991; *Ruppia*, *Zannichellia* and *Althenia* in south-western Europe, Verhoeven, 1980; rice-field aliens in the US, Barrett et al., 1993; *Utricularia* species of seasonal lakes in Nicaragua, Crow, 1993).

4.1.5. Mechanical damage—the effect of water flow and wind-induced waves

The vegetation of running waters is strongly influenced by water flow (Dawson, 1988). Very high or turbulent flows generally preclude the development of aquatic vegetation or restrict its development to patches scattered in non-turbulent, slow-flow refugia (in margins and islands or behind obstacles in the substrate). Very low flows allow the development of vegetation characteristic of static waters, such as ponds and lakes (Dawson, 1988). In addition, seasonal changes in water flow have strong effects on the aquatic flora and they tend to select for species able to re-colonise the riverbed and complete their cycle during the favourable periods (e.g., herbaceous perennials, Dawson, 1988). Fluviatile ecosystems include an enormous diversity

of habitats, ranging from fast-flowing, turbulent headwaters; through streams and rivers with slow, rapid or alternating flow; to slow-flowing, deep, sometimes turbid rivers (Dawson, 1988). Most of this variation is present within single watersheds. Differences in climatic regimes, geologic substrata, shading by gallery forests, etc. among different watersheds super-impose a higher level of habitat heterogeneity on the diversity of fluviatile habitats described above. Within a given watershed, the capacity of the aquatic vegetation to colonise the different habitats will be further influenced by the directional character of water-mediated dispersal: downstream waters are more likely to receive new immigrants (species and genotypes) than upstream tributaries (Gornall et al., 1998).

In shallow lakes, wind-induced waves influence aquatic plant growth through direct (mechanical damage) and indirect effects (e.g., increased sediment siltation; Vermaat et al., 2000). In most regions, winds tend to prevail in certain directions. The interaction between the shape of the lake and the predominant wind directions results in within-lake variation in wind-wave exposure. Differences in exposure are frequently associated with different types of sediment, and the combination of both factors has been reported to result in changes in competitive hierarchies (Kautsky, 1991), species composition and abundance (Duarte and Kalff, 1988; Vestergaard and Sand-Jensen, 2000a) and within-species phenotypic variation (Idestam-Almquist, 1998).

4.1.6. Nutrient availability

Nutrient availability in the sediment and water column is known to affect the composition of the community of aquatic primary producers. Submerged plants are the most affected, since nutrient rich conditions also affect the light climate due to the growth of phytoplanktonic and ephiphytic algae. During this century, widespread fertilisation with phosphorus and nitrogen due to cultural eutrophication has illustrated dramatically the impact of nutrient availability on such communities. As a consequence, species typical of oligotrophic conditions have become rare in most rivers and lakes of Europe and North America (Sand-Jensen et al., 2000; Riis and Sand-Jensen, 2001). Experimental and field evidence has indicated that nutrient availability affects the cover, biomass yield, competitive ability and community composition of submerged (Barko and Smart, 1986; Chambers, 1987; Chambers and Kalff, 1987; Duarte and Kalff, 1988), amphibious and emergent plants (Keddy et al., 2001).

Nutrient availability varies at different scales. Microscale differences can be related, for example, to the presence of dense vegetation with sediment-oxidising capabilities. Within-lake variation in sediment fertility is often related to sediment granulometry, which in turns reflects wind and wave exposure. These small-scale differences are likely to be important in nutrient-poor lakes and rivers; in eutrophic waterbodies, nutrient supply through the water column

frequently offsets nutrient limitation (Duarte and Kalff, 1988). Lake position within the watershed also influences nutrient availability, which tends to increase from upper tributaries and highland lakes to lowland waterbodies. Finally, large-scale variation results from decreased nutrient availability at high latitudes due to climatic constrains to mineralisation in the water, soil and sediments.

4.1.7. Sediment anoxia

Most aquatic habitats have sediments with important amounts of organic matter and experience limited inflow of dissolved oxygen from the overlying water (Wetzel, 1988; Duarte et al., 1994). The intense bacterial metabolism produces anoxic, reducing conditions, which result in decreased rates of mineralisation and in the accumulation of fermentation endproducts (volatile fatty acids, hydrogen sulphide) that are toxic to many plants. Adaptations to anaerobic sediment conditions in aquatic plants include internal gas lacunal systems that move oxygen from the atmosphere or the photosynthetic tissues into the root tissue (Amstrong et al., 1996; Vretare and Weisner 2000), and metabolic adaptations to produce non-toxic end products during glycolysis (Wetzel, 1988). Root oxygen supply prevents accumulation of toxic respiratory end-products, and allows for diffusion into the sediment to form an oxidised rhizosphere microzone that reduces the toxicity of fermentation products and increases nutrient availability to the plant (Wetzel, 1988). This mechanism can be fairly efficient (so that aerenchyma is able to maintain adequate root oxygenation under partial oxygen depletion; Lorenzen et al., 2001) and may even result in major changes in sediment geochemistry (Roden and Wetzel, 1996; Nat and Middelburg, 1998) and in the release of rhizosphere-generated greenhouse gasses to the atmosphere (Brix et al., 1996; Beckett et al., 2001).

Sediments of the littoral zone of lakes and of running waters are sorted by water movements into particle size gradients (Wetzel, 1988). Exposed and fast-flowing sites tend to have coarser sediments with lower organic content, while in sheltered sites and densely vegetated waters, organic content tends to be high. As a result, considerable spatial variation in sediment composition and geochemistry (resulting in variable levels of sediment anoxia) can be observed within lakes or small rivers. Variation between lakes can also be observed at both local (depending, for example, on the position within a watershed or drainage basin) and regional scale (depending, for example, on watershed geomorphology). These differences are likely to result in changes in the aquatic plant community; for example, differences in root aeration have been linked to plant distribution of wetland species (Sorrell et al., 2000) and to changes in sediment geochemistry (Nat and Middelburg, 1998). Although little is known on submerged freshwater species, a recent review on the effect of sediment anoxia on seagrass growth and survival reported differences among species and environments (Terrados et al., 1999).

Intraspecific variation in the morphology of the lacunar system along depth gradients has also been observed in some aquatic species (Sorrell and Tanner, 2001).

For a great majority of the environmental variables described above, most variation takes place at a small scale (within waterbodies, and among waterbodies within the same watershed). For example, the community composition of 82 Danish lakes varied according to alkalinity and trophic status, but there was no correlation between the geographic distance among lakes and the similarity of their submerged plant communities (Vestergaard and Sand-Jensen, 2000a). This small-scale environmental mosaic tends to be repeated regionally—only in this sense should the aquatic environment be considered uniform. The variability of ecological conditions among neighbouring lakes makes aquatic habitats even more isolated than generally believed: dispersal is likely to be limited not only by the number of waterbodies in the neighbourhood, but also by the availability of suitable habitats within these neighbouring lakes. Combined with the low number of individuals per population that results from the limited size of many aquatic habitats, reduced dispersal might impose a strong influence on differentiation: populations are too small and isolated to survive local extinction and genetic erosion processes. However, clonal multiplication provides an effective method to reduce genet mortality and thus retard the loss of genetic variation within populations (see below). The combination of small-scale environmental variation (within waterbodies and between neighbouring ones) and genet longevity (resulting from clonal growth and multiplication) is, in turn, likely to promote the evolution of broad plastic responses.

4.2. Clonal reproduction

Most aquatic species show prolific clonal propagation or perennation, often in association with limited sexual reproduction (Les 1988; Barrett et al., 1993). Indeed, clonal growth and propagation has generally been assumed to be more abundant in aquatic habitats than in terrestrial ones (Sculthorpe, 1967; Hutchinson, 1975; Grace, 1993; Duarte et al., 1994). Different authors have argued that the widespread occurrence of clonality among aquatic plants serves the primary function of increasing genet survival under conditions that severely inhibit or restrict the success of sexual reproduction (as discussed by Grace, 1993; see also Sculthorpe, 1967). These conditions include decreased pollination success, particularly for submerged species (Duarte et al., 1994); unsuitable ecological conditions for seed production, maturation, germination, and seedling establishment (Barrett et al., 1993); low reproductive success arising from the small population size characteristic of many aquatic habitats (due for example to the absence of compatible mating types and to the harmful effects of inbreeding; Barrett et al., 1993; Charpentier et al., 2000); and low reproductive success arising from hybridisation (Barrett et al., 1993; Les and Philbrick, 1993). However, clonal spread

may itself contribute to the limited success of sexual reproduction, e.g., by reducing pollination success in self-incompatible species (Charpentier et al., 2000).

In addition, asexual reproduction has an enhanced value in aquatic environments (Grace, 1993). By enhancing year-to-year survival, asexual reproduction may reduce the selective value of sexual reproduction as a means of local persistence (Grace, 1993), opening the way for a number of adaptations that promote outbreeding and dispersal at the cost of increased risk of low or stochastic reproductive success. For example, the aquatic environment provides optimal conditions for the production of low-cost propagules (Grace, 1993). Detached plant fragments have low production costs, are able to capture nutrients while dispersal and establishment take place, and may disperse over considerable distances within lakes and slowly flowing waters. Clonal fragmentation combined with plant buoyancy also provides a good solution to another typical feature of the aquatic environment: shading through the water column.

Comparative work has confirmed that clonal species are more frequent in wet habitats, and in aquatic habitats in particular (van Groenendael et al., 1996). Van Groenendael et al. (1996) have argued that the four habitat types where clonal species predominate (respectively characterised by wet, nutrient-poor, cold and shaded conditions) present abiotic limitations to the growing conditions of plants, as indicated by their low species richness. Submerged habitats tend to have reduced irradiance, nutrient availability is often low due to low rates of mineralisation in the sediment and carbon limitation often limits photosynthesis and growth (Bowes, 1987; Duarte et al., 1994; Wetzel, 1988). Hence, clonal growth and fragmentation seems to be best suited for the particular set of ecological conditions that characterise aquatic habitats.

Different modes of clonal growth and reproduction allow for subsequent specialisation within the aquatic environment. Species with splitter-spreading architecture are particularly abundant in most submerged and floating habitats, which tend to be shaded, where nutrient supply through the water column can be substantial and where resource acquisition by the plant fragment provides a cheap solution to alleviate carbon limitation. Species with packed, tightly connected systems, on the other hand, predominate in 'drier' aquatic systems (lake shores and flooded areas), where the opportunity for fragment dispersal is greatly reduced. Packed-connected architecture is also common among the submerged flora of cold, oligotrophic lakes and in nutrient-poor sediments, where it favours clone persistence, site occupation and the monopolisation of the nutrients present (van Groenendael et al., 1996).

The greater representation of monocots than dicots among the aquatic flora (Sculthorpe, 1967; Grace, 1993; Duarte et al., 1994; van Groenendael et al., 1996; Jacobs and Wilson, 1996) is probably related to the higher capacity of monocots to reproduce asexually (Grace, 1993; Duarte et

al., 1994). However, the high phylogenetic relatedness of most aquatic species precludes a comparative evaluation of whether the acquisition of clonal growth and propagation was a pre-requisite for the successful colonisation of the aquatic environment (van Groenendael et al., 1996).

All in all, the widespread occurrence of clonal growth, fragmentation and perennation does not necessarily reflect a response to conditions that reduce the opportunities for sexual reproduction. This might be the case for submerged plants, but clonal reproduction is also widespread among floating, emergent and amphibious plants. Alternatively, or complementarily in the case of submerged plants, clonality provides a suite of traits that is selectively advantageous in aquatic environments. Whether reduced sexual reproduction preceded, followed or coevolved with the acquisition of clonality among the aquatic vascular plants remains largely unknown, given the variety of ecological and genetic factors that relate to reduced sexual reproduction (Barrett et al., 1993).

These considerations are particularly relevant when addressing the relative contribution of clonal growth and multiplication to the generality of broad distributions among the aquatic vascular plants. In the first place, its influence on the maintenance of viable populations in the face of reduced sexual reproduction and small population sizes most likely represents a significant contribution to the maintenance of population ranges. In particular, range-limit populations are particularly prone to local extinction due to climatic constraints, reduced competitive ability (Woodward and Williams, 1987; Woodward, 1988) and poorer reproductive performance (García et al., 2000). In these populations, clonal perennation is most likely to contribute to increased species ranges. In addition to this, clonal growth and fragmentation provides aquatic plants with a highly competitive growth form and a rapid method of within-population spread. The competitive displacement of non-clonal species and genotypes has probably contributed to the decreased importance of sexual reproduction among the aquatic species. This, in turn, may represent a significant contribution to the low levels of taxonomic and genetic differentiation observed among the aquatic vascular plants.

4.3. High dispersal rates

The broad distribution ranges of many aquatic macrophytes have often been taken as compelling evidence of high dispersal rates. However, given the long persistence of clonal plant populations (as exemplified for example by the maintenance of relict, asexual populations of the hybrid *Potamogeton x suecicus*, which probably date from the Weichselian glacial period; Hollingsworth et al., 1996a; see also Fig. 2), effective dispersal rates could actually be much lower than generally considered. On the one hand, it is important to note that dispersal functions that peak locally but have thick tails (as one can easily expect from waterfowl-mediated dispersal) can result in very fast dispersal, particularly in combination with adequate ecological conditions and widespread availability of unoccupied habitats (Clark, 1998). On the other hand, the higher frequencies of invasion observed in disturbed ecosystems suggest that habitat occupation may restrict effective dispersal more than propagule dispersal rates (Rejmánek, 1999). The broad distributional patterns of native species and the high dispersal rates of alien species could thus reflect a high colonisation ability in unoccupied habitats combined by high persistence following their occupation, rather than high rates of effective dispersal (see De Meester et al., 2002, for a discussion of priority effects in zooplankton).

Dispersal of sexual and asexual propagules of aquatic plants is generally assumed to be common, largely due to passive transport by migratory waterbirds (Darwin, 1859; Guppy, 1906; Ridley, 1930; De Vlaming and Proctor, 1968). Many authors have argued that compelling evidence is provided by existing plant distributions that match migration routes, anecdotal observations and experimental-feeding experiments (Ridley, 1930; Hutchinson, 1975; Cook, 1987; Jacobs and Wilson, 1996). On the one hand, bird-mediated passive transport of plant seeds, both internal and external, is probably a frequent process in the field, at least at local scale (Figuerola and Green, 2002). Many species of waterfowl are known to consume large amounts of aquatic plant seeds (Thomas, 1982; Green et al., 2002; Figuerola and Green, 2002; but see also Clausen et al., 2002). Experimental feeding has shown that the seeds of a variety of species survive gut passage and may show long passage times (De Vlaming and Proctor, 1968; Proctor, 1968; Agami and Waisel, 1986; Smits et al., 1989; Holt, 1999; Charalambidou and Santamaría, 2002). In some cases, gut passage enhanced seed germination (Lohammar, 1954; Agami and Waisel, 1986; Smits et al., 1989; L. Santamaría, unpublished). Observations of seeds recovered from waterfowl droppings have shown that they may be fairly abundant and largely viable, suggesting that (short-distance) transport can be rather common (Green et al., 2002; J. Figuerola, unpublished). Direct observations of shot and captured birds have shown that external transport of seeds may occur, being more common for emergent and wetland plants than for floating and submerged species (Hutchinson, 1975; Vivian-Smith and Stiles, 1994; J. Figuerola and A.J. Green, unpublished). On the other hand, however, the amount of evidence concerning the transport of asexual propagules and plant fragments is still fairly limited. Recovery of externally and internally transported, asexual propagules has been rare and largely anecdotal (Hutchinson, 1975).

Most aquatic species, including those classically considered to be endo-zoochorous (such as *Potamogeton pectinatus*), are also water dispersed (Duarte et al., 1994). The seeds of many species have structures that allow them to float at the water surface (e.g., pulpy arils in *Nymphaea*, hydrophobic structures in *Nymphoides*, aeriferous exocarps in *Potamogeton*, aeriferous testas in *Iris*, glumes in *Scirpus*),

where they can travel long distances aided by wind or water currents. The buoyancy of plant fragments is also well suited for dispersal, while specialised organs for asexual perennation tend to be heavier than water (or buried in the sediment) and will thus travel shorter distances. In summary, it is fair to say that both sexual and asexual propagules show significant dispersal ability within and among hydrologically connected waterbodies. Despite the common believe that asexual propagules are best suited for dispersal (Hutchinson, 1975; Duarte et al., 1994; Rejmánek, 1999), they seem less likely to disperse to isolated waterbodies and among unconnected watersheds (with the exception perhaps of very small plants, such as *Riccia*, *Azolla* or *Lemna*). For example, Hollingsworth et al. (1996b) concluded that sexually derived propagules (primarily seeds) are the most likely responsible for gene flow in *P. pectinatus*.

Despite a high potential for propagule dispersal, effective dispersal rates may be limited by reduced establishment of immigrant propagules, particularly in habitats where they have to compete with established populations of highly clonal species. It is generally argued that non-dormant asexual propagules, in particular plant fragments, have a higher potential for dispersal due to their higher establishment capacities. These propagules are however produced and dispersed during the growing season, when competition in recipient populations is maximal. Sexual propagules and dormant asexual ones, on the other hand, might compensate for their low competitive ability by their early arrival to the recipient populations, before competition is intense.

The alleged distributional evidence for long-distance dispersal may thus largely relate to rare events that create highly conservative biogeographic patterns due to the long persistence of clonal populations. While asexual propagules are probably of importance for short-distance and local dispersal (within hydrological units), sexual propagules are more likely to result in regional and long-distance dispersal (between hydrological units). The combination of these dispersal patterns and the patterns of habitat heterogeneity presented above suggest that most environmental variation will be encountered at a geographic scale at which asexual multiplication and dispersal predominate. This should promote the evolution of phenotypic plasticity ('general purpose genotypes'). The smaller importance of large-scale environmental heterogeneity, combined with the low frequency of effective colonisation by sexual propagules that result from priority effects in clonal populations (De Meester et al., 2002) probably contributes to the low levels of taxonomic, genetic and ecotypic differentiation found among the aquatic angiosperms.

4.4. Plasticity and general-purpose genotypes

I have argued above that aquatic plants should show high levels of plasticity, in particular for those factors that vary over small spatial scales, or over short-term temporal scales.

The assessment of the relative contribution of plasticity and genotypic variation to phenotypic variation in aquatic plants is however difficult due to the scarcity of studies that specifically report the reaction norms of different genotypes. Many authors claiming to report plastic variation are reporting instead phenotypic variation among propagules collected at various sites or populations (i.e., from a unknown mixture of ramets and genets) and randomly distributed over various treatments (e.g., Kautsky, 1991; Idestam-Almquist and Kautsky, 1995; Hootsmans et al., 1996).

A topic that has received large interest has been carbon uptake in submerged plants. Phenotypic plasticity in carbon metabolism seems to be a major feature of submersed aquatic plants (Maberly and Spence, 1983; Sand-Jensen, 1987; Bowes and Salvucci, 1989), in particular in response to temporal variation in carbon availability (Sand-Jensen and Gordon, 1986; Bowes and Salvucci, 1989; Madsen and Sand-Jensen, 1991) or inundation (Robe and Griffiths, 1998, 2000) and to within-lake variation in DIC availability (Spencer et al., 1994; Fig. 5). Those are very significant modifications, which often involves major changes in plant metabolism, including biochemical and morphological variation (Bowes and Salvucci, 1989).

Another important area of research concerns inundation gradients. For example, *Phragmites communis* showed significant plastic variation in response to within-lake inundation gradients (Vretare et al., 2001). Small-scale, ecotypic differentiation reported along inundation gradients or between exposed and sheltered sites typically involved differences in the plastic response to factors that varied between these local habitats. For example, low-meadow *Glaux maritima* plants responded less plastically to reduced light and inundation (Jerling and Elmgren, 1996) and *Potamogeton pectinatus* from sheltered sites showed higher phenotypic variation in response to variation in sediment type and exposure, than plants collected in exposed sites (Idestam-Almquist and Kautsky, 1995).

Significant variation in plant morphology and growth in response to light and temperature has also been reported for a number of aquatic plants (e.g. Barko and Smart, 1986; Barko et al., 1982; Hootsmans et al., 1996; Vermaat and Hootsmans, 1994), but the relative contribution of the genetic and/or plastic components was rarely studied. A comparison between the responses of different clones of *P. pectinatus* collected over a broad latitudinal gradient suggested broad thermal tolerance and significant plastic responses to temperature, but limited geographical variation (Pilon and Santamaría, 2002; Fig. 4). Acclimation was largely achieved by morphological, rather than physiological changes. Research on temporal variation in the temperature response of photosynthesis and respiration of three submerged species also indicated broad thermal tolerances, but limited seasonal acclimation (Pilon and Santamaría, 2001). Similarly, *Phragmites australis* showed significant geographic variation in phenology (length of the growing season, time of flowering) along a geographic cline (Clev-

ering et al., 2001), but photosynthetic plasticity within genotypes was generally larger than genotypic differences among four latitudinally distant populations (Lessmann et al., 2001). Although much more research is required in this area, published evidence suggests that climatic gradients tend to result in phenological variation among populations (frequently involving the time of reproduction; Pilon et al., 2002), while variation in physiological and morphological responses is fairly limited.

5. Conclusions

Aquatic vascular plants generally show broad distributional ranges. Climatic factors seem to have limited effects on plant distributions, largely restricted to the determination of major disjunctions (tropical–temperate–subarctic). Existing distributions suggest that dispersal should have been frequent enough to assure the quick colonisation of extensive areas following glacial retreat. Dispersal limitation is still apparent, however, in isolated continents or islands and in continental areas separated by geographic barriers.

Aquatic vascular plants also show limited taxonomic differentiation. It is possible that with the application of new taxonomic criteria (for example, the combination of reproductive isolation and ecological differentiation proposed in the ecogenetic species concept; Levin, 2000) and tools (for example, molecular markers), broadly distributed species will be shown to be composed of groups of sibling species. In a few cases where this has already happened, however, sibling species still have broad geographic ranges. In agreement with previous reviews, recent work has revealed limited genetic variation within aquatic plant species. Variation within populations is particularly low. In contrast, variation among populations seems to be rather high, mainly due to the persistence of long-lived clones. Finally, ecotypic differentiation has been reported in a few cases, often related to factors that constrain clonal reproduction (salinity and ephemeral inundation). Ecotypic differentiation often occurred over small distances, suggesting that it is caused by selection pressures rather than by reduced dispersal.

I have argued that the alleged uniformity and 'benign' character of the aquatic environment is a misrepresentation of this type of habitat. Aquatic habitats are heterogeneous environments, but this heterogeneity largely occurs at relatively small scales (within waterbodies and among neighbouring ones). This small-scale environmental mosaic tends to be repeated regionally, and it is only in this sense that the aquatic environment should be considered uniform. Aquatic habitats also represent a stressful environment for plants, characterised by low carbon availability, shaded conditions, sediment anoxia, wave exposure, significant restrictions to sexual reproduction, and sometimes also osmotic stress and limited nutrient supply. I propose that the generality of broad distributions and low differentiation among the aquatic flora is best explained by a combination of: (1)

selection for stress-tolerant taxa, which typically tend to show broad tolerance (plastic) ranges. (2) The selective advantages provided by clonal growth and multiplication, which provides an adequate tool-kit to cope with environmental stress, reduces genet mortality and increases the viability of (typically) small-sized populations. (3) Relatively high long-distance dispersal of sexual propagules within the time scale set by the long live-span of asexual clones, and high local dispersal of asexual propagules at a much shorter time scale. (4) The generality of broad plastic responses, promoted by the combination of clonal growth, long-distance dispersal of sexual propagules, small-scale spatial heterogeneity and temporal variability. As a consequence, aquatic plants have a tendency to have general-purpose genotypes that occupy large areas and show high clonal persistence.

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