RESEARCH ARTICLE

Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes

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Abstract Theories that link plant strategies and abiotic filters discriminate between three strategies: competitive, ruderal or stress-tolerant species, and suggest that functional diversity is higher at intermediate values along the gradients of productivity and disturbance. The mechanism by which abiotic filters screen plant traits in aquatic plant communities has been poorly tested and has led to contrasting results. The present study aimed to test whether functional diversity and abundance of life-history traits corresponding to morphology, fecundity and longevity of aquatic plants were linked to disturbance and productivity. Fifty-nine shallow lakes that were arranged along a gradient of productivity (estimated through total phosphorus concentration) and drought-disturbance frequency were sampled for aquatic plants. Species traits were documented and functional diversity was calculated (richness, dispersion and evenness) for each lake. Increasing total phosphorus concentration was associated with decreased functional richness and dispersion but not functional evenness. Functional diversity did not differ according to disturbance frequency, regardless of the index that was measured. High productivity favoured floating species with storage organs and vegetative reproduction, especially at low disturbance frequency. For all disturbance frequencies, low productivity favoured small species without storage organs and sexual reproduction. The present study partly supports the theoretical model. At high productivity levels, because phytoplankton is a better competitor for light than aquatic plants, plant traits are screened stringently, and species with traits that allow them to reach the photic zone are selected.

Introduction

Several sets of plant life-history traits have been proposed as adaptations to factors of environmental disturbance and productivity (e.g., Southwood 1977; Grime 1979; Paine and Levin 1981). Grime (1979) predicts 3 strategies, ruderal, stress-tolerant and competitive (C-S-R theory), excluding the possibility for plant species to grow in an environment characterised by both a high degree of disturbance and low productivity. However, the exclusion of plant species in case of simultaneous disturbance and limitation of resources is highly questionable (Grubb 1985; Westoby 1998). The Kautsky model (1988), drawn from observations on aquatic macrophytes, led to the definition of not only three but four strategies (C-S-R-B), splitting the stress-tolerant strategy into 'stunted' and 'biomass-storer' species according to high or low disturbance, respectively. Ruderal species are characterised by small growth forms with low longevity and a large production of seeds, with the latter being the main type of perennating organs. Competitive species are characterised by growth forms that optimise the access to light (tall or floating), either a long or relatively short longevity, a small production of seeds, and dormant buds as alternative perennating organs. Stunted and biomass-storer species are characterised by a high longevity, a low seed production and storage systems

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in stems or roots. Stunted species tend to be very small, whereas biomass-storers are large species.

As a result, Grime (1973) postulated that functional diversity had a humpbacked relation to stress and disturbance. At a low stress or disturbance level, competitors may dominate communities. At high levels of disturbances or stress, most species are predicted to be of type R (ruderals) or S (stress tolerant), respectively. In all of these situations, functional diversity is supposed to be low. By contrast, for moderate levels of disturbance and productivity, several functional types may coexist. Modelling has corroborated these patterns of functional diversity in response to environmental strains (Colasanti et al. 2001). However, we know little about how far environmental factors effectively impact functional diversity (Petchey and Gaston 2007).

In their review, Wilson and Lee (2000) claimed that few studies have really tested CSR or CSRB theory, which partly failed as a predictive model at the community level. Such models have been even more rarely tested for aquatic plant communities (but see Bornette et al. 1994; Willby et al. 2000; Riis et al. 2001). These few studies suggest that aquatic plants may fit better with the predictions than what is observed among terrestrial plants. One possible reason for this is the low effect of gravity on organisms in aquatic ecosystems. In such a situation, most species are characterised by few support tissues (Rascio 2002), and, thus may be more vulnerable to disturbance (Bornette et al. 2008). In the same way, decreasing nutrient stress increases competition, initially among aquatic plants, but later also between aquatic plants and phytoplankton, leading ultimately to plant disappearance (Declerck et al. 2005). Consequently, we suggest that aquatic plants may be a good subject for testing the conceptual models that link stress, disturbance and plant traits, and we aimed in the present paper to determine both whether key aquatic plant traits are shaped by nutrient stress and disturbance as well as how such factors rule functional diversity.

For this purpose, we studied how life-history traits of aquatic plant communities were shaped along gradients of productivity and disturbance frequency. The selected life-history traits were key traits involved in plant fitness, i.e., those related to morphology, longevity and fecundity. Firstly, we tested whether functional diversity was higher at intermediate levels of productivity and disturbance frequency. Secondly, we hypothesised that life-history traits were shaped by disturbance and productivity as a way of validating the hypotheses suggested by the conceptual models of Grime and Kautsky: (1) concerning morphology, species with leaf arrangements that increase light availability (tall forms or floating-leaved) were hypothesised to be more abundant at high productivity,

and tall forms were hypothesised to be more abundant at low disturbance frequencies; (2) concerning longevity, we assumed that perennial species would be more abundant at low disturbance frequencies and at low productivity; and (3) concerning fecundity, we hypothesised that species with a high number of reproductive organs would be more abundant at high disturbance frequencies and high productivity.

Shallow lakes represent good systems for testing such hypotheses. The nutrient content of lakes is influenced by management practices around and on lakes, and consequently varies greatly among lakes within the same landscape, ranging from mesotrophic to hypertrophic (Hansson et al. 1998; Wezel et al. 2011). The management of shallow lakes sometimes involves alternation between wet and dry periods, the frequency of which generates a hydroperiod gradient from ephemeral to near permanent, leading to a gradient of disturbance frequencies among lakes (De Meester et al. 2005; Williams 2005).

Materials and methods

Study sites

The study was conducted in the Dombes region of southeastern France (46°00′00″N, 05°01′00″E), which is characterised by more than 1,000 man-made shallow lakes dispersed in an agricultural landscape of pastures and crop fields (see Appendix Table 2 for key environmental variables of shallow lakes in the Dombes region). The whole region of the Dombes is characterized by decalcified clay soils. As a consequence, all the lakes have similar slightly acid characteristics. Their median average depth is very low at 0.7 m, and ranges up to 1.1 m. The management of the lakes consists in alternating fish farming and crop production in the same area. The lakes are emptied completely every 4–7 years for one full year for cereal cultivation on the lake bottom. Drying and cropping is a high-level disturbance for natural aquatic plant communities, as all vegetative individuals are destroyed during this period. After this dry year, lakes are filled again with water drained from the lake catchment.

Fifty-nine shallow lakes were randomly selected and sampled, either in 2008 (29 lakes) or 2009 (30 lakes). Their surface area varied from 2.5 ha for the smallest lake to 79 ha for the largest ones. Disturbance frequency was defined as how often a disturbance event occurred, which is commonly measured as the time since the last disturbance (Shea et al. 2004). In the present set of lakes, the last dry year was 1 year prior to sampling for 11 lakes, 2 years prior to sampling for 18 lakes, 3 years prior to sampling for 15 lakes and 4 or more years prior to sampling for 15 lakes.

Sampling of established vegetation

The established vegetation was sampled in summer, during the second half of June. For all lakes, aquatic vegetation was systematically sampled in the aquatic zone along five transects parallel to the inflow. Two were located along the helophyte belts on each side of the lake, one was located in the centre of the lake, and two were located between the central transect and each side transect. Side transects were positioned in the open water zone at a distance of 5 m from the helophyte belts to avoid shade by riparian vegetation. Quadrats of 4 m² separated by 50 m were regularly distributed along each transect so that the number of quadrats sampled increased proportionally with lake area. For each quadrat, the percentage cover of submerged and floating aquatic plants (angiosperms and Characeae) was recorded using Braun-Blanquet cover-abundance estimates (1 = 0–5%; 2 = 5–25%; 3 = 25–50%; 4 = 50–75%; 5 = 75–100%). The Braun-Blanquet scores for each species were then converted to mean values of percentage cover (2.5; 15; 37.5; 62.5 and 87.5%) to allow for statistical analysis (van der Maarel 2007).

Helophytes were not recorded because they do not experience drought disturbances and nutrient constraints in the same way as the aquatic vegetation of open water.

Species traits

Information on species trait attributes was obtained from Grime et al. (1990), Willby et al. (2000) and personal observation (concerning leaf arrangement; see Appendix Table 3). Morphology was characterised by leaf arrangement (rosette, caulescent or floating) and plant height (small, i.e., average size approx. <30 cm; medium, i.e., average size approximately between 30 and 60 cm; or tall, i.e., size ranging from 60 cm to more than 1 m). Floating species were separated between free-floating species and tall rooted species with floating leaves, the latter being called "tall floating". Species longevity discriminated between annual species and perennial species, and between species with or without storage organs (dormant buds for pseudo-annuals and rhizomes or tubers for true perennials). Fecundity was the number of reproductive organs year^{-1} individual^{-1}, and it ranged from medium (10–100) to high fecundity (100–1,000). The reproductive pattern was also identified by distinguishing species reproducing only sexually (seeds) or both by sexual and vegetative reproduction (seed + rhizomes, stolons, dormant buds, turions or fragmentation). Some inevitable redundancy may occur between these traits. Indeed, the distinction between vegetative parts serving for reserve and those for dispersion is complex among aquatic plants, as many organs for vegetative reproduction are also organs of perennation (Van der Pijl 1972; Barrat-Segretain 1996).

Lake productivity

Total phosphorus served as a surrogate variable for potential lake productivity (Leibold 1999; Jeppesen et al. 2000). Total phosphorus concentration was measured in water samples collected from April to July 2008 or 2009 in all lakes, when the recruitment and growth of aquatic plants took place. The sampling was done every 2 weeks in April and every week from May to July. Samples were collected at the deepest location, i.e., near the outlet of each lake, in the upper 50 cm of the water column with a Van Dorn water sampler.

Total phosphorus content was assessed in unfiltered water using the acid persulphate digestion and colorimetric methods, following the standard procedures of the Hach® methods (HACH Company, Loveland, Colorado, USA, DR/2400 Spectrophotometer Procedure Manual, Hach Company, 2002). Lakes ranged from oligo-mesotrophic to hyper-eutrophic, according to the nomenclature of Søndergaard et al. (2005) and the oligotrophic part of the trophic gradient was therefore lacking in our sampled of lakes.

Data analysis

Functional diversity indices

The functional diversity of a community is usually approximated through measurements of traits and described by three kinds of indices, which can be combined to calculate different facets of functional diversity: functional richness, functional evenness and functional divergence (Mason et al. 2005). Many methods to measure each index have been proposed in the literature (see the reviews of Mouchet et al. 2010; Schleuter et al. 2010). In the present study, we used indices developed by Villéger et al. (2008), which are considered appropriate for revealing assembly rules that underlie community structure (Mouchet et al. 2010). Their functional richness index (FRic) efficiently differentiates assembly rules regardless of species richness; their functional divergence index (FDiv) has the highest power value regardless of the assembly rule or the richness value; and their functional evenness index (FEve) is the only one that allowed us to consider simultaneously several life-history traits (Schleuter et al. 2010).

The FRic for categorical traits was measured as the number of unique combinations of trait attributes (Laliberté and Legendre 2010). The FDiv cannot be computed for categorical traits, so it was replaced by the index of dispersion (FDis) developed by Laliberté and Legendre (2010)

and summarises both functional richness and FDiv. FDis equals 0 in communities with only one functionally singular species.

Relative abundance of life-history traits

We used an individual trait approach where the relative abundance of each trait attribute was considered individually. The relative abundance of a given trait attribute corresponds to the sum of the relative abundance of all species which display that attribute.

Statistical tests

Total phosphorus concentrations were $\log_{10}$ transformed before statistical analyses to meet assumptions of normality (validated using Shapiro tests). The relationships between species richness and environmental parameters (area, disturbance frequency, productivity and connectivity) were assessed using the general linear models analysis of covariance (GLM ANCOVA) with a binomial model (values of the three indices of functional diversity and data of relative abundance ranging between 0 and 1). The assumption of independence of the 2 covariates (productivity and disturbance frequency) was verified prior to the ANCOVA; total phosphorus concentration did not differ according to the number of years since the last summer drying (ANOVA: $F_{3,60} = 2.11$, $p = 0.11$), although it tends to be lower the first year after summer drying.

R software was used for all statistical analyses (R Development Core Team, Vienna, Austria, R Foundation for Statistical Computing, 2008), and the ''FD'' R package was used to implement distance-based FD Framework (Laliberté and Shipley 2010).

Results

Relationships between functional diversity and environmental parameters

Lakes may be considered as islands in a terrestrial landscape, and, according to the theory of island biogeography (MacArthur and Wilson 1967), lake size may affect species richness in a positive or negative way (MacArthur and Wilson 1967; Scheffer et al. 2006). To test whether there was a possible bias due to the effect of lake area on diversity, we added lake area in the GLM ANCOVA. Lake area was not correlated with functional richness or functional diversity ($F_{1,59} = 0.90$, $p = 0.35$; $F_{1,59} = 1.84$, $p = 0.18$, respectively), and was consequently deleted from the model.

Functional richness and functional dispersion were negatively correlated with total phosphorus concentration and did not differ according to the number of years since the last summer drying (Table 1; Fig. 1). They were generally high at low total phosphorus concentrations, but ranged from high to very low at high total phosphorus concentrations. Functional evenness was not correlated with total phosphorus concentration and did not differ according to the number of years since summer drying (Table 1).

Relationship between relative abundance of life-history traits and stress and disturbances
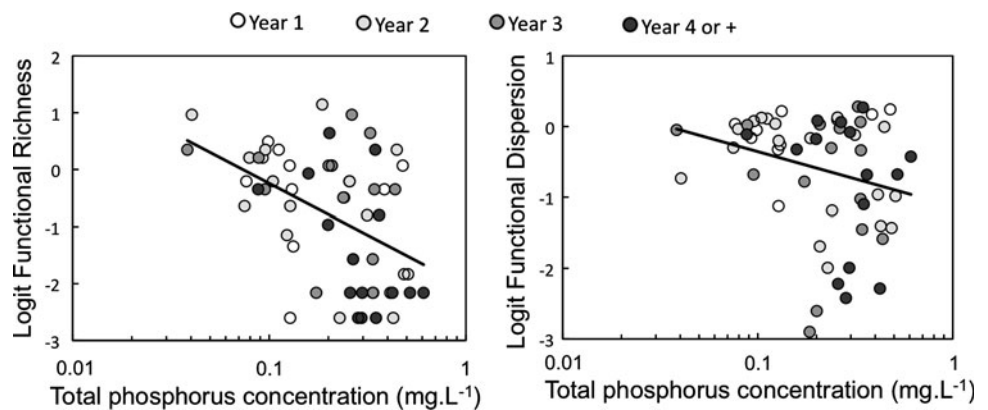
Morphology

The relative abundance of tall floating and free-floating species was positively correlated with total phosphorus concentration but did not differ according to the number of years since the last summer drying (Table 1). The relationship between relative abundance of tall caulescent species and total phosphorus concentration was hump-shaped; it did not differ according to the number of years since the last summer drying. The relative abundance of medium caulescent species tended to be negatively correlated with total phosphorus concentration, while the relative abundance of small caulescent species was negatively correlated. Abundance of medium and small caulescent species did not differ according to the number of years since the last summer drying. The relative abundance of medium rosette species tended to be negatively correlated with total phosphorus concentration and was higher the 1st year after summer drying but did not significantly differ among the following years. The relative abundance of small rosette species was not correlated with total phosphorus and did not differ according to the number of years since summer drying.

The modelling of the distribution of morphological traits was based on significant relationships between traits and abiotic pressures, and showed the distribution of traits along productivity and disturbance gradients (Fig. 2). In the 1st year, small caulescent and medium rosette species were dominant in the lakes having the lowest total phosphorus concentrations among the whole set of lakes (approximately <0.05 mg L^{-1}), and tall caulescent and medium rosette species were dominant in the lakes that had intermediate total phosphorus concentration (approximately between 0.05 and 2 mg L^{-1}). From the 2nd years onwards, medium rosette species became scarce. Tall floating and free-floating species were dominant at high total phosphorus concentrations (approximately >2 mg L^{-1} in our data set), whatever the number of years since summer drying.

Table 1 Results of the GLM ANCOVA relating environmental variables, functional diversity and relative abundance of life-history traits (values that are statistically significant at the 5% level ($p < 0.05$) are indicated in bold)

	Total phosphorus concentration		Summer drying		Total phosphorus concentration x summer drying	
Functional diversity						
Functional Richness	$F_{1,59} = 13.72$	$p = 0.0005$	$F_{3,59} = 0.94$	$p = 0.43$	$F_{3,59} = 1.02$	$p = 0.39$
Functional dispersion	$F_{1,59} = 4.26$	$p = 0.04415$	$F_{3,59} = 1.24$	$p = 0.31$	$F_{3,59} = 0.58$	$p = 0.63$
Functional evenness	$F_{1,59} = 0.38$	$p = 0.54$	$F_{3,59} = 0.29$	$p = 0.83$	$F_{3,59} = 0.53$	$p = 0.67$
Morphology						
Free floating	$F_{1,59} = 6.81$	$p = 0.012$	$F_{3,59} = 0.06$	$p = 0.98$	$F_{3,59} = 1.72$	$p = 0.17$
Tall floating	$F_{1,59} = 4.43$	$p = 0.04$	$F_{3,59} = 1.37$	$p = 0.26$	$F_{3,59} = 0.39$	$p = 0.76$
Tall caul.	$F_{1,59} = 6.42$	$p = 0.015$	$F_{3,59} = 1.90$	$p = 0.14$	$F_{3,59} = 0.72$	$p = 0.55$
Tall caul.: polynomial	$F_{1,59} = 5.47$	$p = 0.023$				
Medium caul.	$F_{1,59} = 2.88$	$p = 0.096$	$F_{3,59} = 1.68$	$p = 0.18$	$F_{3,59} = 2.19$	$p = 0.10$
Small caul.	$F_{1,59} = 8.13$	$p = 0.0063$	$F_{3,59} = 0.11$	$p = 0.95$	$F_{3,59} = 1.46$	$p = 0.24$
Medium ros.	$F_{1,59} = 3.15$	$p = 0.082$	$F_{3,59} = 6.35$	$p = 0.0009$	$F_{3,59} = 1.05$	$p = 0.38$
Small ros.	$F_{1,59} = 1.27$	$p = 0.27$	$F_{3,59} = 0.51$	$p = 0.68$	$F_{3,59} = 0.05$	$p = 0.98$
Longevity						
Annual						
Without storage organs	$F_{1,59} = 8.99$	$p = 0.004$	$F_{3,59} = 0.69$	$p = 0.2$	$F_{3,59} = 1.35$	$p = 0.27$
With storage organs	$F_{1,59} = 2.56$	$p = 0.12$	$F_{3,59} = 0.06$	$p = 0.98$	$F_{3,59} = 1.33$	$p = 0.27$
Perennial						
Without storage organs	$F_{1,59} = 3.33$	$p = 0.082$	$F_{3,59} = 4.45$	$p = 0.0075$	$F_{3,59} = 0.38$	$p = 0.77$
With storage organs	$F_{1,59} = 1.27$	$p = 0.27$	$F_{3,59} = 0.46$	$p = 0.7$	$F_{3,59} = 0.23$	$p = 0.88$
Fecundity						
Medium number of reproductive organs						
Only seed	$F_{1,59} = 7.8$	$p = 0.007$	$F_{3,59} = 1.04$	$p = 0.38$	$F_{3,59} = 2.26$	$p = 0.09$
Seed + vegetative propagules	$F_{1,59} = 0.90$	$p = 0.35$	$F_{3,59} = 0.51$	$p = 0.68$	$F_{3,59} = 0.38$	$p = 0.76$
High number of reproductive organs						
Only seed	$F_{1,59} = 0.87$	$p = 0.36$	$F_{3,59} = 10.18$	$p = 2.10^{-5}$	$F_{3,59} = 0.24$	$p = 0.87$
Seed + vegetative propagules	$F_{1,59} = 0.36$	$p = 0.55$	$F_{3,59} = 1.98$	$p = 0.26$	$F_{3,59} = 0.58$	$p = 0.63$

Fig. 1 Relationships between functional richness (*left*), functional dispersion (*right*) and total phosphorus concentration to the number of years since summer drying (indicated by a *shaded point* for each lake). *Lines* correspond to significant negative relationships between functional richness and total phosphorus concentration, and between functional dispersion and total phosphorus concentration

Longevity

The relative abundance of annual species without storage organs was negatively correlated to total phosphorus concentration, whereas the relative abundance of annual species with storage organs (perennating through turions as storage organs) was not correlated to total phosphorus concentration. The relative abundance of both categories of species did not differ according to the number of years since summer drying.

The relative abundance of perennial species without storage organs tended to be negatively correlated to total
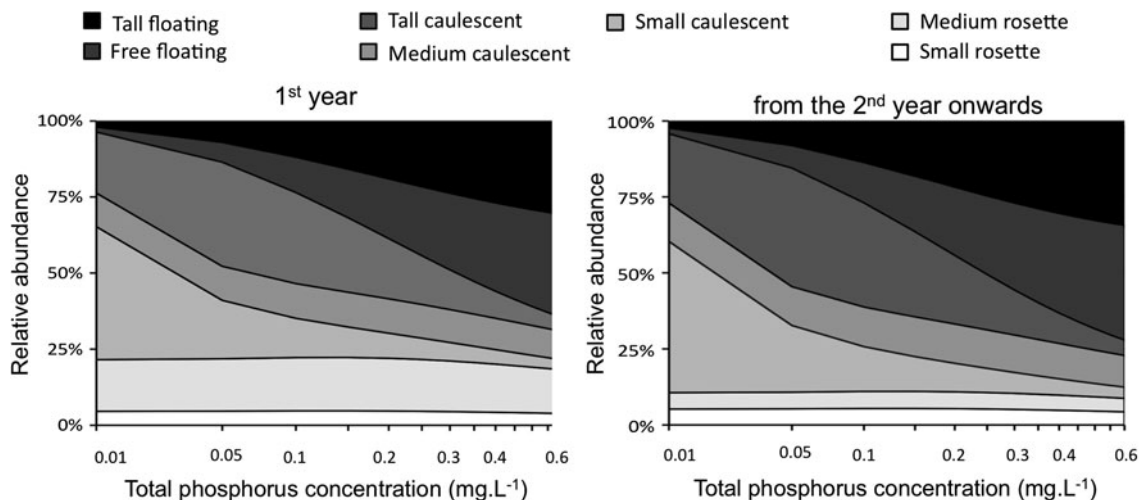
Fig. 2 Modelling of the relative abundance of plant growth forms according to total phosphorus concentration the 1st year after summer drying (*left*) and from the 2nd year onwards (*right*)

phosphorus concentration and was higher the first year after summer drying, but did not differ among the following years. The relative abundance of perennial species with storage organs was not correlated to total phosphorus and did not differ according to the number of years after summer drying.

Modelling of the distribution of longevity traits based on a significant relationship between traits and abiotic pressures is presented in Fig. 3. The abundance of annual and perennial species was similar at lowest total phosphorus concentration, but perennial species became dominant when the total phosphorus concentration increased, especially from the 2nd year onwards. Species without storage organs were dominant at lowest total phosphorus, especially in the 1st year for perennial species, whereas species

with storage organs were dominant at high total phosphorus concentrations.

Fecundity

The relative abundance of species reproducing only with seeds and having a medium number of reproductive organs was negatively correlated to total phosphorus concentration and did not differ according to the number of years after summer drying. The relative abundance of species reproducing only with seeds and having a high number of reproductive organs was not correlated to total phosphorus concentration but it was more abundant the first year after summer drying. Concerning species that reproduce with both seeds and vegetative propagules, their relative
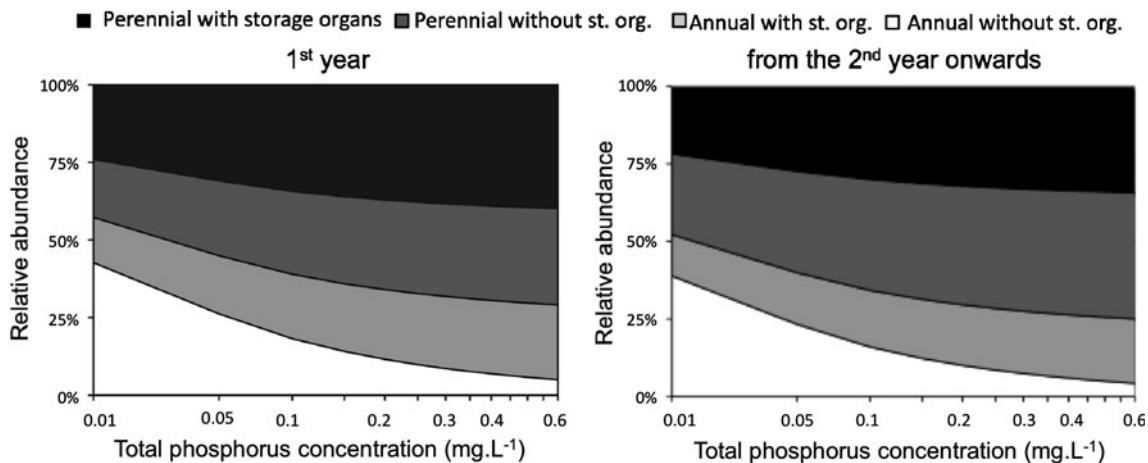

Fig. 3 Modelling of the relative abundance of the different modalities of species longevity according to total phosphorus concentration the 1st year after summer drying (*left*) and from the 2nd year onwards (*right*)

abundance was not correlated to total phosphorus concentration and did not differ according to the number of years after summer drying, regardless of the number of reproductive organs.

The modelling of the distribution of fecundity traits along productivity and disturbance gradients is presented in Fig. 4. Species with a medium number of reproductive organs were dominant throughout both gradients. Among these species, the abundance of those with only sexual reproduction, or with both vegetative and sexual reproduction, was similar at lowest total phosphorus concentration, whereas those with vegetative and sexual reproduction were dominant at high total phosphorus concentration.

Discussion

Functional diversity in the productivity-disturbance framework

Functional richness, dispersion and evenness did not all have the same relationship with productivity and disturbance. Functional richness and dispersion fitted only partly the hypotheses. Indeed, they were lower at high productivity, but did not differ according to disturbance frequency. Functional evenness also did not fit the hypotheses because it did not differ according to either disturbance frequency or productivity.

These results confirm that increasing productivity selects for the more competitive species, leading to low functional richness and functional dispersion at high productivity levels. The absence of any trend for evenness suggests that regardless of functional richness and dispersion, the life-history traits that occur at a given level of productivity are equally abundant in the communities.

Disturbance frequency did not correlate with functional diversity, regardless of the index tested. In our sampling design, disturbances were highly homogeneous among ecosystems (long-term drought and crop cultivation). This technique has been used for several centuries across the Dombes region and probably strongly selected for a set of species able to face these events, regardless of their frequency. The range of disturbance frequencies may also not be sufficiently high for observing any variation through time in trait content.

Our results contrasted with the theory that predicts a humped back relationship between diversity and major abiotic factors (Grime 1979). The only study available (Nielsen 2003) also contradicts the theory, but did not exhibit the same pattern as the one demonstrated in the present study. Indeed, Nielsen (2003) demonstrated that functional richness, diversity and evenness of coastal macrophytes colonising intertidal rocks were lower for higher levels of disturbance (assessed through the biomass of herbivores) and that functional evenness was higher for high productivity (only where herbivore biomass was low).

Distribution of life-history traits in the productivity-disturbance framework

At high productivity and low disturbance frequency, some life-history traits related to the competitive strategy, i.e., tall species with floating leaves or free-floating species, both of which optimise light uptake. Species with storage organs were favoured, contrary to what is expected for competitive species, as such a trait is usually associated with stress-tolerators (Grime 1979). In eutrophic ecosystems, increasing ecosystem productivity leads to increasing competition for light with phytoplankton, which may explain the increasing allocation to storage organs that
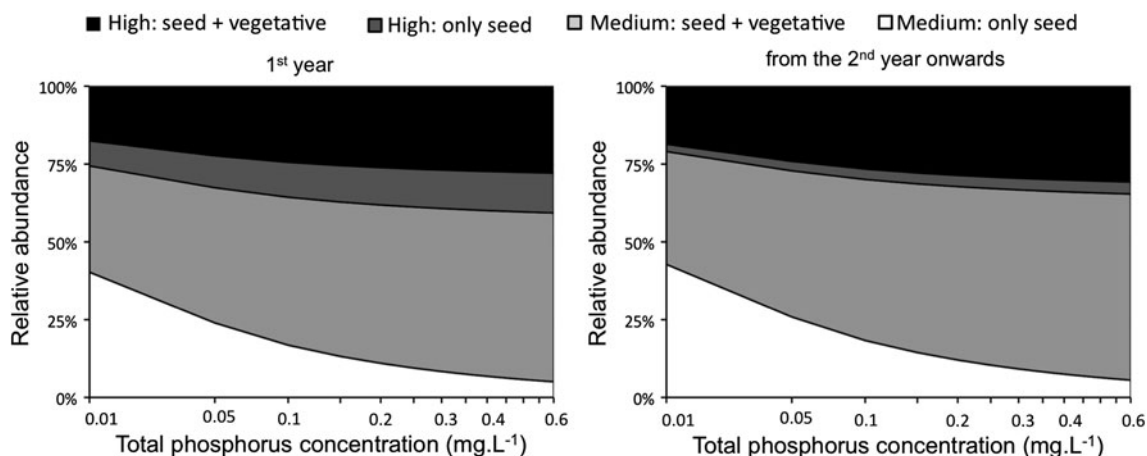

Fig. 4 Modelling of the relative abundance of the different modalities of species fecundity according to total phosphorus concentration the 1st year after summer drying (*left*) and from the 2nd year onwards (*right*)

increase the ability of a plant to reach the photic zone. Furthermore, vegetative propagules, such as turions, or dormant apices may store more reserves than seeds (Klimešová and Klimeš 2007), and may consequently be superior to seeds in terms of reaching the photic zone. Storage organs allowing vegetative reproduction may thus be key traits in defining aquatic plant success, particularly in eutrophic situations. When the disturbance intensity increased, the relative abundance of species with a high number of only sexual diaspores increased, in accordance with what is expected from the ruderal strategy. Drought destroys all vegetative individuals, whereas seeds of many species may persist and withstand desiccation (Klimešová and Klimeš 2007). The high density of seeds found in these ecosystems (Arthaud et al. 2011) is consistent with our results, confirming that drought disturbance favours species with high seed production.

At low productivity, regardless of disturbance frequency, the results were inconsistent with what was expected from the stress-tolerant strategy, i.e., a long established phase and the occurrence of storage organs (Kautsky 1988). Indeed, species without storage organs were the most abundant, and perennial species were as abundant as annual species. This pattern may relate to the higher light availability at low productivity, allowing a strong recruitment from the seed bank because of the lower competition pressure for light by phytoplankton. Furthermore, since evergreen species are absent from our lakes, above-ground biomass is completely lost in winter, resetting the competitive hierarchy and allowing for the maintenance of annual, poorly competitive species even for low disturbance frequency. Concerning fecundity, regardless of the disturbance frequency, the abundance of species reproducing either only sexually or with many various types of vegetative diaspores, was similar, invalidating the expectation that seed-reproducing species (ruderals) dominate at high disturbance intensity. The occurrence of vegetative reproductive strategies at high drought disturbance suggest that either selected vegetative diaspores are able to survive drought and persist long term, or that such species use simultaneously several reproductive strategies in order to cope with the various uncertainties that characterise such habitats. Vegetative diaspores are killed by drought, but may allow rapid regrowth in spring, and seeds, disperse among lakes through water fluxes. Seeds, on the contrary, may permit plants to survive drought. Plant morphology differed according to disturbance frequency. For high disturbance frequency, our results were consistent with what was expected from the 'stunted' strategy, i.e., the dominance of small and medium species. However, at a low disturbance frequency, small and medium species also dominated, contrary to our expectations for 'biomass storers'. Our results also contradict those of Van Geest

et al. (2005) who found perennial tall floating species in floodplain lakes that are temporarily dewatered. However, in this last situation, the disturbance caused by water level fluctuations was of much lower intensity than observed in the present study, and it did not induce sediment drying.

Concluding remarks

The present study partly supported the CSRB model (Kautsky 1988). Strategies may be screened not only by disturbance frequency but also by the nature of the disturbing event. Indeed, sustained droughts kill all vegetative parts of aquatic plants. For such disturbances, community resilience relies strongly on a persistent seed bank or high seed rain. In the present study, the disturbance was drought of very high intensity (1 year of complete drought) in all cases. In natural ecosystems, drought intensity may vary and allow some plants to resist the disturbing event through dormancy (deep anchored rhizomes) or phenotypic plasticity (Barko and James 1998; Greulich et al. 2001; Puijalon and Bornette 2006). Such plasticity may result in an enhanced resistance to drought if the species is able to produce an emerged growth form (as many rosette growth forms do). Plasticity may also induce more resilience, if species are able to switch from sexual to vegetative reproduction, depending on the nature or intensity of the disturbance (Combroux and Bornette 2004; Stöcklin and Winkler 2004). Such contrasting ways of facing disturbances may complicate the pattern of traits along the disturbance gradient, compared to the situation observed in the present study.

Several traits were not considered in the present study but may be considered in further research on plant survival strategies along productivity gradients, as they may greatly affect the tolerance of species to productivity. During the recruitment phase, seedlings must tolerate the shading effect of phytoplankton. Two traits may be informative regarding this tolerance: the quantity of resources stored in the seed and the seedling relative growth rate in the shade (Ganade and Westoby 1999). The light compensation point of species may also strongly determine the species tolerance to light stress induced by the competition between aquatic plants and phytoplankton (Spencer and Rejmánek 2010), which prompts the question of whether there is an uncoupling of juveniles and adult plant with respect to this trait.

Appendix

See Tables 2, 3

Table 2 Water, sediment and site parameters of samples of the shallow lakes of the Dombes region, France (Wezel et al. 2011)

Parameter	Mean	Minimum	Maximum	SD	N
Site parameters					
Lake area (ha)	13.4	2.3	79.6	11.9	83
Lake depth median (m)	0.68	0.28	1.10	0.18	59
Lake volume (m^3)	85,15	14,622	444,830	82,924	59
Ratio lake/catchment area	1.2	0.1	12	2.1	61
Summer water parameters					
Total P median (mg/m^3)	274	29	609	136	83
Total N median (g/m^3)	2.85	1.32	6.68	1.03	83
Chlorophyll-a median (mg/m^3)	94	3	474	90	83
Chlorophyll-a maximum (mg/m^3)	471	16	2,547	478	83
Sediment parameters					
Available P (mg/kg)	209	43	664	118	83
Organic matter (g/kg)	37.54	13.30	85.91	12.52	83
Total N (g/kg)	2.20	0.60	4.17	0.57	83
Calcium (g/kg)	2.17	0.65	10.52	1.60	83
pH	6.34	4.925	7.93	0.54	83

Table 3 Table for the species traits according their morphology, longevity and fecundity (Grime et al. 1990; Willby et al. 2000 and personal information)

Species	Morphology	Longevity	Fecundity	Species	Morphology	Longevity	Fecundity
Alisma gramineum	MR	A	Hv	*Potamogeton berchtoldii*	SC	Ar	Hv
Alisma plantago-aquatica	MR	P	H	*Potamogeton crispus*	TC	Pr	Hv
Callitriche hamulata	SC	P	Mv	*Potamogeton gramineus*	TC	Pr	Mv
Ceratophyllum demersum	FF	Pr	Mv	*Potamogeton lucens*	TC	Pr	Mv
Chara braunii	SC	A	Hv	*Potamogeton natans*	TC	Pr	Hv
Chara globularis	SC	P	Hv	*Potamogeton nodosus*	TF	Pr	Hv
Damasonium alisma	MR	P	H	*Potamogeton obtusifolius*	MC	Ar	Hv
Elatine alsinastrum	MC	P	M	*Potamogeton pectinatus*	TC	Pr	Hv
Elatine hexandra or *E. triandra*	SC	A	Mv	*Potamogeton pusillus*	SC	Ar	Hv
Eleocharis acicularis	SR	P	Mv	*Potamogeton trichoides*	SC	Ar	Mv
Glyceria fluitans	MC	Pr	Hv	*Potamogeton x angustifolius*	TC	Pr	Mv
Hydrocharis morsus-ranae	FF	Pr	Mv	*Ranunculus flammula*	SR	P	Hv
Juncus articulatus	MR	P	Hv	*Ranunculus peltatus*	MC	P	Hv
Lemna gibba	FF	Ar	Hv	*Ranunculus sceleratus*	MR	A	Hv
Lemna minor	FF	Ar	Hv	*Riccia fluitans*	FF	Ar	Hv
Ludwigia palustris	MC	Pr	H	*Rorripa amphibia*	MR	Pr	Hv
Luronium natans	SR	P	Mv	*Sagittaria sagittifolia*	MR	Pr	Hv
Marsile aquadrifolia	SR	P	Hv	*Sparganium angustifolium*	MR	Pr	Hv
Mentha aquatica	MC	Pr	Mv	*Sparganium emersum*	MR	Pr	Hv
Myriophillum spicatum	TC	Pr	Mv	*Spirodela polyrhiza*	FF	Ar	Hv

Table 3 continued

Species	Morphology	Longevity	Fecundity	Species	Morphology	Longevity	Fecundity
Najas marina	TC	A	M	*Trapa natans*	TF	Ar	Mv
Najas minor	MC	A	M	*Utricularia australis*	FF	Ar	Mv
Nitella spp.	SC	A	Hv	*Utricularia intermedia*	FF	Ar	Mv
Nymphoides peltata	TF	Pr	Mv	*Utricularia ochroleuca*	FF	Ar	Mv
Oenanthe aquatica	MR	P	Hv	*Utricularia vulgaris*	FF	Ar	Mv
Polygonum amphibium	TF	Pr	Mv	*Zannichellia palustris*	SC	Pr	Mv
Potamogeton acutifolius	MC	Ar	Hv				

Morphology: *SR* small rosette, *MR* medium rosette, *SC* small caulescent, *MC* medium caul., *TC* tall caul., *FF* free floating, *TF* tall floating; Longevity: *Pr* perennial with storage organs, *P* perennial without st. org., *Ar* annual with st. org., *A* annual without st. org.; Fecundity: *Hv* high number of reproductive organs, seed and vegetative propagules, *H* high number of rep. org. only seed, *Mv* medium number of rep. org., seed and veg. prop., *M* medium number of rep. org., only seed

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