

Plant response strategies to stress and disturbance: the case of aquatic plants

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The environmental factors controlling the establishment and development of plants in different ecosystems are of two types, stress and disturbance. The effects of stress or disturbance on aquatic systems are discussed in relation to the following questions:

Can we predict the state and rate of recolonization after a disturbance? What are the strategies of recolonization developed by plants? How high is the resilience of a disturbed system? Two theories, the intermediate disturbance hypothesis, and the patch dynamics concept proposed to predict the composition, structure and dynamics of plants due to physical-chemical factors, were tested on two scales, that of communities and that of species, within two alluvial floodplains (the Rhine and the Rhône systems in France).

With regard to the change of community on a larger scale (i.e. the whole network of the cut-off channels in the floodplain), large gradients of connection and disturbance induce high diversities within communities. Moreover, the highest flood disturbance induces a higher species richness and the occurrence of a particular species. The change in species is analysed using biological traits (morphological, reproductive or physiological). In the floodplain of the river Rhône, the response of plants corresponds well to theory, i.e. that habitats with an intermediate disturbance are richer than more or less disturbed habitats. So we can predict, through the biological traits, the functioning of a habitat. The last remaining question is that of the resilience of the system, which can be discussed in terms of species competition and the risk of biological invasion after an opening of habitat.

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1. Introduction

Stress is defined according to Grime (1979) as the external constraints which limit the dry matter production rate of all or a part of vegetation, whereas disturbance consists of the mechanisms limiting plant biomass by causing its destruction. According to Pickett and White (1985), a disturbance means any relatively discrete event in time that disrupts an ecosystem, its community and population structure, and changes substrate availability or the physical environment. Disturbance is often considered as an unpredictable event. These two processes structure habitats and can explain the distribution and dynamics of plants.

Aquatic plant habitats in both running and steady waters are characterized by high spatial and temporal variations

of physical and chemical parameters. These aquatic habitats represent stressful environments, which are characterized for example by low carbon availability, low or excess of nutrients, shaded conditions, mechanical damages by currents and waves. Thus plants are subjected to these more or less frequent changes and are usually considered to be stress-tolerant. However, aquatic plants have large distributional ranges. The broad distribution of taxa among aquatic plants results from dominance of best-fitted genotypes, widespread clonality and a high phenotypic plasticity (Barrett *et al* 1993; Santamaria 2002). These authors observe that within genetic species and population variations are low, but variations among populations can be high. Ecotypic differentiation is related to factors that constrain clonal reproduction, such as stress

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(e.g. salinity, light, nutrient content) and disturbance (ephemeral inundation). These two factors control the heterogeneity of aquatic habitats at relatively small scales, which could explain the large pattern of biological traits developed by aquatic vascular plants. This small scale environmental mosaic tends to repeat itself regionally.

The plant strategy approach assesses the connection between submerged aquatic plants and environmental pressures. In lakes, for example, Murphy *et al* (1990) show that a high incidence of stress-tolerant traits occurred in habitats stressed by low nutrient availability and low pH, whereas competition and disturbance-tolerant traits were more frequent in communities of two productive lakes impacted by water level fluctuations.

The questions are:

What are the strategies developed by aquatic vascular plants after a disturbance or a stress?

Can we predict the rate and state of recolonization after disturbance?

What is the resilience of an aquatic habitat, in its capacity to restore its structure and functioning? In this case the difficulty lies in the definition of a reference point.

We analyse plant response at different levels: the level of species through their biological traits, and the level of communities in relation to their specific richness and floristic composition. Examples are chosen in fluvial hydro-systems, where disturbance caused by floods is relatively frequent. Can we distinguish the effects of competition, constraint or disturbance under these conditions? Finally, what is the capacity of invasive plants according to their biological traits, in colonizing new opened habitats after a disturbance?

A few theories and models have been proposed to explain and predict distribution and dynamics of plants according to stress and/or disturbance, which have been tested in floodplains.

2. Response of plant communities

2.1 *Species richness*

The hypothesis of intermediate disturbance (Connell 1978), which means disturbance with intermediate frequency and magnitude, allows fast-growing ruderal species and competitive species to co-occur, favouring a great richness and diversity of species. In fluvial hydro-systems, the disturbance frequency caused by floods depends on the connectivity between cut-off channels and the river.

The hypothesis was that intermediate connectivity enables inputs of propagules in the wetlands without impeding recruitment and intermediate nutrient supply of the latter. On the contrary high connectivity impedes recruitment either by overfrequent flood scouring or by supplying hypertrophied turbid surface waters, which reduces

species richness. Low connectivity (or disconnection) too decreases or suppresses flood scouring and succession rejuvenation and consequently allows competition to eliminate less competitive species with no recruitment of new species brought by floods.

An example, taken from the Rhone fluvial hydrosystem (Bornette *et al* 1998), shows that the most frequently flooded channel presents the highest species-richness of up to 31 species, whereas channels with low sinuosity and flooded at intermediate frequencies are either species-poor (6–8 species) or at an intermediate richness (24 species) (figure 1). A first species-poor group is closely connected to the river, the water of which is nutrient-rich and turbid, while a second group was species-poor because of groundwater supplies with nutrient-poor water, which probably is a limiting factor for plant growth and recruitment. The group at intermediate richness is influenced by floods that partly scour substrate and plants and afford regeneration niches for transported propagules. Moreover, the origin of water supply in the cut-off channels influences the specific richness. The effects of connectivity appear much more complex than hypothesized, so that surficial connectivity between river and wetlands cannot be reduced to a single phenomenon of disturbance.

In the Rhine hydrosystem on the contrary, it seems that there is no clear connection between species richness and the degree of connectivity. The maximum richness is around 20 hydrophyte species, and reaches almost as many sites belonging to each of the three classes of connection (disconnected, temporarily connected and permanently connected). The richest sectors are those which have different types of water supply from groundwater and surface water. However, one of the richest channels, a drainage canal disconnected from the Rhine, is only fed by groundwater which is influenced by seepage from the nutrient-rich waters of the Rhine. The drainage waters are clear and eutrophied. This is also indicated by a macrophyte community rich in eutrophic species (table 1).

The species richness of the Rhine is lower than that of the Rhône (Bornette *et al* 1998). In this latter system, the braided lateral arms present higher frequencies of overflowing than those of the Rhine and also a higher meandering. A higher degree of disturbance by floods explains this difference. The floods cause a scouring of the substrate, which is then recolonized by pioneer species which cohabit with species tolerant to flood, and this increases the diversity. This is not the case in the Rhine system because of its canalization, even in flooded zones where the dynamics of floods is highly reduced.

2.2 *Floristic composition*

Flood disturbance opens habitats and creates new ecological niches. This results in a large diversity of habitats and

in a community richness presenting a large range of variations. The floristic composition of communities reflects the combination of environmental factors, hydrological and chemical factors as such. In the Rhine river floodplain we identify up to 5 plant communities in the connected, probably disturbed sector and only two in the partly connected less disturbed sector (table 1). Aquatic macrophyte communities are mesotrophic to eutrophic, depending on the origin and quality of waters. Moreover, the floods allow the alternating of deposit areas with slow flowing waters and erosive areas with high current velocity within the channel. This allows a development of species which are adapted either to coarse substrate or to fine deposits (silty-clay). *Potamogeton pectinatus* for example, a eutrophic species, occurs in both running and stagnant water, whereas *Ceratophyllum demersum* grows only in stagnant water. In mesotrophic water, *Lemna trisulca* is abundant in calm water whereas *Berula erecta* prefers coarse substrate with high velocity (Trémolières M and Szwab A, unpublished results). Trophic seems to strongly influence the distribution of macrophytes.

This community diversity can be explained by the combination of two main factors, the degree of disturbance and the type and importance of water feeding (supply by river water and/or groundwater), as has also been shown by Bornette *et al* (1998).

However it seems that the seasonal fluctuations of hydraulic disturbances affect vegetation more in terms of abundance, whereas qualitative change in species composition occurs at an interannual rate at which a succession

can occur when the disturbances are less frequent. Thus a channel close to the river is maintained at a steady state by the regular floods; the disturbance washes away fine deposits and rejuvenates vegetation mosaic. In a less disturbed channel the maintenance of fine sediments authorizes a succession trend, which is however slowed down by groundwater supply (Bornette *et al* 1994). The disturbance frequency and duration explain both the seasonal and interannual change in floristic composition within a channel, which permits the relative stability of a vegetation mosaic, but depends on the spatial scale of observation.

The distribution of vegetation is explained by their biological traits, morphological and physiological, the combination of which forms the colonization strategies of plants.

3. Strategies of species

The most common model was proposed by MacArthur and Wilson (1967) and considered two types of contrasted strategies, *r* and *K*. The *r*-strategy selects species with a high reproduction and thus insures a maximization of the rate of regrowth (*r*). The *K*-strategy concerns species which allocate nutrient resources to the structure and functioning of the organism (maximization of *K* which is the carrying capacity of a mature ecosystem for the organism).

The well-known model of Grime (1979) defined three primary ecological strategies, *C*-competitive, *S*-stress and *R*-ruderal, rephrased as *C*-competitive, *D*-disturbed, *S*-stressed aquatic environments by Murphy *et al* (1990) in lakes.

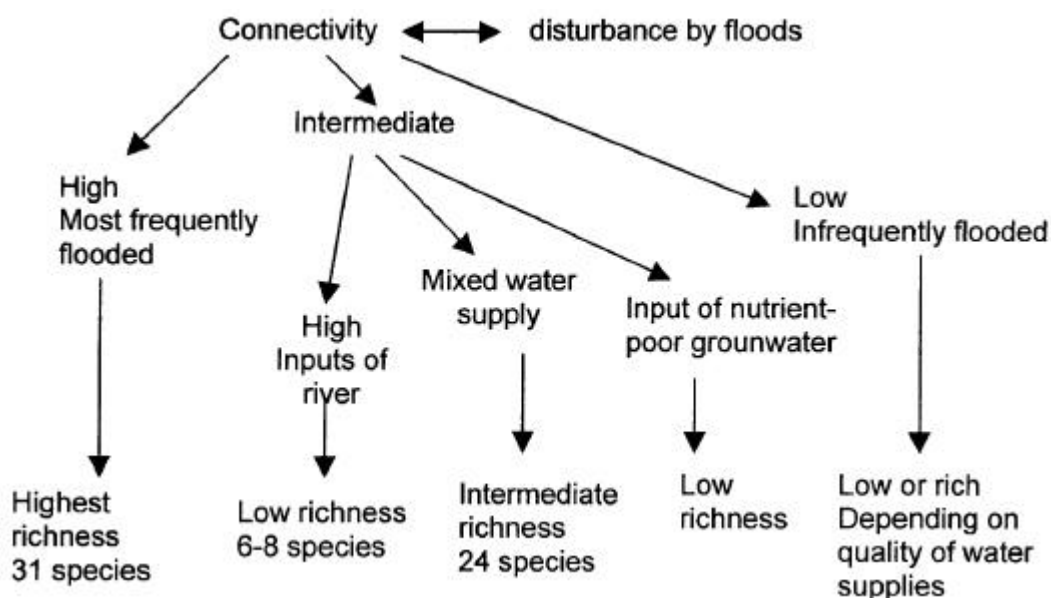


Figure 1. Scheme of relationships between disturbance and specific richness (modified from Bornette *et al* 1998).

Two theories, the 'patch dynamics concept' proposed by Pickett and White (1985) and the habitat templet of Townsend (1989) consider the effects of disturbance for explaining the processes of structure and dynamics of communities and include the strategies developed by species. The basics of the first theory are that firstly, every ecological system is a patch mosaic at various scales of observation, secondly the dynamics of communities differ according to a degree of spatial and temporal heterogeneity of environment. In other words, the disturbance is often patchy, and is distributed in time.

Townsend (1989) considers that different processes control communities according environmental variability (figure 2):

– A level of intermediate temporal variation in a homogeneous environment presents an intermediate specific richness, which corresponds to the model of phased succession, i.e. all the successional stages are present in a spatial homogeneous environment.

– High spatial heterogeneity corresponds to a high specific richness. In this case, we distinguish several patterns of communities:

(i) Firstly when the temporal heterogeneity is low, the pattern corresponds to the 'niche controlled' populations. The main factor which controls the populations is the competition and coexistence of populations in a same habitat and is possible only if they differ in one-dimension of their ecological niches.

(ii) An intermediate temporal heterogeneity leads to two models:

– '*Dominance controlled*' communities: the result of competition between species with different ecological strategies which occur during the succession. The pioneer species which colonize new substrate after a disturbance have *r*-strategy and are replaced by species with *K*-strategy, during the succession. Communities form a patch mosaic at different succession stages.

– '*Founder controlled*' communities: The first species which grow on the new site are again of *r*-strategy type, but there is no replacement by more competitive species. The structure of communities depends on the strategies of the first colonizers and the result of colonization is unpredictable, which corresponds to a 'competitive lottery' model.

(iii) A high temporal heterogeneity leads to 'mobility controlled' communities without competition and high mobility of organisms which control the structure of communities (figure 2).

These theories were tested on macrophyte communities of former channels of the Rhone river (Bornette *et al* 1994; Barrat-Segretain and Amoros 1996). Temporal heterogeneity is produced by frequency and magnitude of flood scouring. Spatial heterogeneity is similar for all the stations and is related to change in substrate granulometry. These authors try to predict the recovery pattern of the communities and strategies of species.

As predicted by theory, in the most frequently disturbed station the species developed *r*-strategies in station C. The recovery is fast which demonstrates the high resilience of the system.

The station with intermediate temporal heterogeneity was colonized by *r*-selected species and *K*-selected species

Table 1. Relationships between connectivity, communities and specific richness.

	Number of communities and trophic level	Characteristic species	Specific richness of the dominant community (the whole sector)
Connected	3–5 according to intensity or frequency of hydrological connection Eutrophic	<i>Elodea nuttallii</i> , <i>Myriophyllum spicatum</i> , <i>Ranunculus fluitans</i> , <i>Ceratophyllum demersum</i> , <i>Potamogeton perfoliatus</i>	18–21 without algae (25)
Partly connected	2 Eutrophic Mesotrophic (groundwater seepage)	<i>Potamogeton nodosus</i> , <i>Potamogeton lucens</i> , <i>Ranunculus fluitans</i> , <i>Nuphar lutea</i> , <i>Sparganium emersum</i> (calm waters) <i>Callitriche obtusangula</i> , <i>Lemna trisulca</i> , <i>Elodea canadensis</i>	10–14 (27)
Disconnected with a mixed feeding by surface water and groundwater (Steingriengiessen)	4 Eutrophic Meso-eutrophic (groundwater seepage)	<i>Potamogeton pectinatus</i> , <i>Myriophyllum spicatum</i> , <i>Potamogeton perfoliatus</i> , <i>Ceratophyllum demersum</i> , <i>Elodea nuttallii</i> <i>Berula erecta</i> , <i>Callitriche obtusangula</i> , <i>Zannichellia palustris</i> , <i>Hippuris vulgaris</i>	10 (28) 21
Disconnected Supply by groundwater	2 Mesotrophic	<i>Berula erecta</i> , <i>Callitriche obtusangula</i> , <i>Potamogeton friesii</i> , <i>Hildenbrandia rivularis</i> , <i>Mentha aquatica</i>	12 (26)

but the recovery is predictable and the resilience is intermediate (station B). The less frequently disturbed station A presents cohabitation of *r*-selected and *K*-selected species. The macrophyte community can be said to be 'dominance controlled'. However the recovery is slow (more than 5 months).

The species traits were analysed according to a degree of disturbance. Among species traits, 13 were retained

e.g. potential size, reproductive period, anchorage, regeneration potential, vegetative dissemination (table 2). The species traits present a common structure with the distribution of species in the floodplain habitats, i.e. species with the same traits occur in the same type of habitat; and this common structure is well related to a gradient of connectivity and thus to the disturbance frequency. Thus the relationship between species traits and habitat utilization

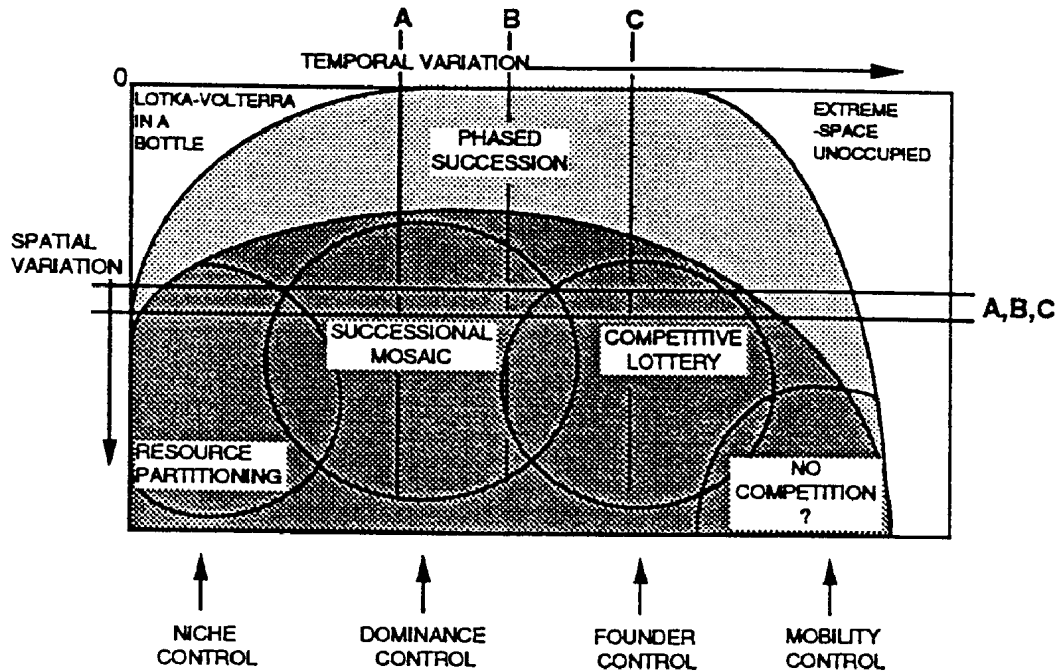


Figure 2. Model of population responses according to a gradient of spatial and temporal heterogeneity as defined by Townsend (1989) and position of three study sites of the Rhône floodplain (A, B, C) (Barrat-Segretain and Amoros 1996).

Table 2. Species traits according to a gradient of flood disturbance frequency (from Bornette *et al* 1994).

Species traits	<i>P</i>	Channels least disturbed	Channels isolated from the river, temporarily flooded	Channels connected far from the river	Channels close to the river the most frequently disturbed
Size	±	Small or large	Intermediate	Intermediate	Intermediate
Number of descendants per cycle	-	Many	Few	Few	Few
Reproductive period	?	Spring	Spring to summer	Spring to summer	Spring to summer
Attachment to substrate	+	Low to high	Low to high	Low to high	High
Body flexibility	±	Low	Intermediate	Intermediate	Intermediate
Regeneration potential	±	Low to high	Intermediate to high	Intermediate to high	Intermediate to high
Vegetative dissemination	+	Low to high	High	High	High
Seed dissemination	?	Anemochory	Hydro/zoochory	Hydro/zoochory	Hydro/zoochory
Sedimentation tolerance	?	High	Low to high	Low to high	Low to high
Growth form	?	Non-anchored, floating leaves	Anchored, floating leaves	Anchored, floating leaves	Submersed or heterophylly

In column *P* comparison with prediction of Townsend and Hildrew (1994) '+', agreement; '-', disagreement; '±', partly agreement; '?', no prediction available.

is highly significant. For example the species which colonize the disconnected habitats are often of a smaller size, less tolerant to water level variations, not anchored such as Lemnids or of a higher size, but anchored (*Nuphar lutea*). The stands with frequently removed substrate select anchored plants with a high vegetative reproduction.

Hence it could be possible to predict the major species traits which can occur in a habitat affected by one or another disturbance (frequency, period, intensity).

4. Plasticity of species and response to disturbance

Phenoplasticity is the response of a genotype to environmental changes. Among plants phenoplasticity depends on spatial structure and architecture, ontogenic variations (predictable change during the growth), and finally environmental factors. High levels of plasticity occur in aquatic habitats characterized by factors that vary over small spatial or over short-term temporal scales. An inundation gradient can be the main factor which induces a significant plastic variation.

We can distinguish passive or inevitable plasticity as a consequence of a nutrient limitation or a disturbance, and active plasticity (figure 3, Garbey 2003) as a change in plant form for a better adaptation to the environment; in this latter case it renders to plants a selective value which allows

them to remain in a disturbed habitat for example. These types of plasticity have energetic, genetic and morphological costs. If the global costs are less than the benefits, the plasticity is considered as adaptative, if not, plasticity is non adaptative, which is rare in nature.

Plasticity could explain the colonization of species in habitats with different degrees of disturbance. Thus immediately after a disturbance, there is a pulse of recruitment under conditions of weak competition: the species which colonizes the new environment produces turions or other non subterranean vegetative organs species that disseminate both by lateral spread and regeneration.

Four examples of plastic species can be given to explain the influence of disturbance or stress on species traits change: two common species relatively largely distributed, *Ranunculus peltatus* in soft waters (Garbey *et al* 2003) and *Potamogeton pectinatus* (fennel pondweed) in brackish and freshwater (e.g. Kautsky 1987; Spink *et al* 1993), two rare species *Luronium natans* (Greulich *et al* 2000a,b) and *Potamogeton coloratus*.

Plants in upstream nutrient-poor undisturbed sites adopted S-strategy with a small size and achieved little sexual reproduction (figure 4). Plants in nutrient rich undisturbed sites have long branching shoots which correspond to C-strategy whereas plants in weakly shaded (unstressed), disturbed sites were small but produced many flowers (R-strategy). This species adopted different types of strategies

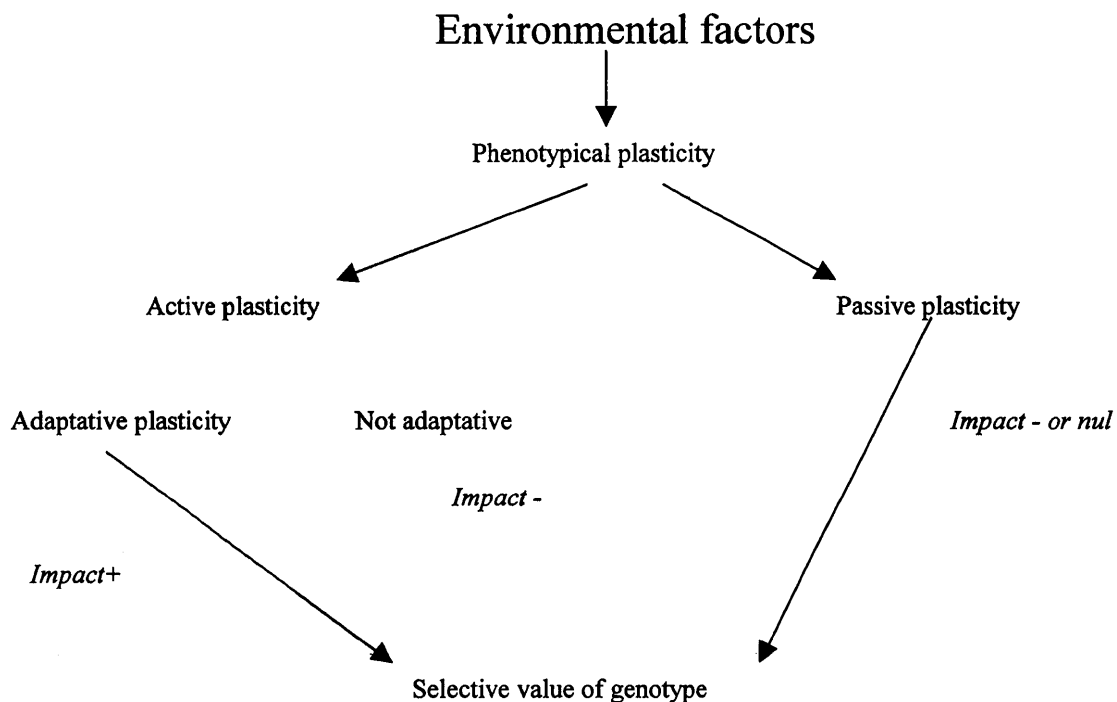


Figure 3. Scheme of relationships between environmental factors and genotype selection (from Garbey 2003).

according to morphological traits adapted to the physical environment more than to the chemical one. The plasticity gives it advantages that explain its ability to colonize different types of habitats.

A rare species such as *L. natans* which occurs usually in the unproductive habitat of the *Littorelletea* communities, which is typical for acidic and poor water, was encountered in two disturbed sites among a hundred cut-off channels of the Rhône floodplain. A study of transplantation of this species in different habitats in which it does not occur spontaneously (Greulich *et al* 2000a) shows that *Luronium* is able to colonize half of transplantation sites and persist over a long term and that this persistence depends on processes limiting community plant biomass. The species heterophyllous growth form and the plasticity in biomass allocation according to the nutrient status explain the reason for the growth of *Luronium* even among dominant species within communities of nutrient-rich habitats (Greulich *et al* 2000b). In these conditions *Luronium* allocates more nutrients to floating leaves which increases its competitiveness. Its rarity could be due to insufficient dispersal and recruitment in frequently disturbed stands.

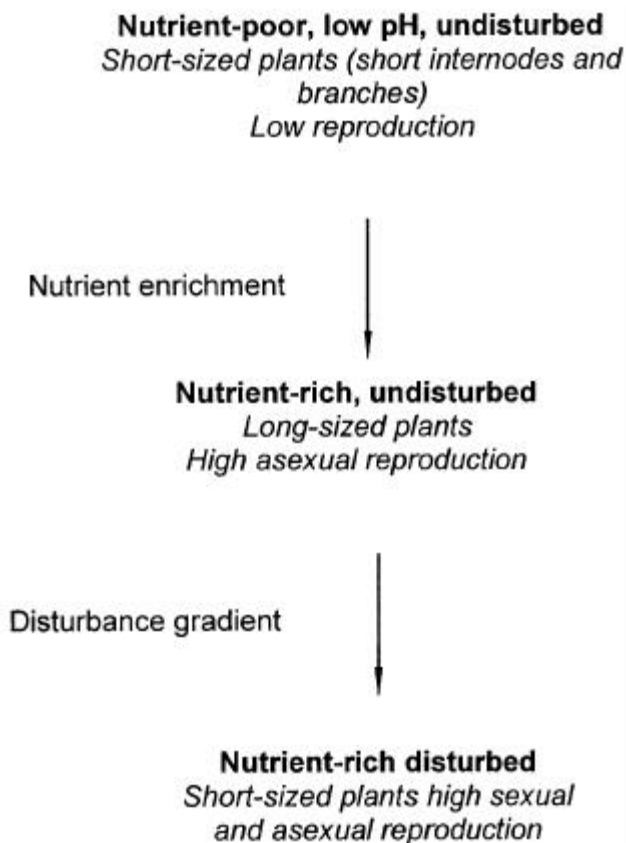


Figure 4. Responses of *R. peltatus* to environmental constraints (from Garbey *et al* 2003).

P. pectinatus, a species relatively common in eutrophic waters, where it can form a dense canopy (Van Wijk 1988) has a very wide distribution as well as in brackish and freshwaters. In a comparison of growth of two species, *P. pectinatus* and *R. penicillatus* in association (Spink *et al* 1993), *P. pectinatus* seems more competitive and this is probably due to its greater plasticity in its growth response. A competitive plant responds to stress with large changes in growth rate (Grime 1979). Thus the *Potamogeton* shoot biomass was seven times smaller in the P-enriched treatment (stress) whereas the *Ranunculus* shoot biomass was only 4.4 times smaller. Moreover the reproductive strategy of *Potamogeton*, flowering and seed production varies according to different degrees of stress (for example exposures to waves, Kautsky 1987). Following Grime (1979), its life cycle can be classified as that of a typical stress-tolerant in more exposed habitat and of a competitive plant in sheltered habitat. Could this high plasticity be related to ecotypic differentiation or only to adapting behaviour to environmental factors?

The case of *Potamogeton coloratus* is specific in that this species is able to colonize undisturbed as well as disturbed systems due to its high regeneration and propagation abilities by vegetative fragments (Bartrrat-Segretain *et al* 1999, 2000). But it is restricted to undisturbed habitats because of its low trophic range (Carbiener *et al* 1990) and its sensitivity to toxicity of ammonia (Rolland and Trémolières 1995). The species' ability to colonize a new site is also the result of the combination of disturbance and stress (nutrient excess, ammonia toxicity).

5. Can invasive plants easily colonize a disturbed habitat?

Disturbance plays an important role by opening habitats and facilitating invasions (Burke and Grime 1996).

Invasion is often favoured by opening habitats. Two invasive species, *Elodea canadensis* and *E. nuttallii* from North America have occurred in Europe in the Alsace floodplain respectively since 1850 and 1950. *E. nuttallii* arrived in 1995 in the Rhône floodplain. These two species colonized numerous waterbodies in floodplains. The colonization occurs through vegetation transported by water, and the connectivity between cut-off channels and river is an essential parameter of their colonization (Barrat-Segretain 2001). Despite a similar pattern of biological traits of both species, *E. nuttallii* seems to replace *E. canadensis* especially after a restoration of a dredged channel. But some differences occur according to the season: *E. nuttallii* develops more roots and a higher length of stem and roots especially in spring and *E. canadensis* more ramifications in summer and autumn depending also on the trophic level. A higher trophic level seems to favour the

expansion of *E. nuttallii*. These traits could explain the better colonization efficiency of *E. nuttallii*. However from the theory proposed by Davis *et al* (2000), a community invasibility should depend on the fluctuation of nutrient availability, i.e. the community susceptibility to invasion is increased by increasing the availability of limiting resources. Moreover, Burke and Grime (1996) show that invasibility is highest in nutrient-enriched sites and still increased by disturbance. A combination of disturbance and eutrophication results in a large increase of nutrient availability and hence increases in invasibility, which is the situation in connected channels of floodplain.

6. What is the resilience of an ecosystem after a disturbance?

The question is how to measure the rate of return to an initial state for a disturbed ecosystem. For example in the case of aquatic vegetation the parameters used for this evaluation are the time for recovering the abundance and richness of species or the floristic composition in disturbed stands by comparison to standard stands. The problem remains in the definition of a reference system. A standard station corresponds to a state which evolves at the same time and space as the disturbed station, it includes

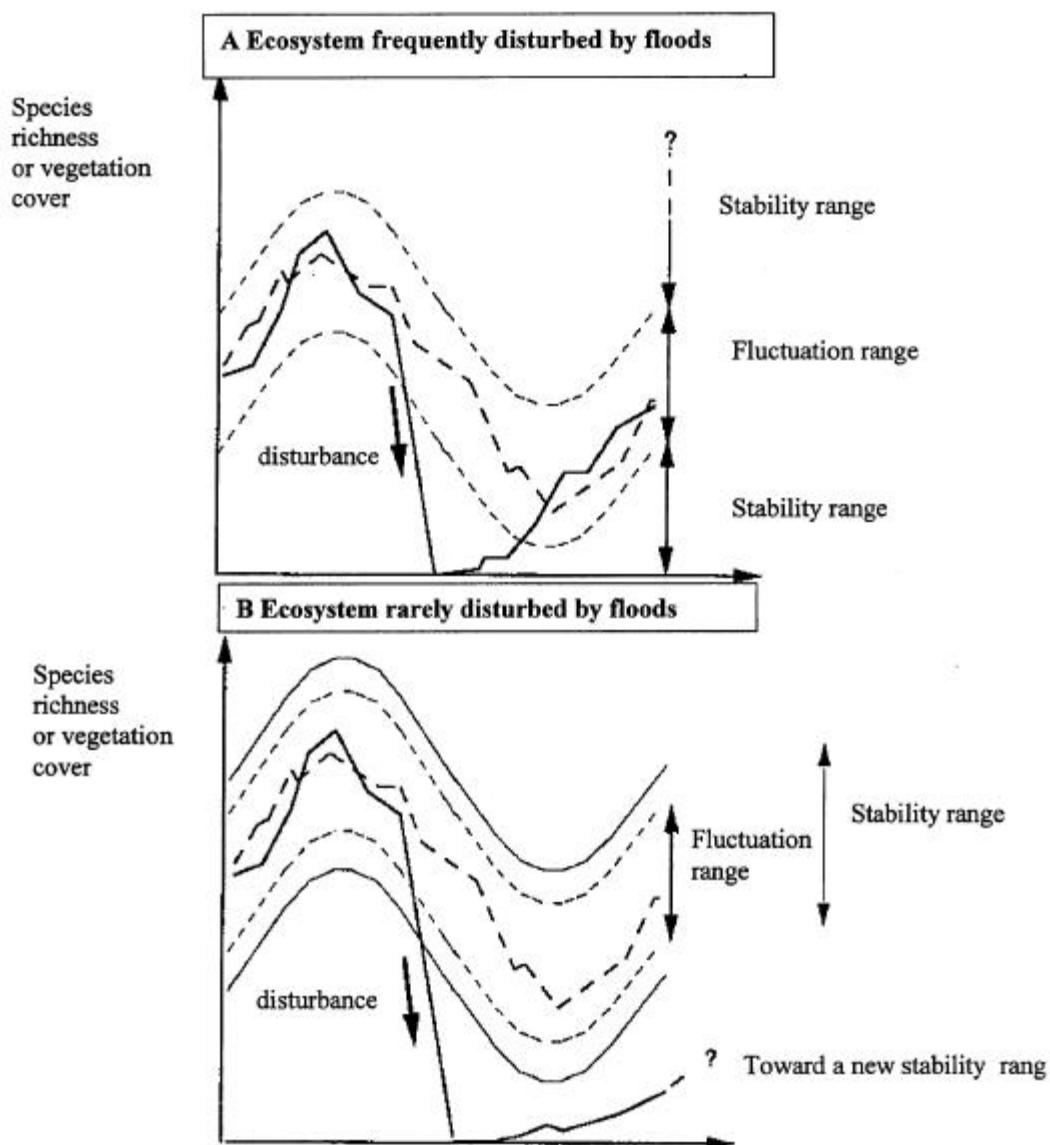


Figure 5. Scheme of change in species richness or cover in reference stands (dotted lines) and disturbed stands (solid lines) in two stations according to disturbance.

seasonal change and natural dynamics (i.e. succession taking place without disturbance).

In a channel frequently disturbed in the Rhône floodplain, the rapidity of return to an undisturbed state is relatively high (some weeks to some months from Bornette *et al* 1994). This high resilience can be attributed to the biological traits such as vegetative reproduction which plays a main role in colonization and dispersion of aquatic plants.

By contrast in a rarely disturbed station, a flood induces a strong sustainable change in the ecosystem structure. The difference between these two situations result in the vegetation stage in the succession. In the first case, the station is preserved in a juvenile stage characterized by pioneer species with *r*-strategy. The system remains in its fluctuation range, whereas in the second case the system goes out of its fluctuation range (figure 5 from Barrat-Segretain 1995). It is probably in a successive stage more advanced than this in the disturbed station. The flood which destroys vegetation eliminates *K*-selected species, and the *r*-selected species colonize these new opened sites.

7. Conclusion

Disturbance by floods creates a mosaic of aquatic habitats and thus heterogeneity within channel and floodplain. It is an important parameter which structures the aquatic systems and maintains their dynamics. As a consequence, this patchy mosaic changes both temporarily and spatially, which explains the high community richness and specific richness at different spatial scales. The recolonization of a disturbed habitat depends on propagule inputs and/or seed banks in a place, the biological capacity of species to settle and grow, and environmental factors such as substrate granulometry and water nutrient supply. These factors change more or less frequently under the disturbance effect. The resilience of a system is related to the evolution step.

Theories such as the patch dynamic concept seem to be valuable to predict relationships between spatio-temporal heterogeneity and characteristics of communities and outlines the role of disturbance in selection of species traits and ecological strategies. However, other factors like the fluctuating nutrient resources can be a constraint (stress) in the selection of species and can interact with disturbance. The combination of these two processes result in an increasing community invasibility.

The macrophyte regeneration, and its growth and development, depend largely on life history traits and strategies. We need some more information on biological traits of species and their relation with habitat utilization. Especially physiological traits have to be more studied. Some species such as *P. pectinatus* have been quite well stu-

died, others less so. The objective is to predict the recolonization potentiality of habitats being disturbed naturally, or artificially by man, and more particularly the risk of the introduction of invasive species. Thus the exotic species strategies need to be known in order to evaluate the risk of invasion. In this context another problem has a role of importance in species phenoplasticity. It is not clear why a species with high plasticity is replaced by another more competitive one or one with higher plasticity. Is this adaptive phenotypes or ecotypic differentiation? Is it a selection of traits more adapted to the new conditions after disturbance?

A recent theory (Davis *et al* 2000) focused on the opportunities for invading species to use more efficient nutrients. Some others emphasized the importance of attributes of invading species. In the *Elodea* invasion model the phosphorus storage is higher in *E. canadensis* than in *E. nuttallii* (results of spring harvest) in nutrient-rich sites when both species grow together, although the second one tends at present to replace the first (Combroux I, Haan-Archipoff G, Laurent P and Trémolières M, unpublished). Seasonal variations have to be taken into account.

We need more experiments on relations between fluctuations of resources availability and specific attributes, such as physiological ones in aquatic systems.

References

- Barrat-Segretain M 1995 *Patch dynamics concept et végétation aquatique: stratégies de recolonization de zones perturbées dans des anciens chenaux fluviaux*, Ph D thesis, University of Lyon, France
- Barrat-Segretain M H 2001 Invasive species in the Rhône river floodplain (France): replacement of *Eodea canadensis* by *E. nuttallii* St John in two former river channels; *Arch. Hydrobiol.* **152** 237–251
- Barrat-Segretain M H and Amoros C 1996 Recovery of riverine vegetation after experimental disturbance: a field test of patch dynamics concept; *Hydrobiologia* **321** 53–68
- Barrat-Segretain M H, Henry C P and Bornette G 1999 Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats; *Arch. Hydrobiol.* **14** 111–127
- Barrat-Segretain M H, Elger A, Sagnes P and Puijalon S 2002 Comparison of three life-history traits of invasive *Elodea canadensis* Michx and *Elodea nuttallii* St John; *Aquat. Bot.* **24** 299–313
- Barrett S C H, Echert C G and Husband B C 1993 Evolutionary processes in aquatic plants populations; *Aquat. Bot.* **44** 105–145
- Bornette G, Amoros C, Castella C and Beffy J L 1994 Succession and fluctuation in the aquatic vegetation of two former Rhône river channels; *Vegetatio* **110** 171–184
- Bornette G, Amoros C and Lamouroux N 1998 Aquatic plant diversity in riverine wetlands: the role of connectivity; *Freshwater Biol.* **39** 267–283
- Burke M J W and Grime J P 1996 An experimental study of plant community invasibility; *Ecology* **77** 776–790

- Carbiener R, Trémolières M, Mercier J L and Ortscheit A 1990 Aquatic macrophyte communities as bioindicators of eutrophication in calcareous oligosaprobe stream waters (Upper Rhine plain, Alsace); *Vegetatio* **86** 71–88
- Connell J H 1978 Diversity in tropical rain forests and coral reefs; *Science* **199** 1302–1310
- Davis M A, Grime J P and Thompson K 2000 Fluctuating resources in plant communities: a general theory of invisibility; *J. Ecol.* **88** 528–536
- Garbey C 2003 *Plasticité phénotypique et compétitivité chez les hydrophytes: étude expérimentale et de modélisation de Ranunculus peltatus Schrank*, Ph.D. thesis, University of Metz, France
- Garbey C, Thiébaud G and Muller S 2003 Morphological plasticity of a spreading aquatic macrophyte, *Ranunculus peltatus*, in response to environmental variables; *Plant Ecol.* (in press)
- Greulich S, Bornette G, Amoros C and Roelofs J G M 2000a Investigation on the fundamental niche of a rare species: an experiment on establishment of *Luronium natans*; *Aquat. Bot.* **66** 209–224
- Greulich S, Bornette G and Amoros C 2000b Persistence of a rare aquatic species along gradients of disturbance and sediment richness; *J. Veget. Sci.* **11** 415–424
- Grime J P 1979 *Plant strategies and vegetation processes* (New York: J Wiley)
- Henry C P, Amoros C and Bornette G 1996 Species traits and recolonization processes after flood disturbances in riverine macrophyte; *Vegetatio* **122** 13–27
- Kautsky L 1987 Life-cycles of three populations of *Potamogeton pectinatus* L. at different degrees of wave exposure in the Askö area, Northern Baltic Proper; *Aquat. Bot.* **27** 177–186
- MacArthur R H and Wilson E O 1967 *Theory of island biogeography* (Princeton: Princeton University press)
- Murphy K J, Rørslett B and Springuel I 1990 Strategy analysis of submerged lake macrophyte communities: an international example; *Aquat. Bot.* **36** 303–323
- Pickett S T A and White P S 1985 Patch dynamics: a synthesis; in *The ecology of natural disturbance and patch dynamics* (eds) S T A Pickett and P S White (Orlando: Academic Press) pp 371–384
- Rolland T and Trémolières M 1995 The role of ammonium in the distribution of the three species of *Elodea*; *Acta Bot. Gallica* **142** 733–740
- Santamaria L 2002 Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment; *Acta. Oecol.* **23** 137–154
- Spink A J, Murphy K J, Smith S M and Westlake D F 1993 Effects of eutrophication on *Ranunculus* and *Potamogeton*; *J. Aquat. Plant Manage.* **31** 113–117
- Townsend C R 1989 The patch dynamic concept of stream community ecology; *J. North Am. Benthol. Soc.* **8** 36–50
- Townsend C R and Hildrew A G 1994 Species traits in relation to habitat templet for river systems; *Freshwater Biol.* **31** 265–276
- Van Wijk R J 1988 Ecological studies on *Potamogeton pectinatus* L. General characteristics, biomass production and life cycles under field conditions; *Aquat. Bot.* **31** 211–258

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