DISTURBANCES AS A STRUCTURING FACTOR OF PLANT PALATABILITY IN AQUATIC COMMUNITIES

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Abstract. Plant palatability plays an important part in the fitness of species and is therefore regarded as a key functional trait. The aim of this study was to relate the palatability of aquatic macrophytes to their distribution in riverine wetlands differing in their exposure to spate flood disturbances. Thirty-three former channels of the Rhône River Basin (eastern France) were characterized in terms of flood-disturbance level. Nutrient richness was also measured to eliminate its potential confounding effect. The coverage of 40 macrophyte species was recorded in these wetlands, and their palatability was assessed through laboratory feeding trials using a generalist consumer, the pond snail *Lymnaea stagnalis*. The consumption rate of *L. stagnalis* ranged from 3.9 mg·g⁻¹·d⁻¹ (for *Hottonia palustris*) to 137.9 mg·g⁻¹·d⁻¹ (for *Sagittaria sagittifolia*) and was used as a palatability index. Plant palatability was unrelated to the nutrient richness of sites but was positively correlated with their flood-disturbance level. However, the strength of this correlation decreased as nutrient richness increased. These results suggest that spate floods promote functional diversity in riverine wetlands, allowing the persistence of the most palatable plant species otherwise eliminated by herbivores, especially in nutrient-poor habitats.

Key words: disturbance; diversity, functional; fluvial dynamics; freshwater macrophytes; herbivory; *Lymnaea stagnalis*; nutrient richness; plant palatability; riverine wetlands; spate floods.

INTRODUCTION

Invertebrate herbivory plays an important part in the geographical distribution and relative abundance of plant species, both in terrestrial (Brulheide and Scheidel 1999, Erneberg 1999), marine (Tamelen 1996, Duffy and Hay 2000) and freshwater systems (Lodge and Lorman 1987, Sheldon 1987). Plant palatability is regarded as a key functional trait, as it governs in part the competitive success of species (Van et al. 1998, Rachich and Reader 1999, Gross et al. 2001). Some plant species can effectively reduce herbivore consumption through morphological adaptations or deterrent chemical compounds (Newman et al. 1996, Cronin 1998, Pennings et al. 1998, Kubanek et al. 2001). Such species should have the ability to persist in habitats where herbivore pressure is high, even under resource-limited conditions (Coley et al. 1985, Sheldon 1987). In contrast, high-palatability species should be restricted to habitats either with low herbivore pressure (Sheldon 1987, Feminella and Resh 1989, Tamelen 1996), or where productivity is sufficiently high to allow plants to compensate for biomass losses (Coley et al. 1985, Jacobsen and Sand-Jensen 1992).

Previous studies have demonstrated that the most palatable species are generally associated with early stages of secondary succession (Grime et al. 1968,

Cates and Orians 1975, Briner and Frank 1998, Elger et al. 2002). Such species are typically fast growing, allocate a large part of their resources to reproduction, and are favored by both high disturbance levels and high nutrient availability (i.e., “ruderal” species, sensu Grime [2001] and Kautsky [1988]). Microcosm experiments demonstrated that ruderal species are the most affected by the presence of herbivores (Fraser and Grime 1999, Buckland and Grime 2000). However, as far as we know, no study has tested the link between the palatability of plant species and their relative abundance in natural communities distributed along a disturbance gradient.

Macrophyte communities in former channels of piedmont rivers are ideal systems for field testing the relationship between disturbance level and plant palatability. Such communities are spatially well delimited, and their species composition is strongly influenced by spate disturbances (Bornette et al. 1998, 2001). These scouring events are brief and unpredictable, and they break or uproot aquatic plants (Henry et al. 1994, 1996). The exposure of former channels to spate scouring depends on their location relative to the active channel and on other geomorphological properties such as their slope and sinuosity. These channels can therefore be ranked along a disturbance gradient.

The purpose of the present work is to determine if the palatability of freshwater macrophyte species is correlated with the disturbance level of their habitat. The hypothesis is that a positive correlation should occur between the palatability of the species and the disturbance levels of the sites where they are the most

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abundant. To avoid a potentially confounding effect of site nutrient richness, which might also be positively correlated with plant palatability (Coley et al. 1985) and could covary with site disturbance level (Bornette et al. 2001), we independently assessed nutrient richness in the wetlands studied, and tested the effect of these two environmental factors on plant palatability.

MATERIALS AND METHODS

The study was undertaken in 33 former channels of the Rhône River Basin, in Eastern France (45°82' N, 5°20' E). Twenty-one of these wetlands were located along the Rhône River, and 12 along one of its tributaries, the Ain River.

Assessment of the environmental characteristics of the study sites

As the direct assessment of flow velocity is not possible during spate floods, disturbance level was assessed through site exposure to spate floods, and through observed effects of disturbance (substrate erosion). Site exposure was estimated through the annual number of days of river overflow in the former channel (each flood event does not exceed four days on average [Combroux et al. 2001]), channel slope, and drainage capacity (mean depth and width). Increasing slope or decreasing drainage capacity of the channel both increase flow velocity, i.e., the scouring effect of floods (Bravard and Gilvear 1996, Gilvear and Bravard 1996). As the Ain and Rhône Rivers differ in their discharge rates, the drainage capacity of the channels studied was normalized per river system to allow comparisons. The net effect of disturbances was assessed through substrate grain size, which provides information on the dominant process, either erosion or deposition, operating in the former channels of a given alluvial floodplain (Poff and Ward 1990, Lamberti et al. 1991). Substrate grain size was visually assessed on 2-m-wide transects crossing the channels and distributed regularly along their upstream–downstream gradient (one per 25 or 50 m, depending on channel length and substrate heterogeneity). The percentage cover of each of the following five grain-size classes was recorded: coarse, diameter (D) = 2–250 mm; sand or sandy silt, D = 0.01–2 mm; silt and clay, D < 0.01 mm; mud; and peat. Substrate grain-size profiles were then established for each channel (relative abundance of each grain-size class, summed abundance = 100%). Normalized principal component analysis (nPCA) was performed on the grain-size table, and the first principal component was used as an integrative grain-size variable for the assessment of flood-disturbance level. The location of each channel j along the disturbance gradient (Dis_j) was provided by the first principal component of a second nPCA performed on overflow frequency, slope, and normalized drainage capacity of the channel, together with the integrative grain-size variable.

Both phosphate and ammonium levels in the water have been recognized to be the main parameters governing nutrient status in aquatic habitats (Kohler et al. 1974, Carbiener et al. 1990). Water samples were collected monthly from each site over one year for chemical analysis. Ammonium N and phosphate contents were measured by colorimetry after standard HACH procedures (HACH Company, Loveland, Colorado, USA). As sediment is able to accumulate phosphorus and to act therefore as an alternative nutrient source for aquatic plants (House et al. 1998), total phosphorus content of the five upper centimeters of sediment was also measured by spectrophotometry on core samples collected at each site. The nutrient content of both water and substrate (water phosphate and ammonium N contents, total sediment phosphorus content) were analyzed through nPCA, and the first principal component was used to define the location of each channel j along the nutrient gradient (Nut_j).

Vegetation sampling

Aquatic vegetation was surveyed on 2-m-wide transects crossing the former channels and distributed regularly along their upstream–downstream gradient (one per 25 or 50 m, depending on channel length and spatial heterogeneity, resulting in 4 to 64 transects per channel). The cover of each occurring species was visually measured and expressed as the relative cover percentage of the species on the transect, using the Braun-Blanquet cover classes (Braun-Blanquet 1932). The average cover percentage of each species was then calculated for each channel.

Assessment of plant palatability

The palatability of 40 macrophyte species was assessed with the pond snail *Lymnaea stagnalis* (L.), which has been successfully used in previous similar laboratory studies (Smits 1994, Elger et al. 2002). The regular diet of this snail includes both decaying and living macrophyte materials, microbenthic algae, and dead animals (Reavell 1980). Contrary to most freshwater gastropod species, *L. stagnalis* presents several attributes indicating that it is adapted to macrophyte feeding. Its big size (30–50 mm shell length on average) allows it to ingest coarse fragments of food, and its digestion of tough cell walls is facilitated by an active ingestion of mineral particles and by an endogenous cellulase activity, higher than for most other freshwater gastropod species (Carriker 1946, Calow and Calow 1975). *Lymnaea stagnalis* has been shown to graze readily on more than 30 macrophyte species among 15 families (Frömming 1956, Gaevskaya 1969, Smits 1994), and can therefore be considered as a generalist consumer.

Lymnaea stagnalis individuals were grown on a lettuce-based diet in aquaria, in filtered water kept close to 22°C, and were used in palatability experiments 12–18 weeks after hatching (shell length: 30.5 ± 1.7 mm).

TABLE 1. Macrophyte species investigated for palatability in laboratory experiments using the pond snail *Lymnaea stagnalis* (L.).

Family	Species	Type of fragments	<i>n</i> †	<i>N</i> ‡
Characeae	<i>Chara major</i> Vaillant	leaves	15	2
	<i>Chara vulgaris</i> L.	shoots	7	1
Nymphaeaceae	<i>Nuphar lutea</i> (L.) Smith	portions of leaves	13	1
	<i>Nymphaea alba</i> L.	portions of leaves	15	2
Ceratophyllaceae	<i>Ceratophyllum demersum</i> L.	shoots	15	1
Alismataceae	<i>Baldellia ranunculoides</i> (L.) Parl.	portions of leaves	15	1
	<i>Luronium natans</i> (L.) Rafin.	portions of leaves	15	1
	<i>Sagittaria sagittifolia</i> L.	portions of leaves	15	2
Lemnaceae	<i>Lemna minor</i> L.	whole plant	15	3
	<i>Lemna trisulca</i> L.	whole plant	15	1
Hydrocharitaceae	<i>Elodea canadensis</i> Michaux	shoots	15	2
	<i>Elodea nuttallii</i> (Planchon) H. St John	shoots	14	2
	<i>Hydrocharis morsus-ranae</i> L.	leaves	15	2
Najadaceae	<i>Najas marina</i> L.	shoots	14	1
Potamogetonaceae	<i>Groenlandia densa</i> (L.) Fourr.	shoots	15	3
	<i>Potamogeton coloratus</i> Hornem.	portions of leaves	15	1
	<i>Potamogeton compressus</i> L.	shoots	15	1
	<i>Potamogeton crispus</i> L.	leaves	15	1
	<i>Potamogeton lucens</i> L.	portions of leaves	15	2
	<i>Potamogeton natans</i> L.	portions of leaves	15	3
	<i>Potamogeton nodosus</i> Poir.	portions of leaves	15	2
	<i>Potamogeton pectinatus</i> L.	leaves	15	3
	<i>Potamogeton perfoliatus</i> L.	leaves	15	2
	<i>Potamogeton pusillus</i> L.	shoots	15	2
Cyperaceae	<i>Eleocharis acicularis</i> (L.) Roem. & Schult.	portions of leaves	15	2
	<i>Scirpus lacustris</i> L.	portions of leaves	15	2
Juncaceae	<i>Juncus articulatus</i> L.	portions of leaves	15	3
Sparganiaceae	<i>Sparganium emersum</i> Rehmman	portions of leaves	13	3
Ranunculaceae	<i>Ranunculus circinatus</i> Sibth.	shoots	15	2
Haloragaceae	<i>Myriophyllum verticillatum</i> L.	whorls of leaves	15	2
Onagraceae	<i>Ludwigia palustris</i> (L.) Elliott	leaves	15	2
Primulaceae	<i>Hottonia palustris</i> L.	leaves	15	2
	<i>Samolus valerandi</i> L.	leaves	14	2
Boraginaceae	<i>Myosotis scorpioides</i> L.	leaves	15	3
Rubiaceae	<i>Galium palustre</i> L.	shoots	15	2
Lamiaceae	<i>Mentha aquatica</i> L.	leaves	15	2
Lentibulariaceae	<i>Utricularia vulgaris</i> L.	shoots	15	1
Callitrichaceae	<i>Callitriche platycarpa</i> Kütz.	shoots	14	2
Hippuridaceae	<i>Hippuris vulgaris</i> L.	whorls of leaves	15	2
Apiaceae	<i>Berula erecta</i> (Hudson) Coville	leaves	15	2

Note: Nomenclature follows Corillion (1975) for Characeae and Tutin et al. (1964–1980) for flowering species.

† Total number of replicates.

‡ Number of populations surveyed.

[mean $\pm$ 1 SD]). Plants were collected in the field, and samples were stored in a greenhouse for up to five days, in dechlorinated tap water aerated and kept below 18°C. The different plant species were presented individually to *L. stagnalis* in a non-choice feeding experiment, to assess their relative palatability through snail feeding rate (Briner and Frank 1998, Wardle et al. 1998). A comparison of the feeding rates of *L. stagnalis* in non-choice and multiple-choice experiments has shown that the ranking of macrophyte species was not significantly affected by the possibility of choice, which indicates

that non-choice tests are prone to correctly order the species in terms of palatability and are little influenced by compensatory feeding (Elger et al. 2002).

The consumption of *L. stagnalis* was recorded on fragments of each plant species and expressed in terms of dry mass following the method described in Elger and Willby (2003). The types of fragment used for each plant species are indicated in Table 1. In the case of species that develop floating (e.g., *Nuphar lutea*, *Potamogeton natans*) or emergent leaves (e.g., *Scirpus lacustris*, *Berula erecta*), only submersed leaves were

used. A relative consumption rate (RCR) was then calculated by dividing the consumption value by the body dry mass of the snail, estimated from its shell length using an allometric model previously described (Elger and Barrat-Segretain 2002).

Palatability experiments took place from the end of May to mid-July 2000. Every week, 4–8 plant species were tested, following a randomly determined order. When possible, plant species were each collected from two or three different sites to include intraspecific palatability variations in the analysis, and therefore calculate a mean RCR value that is representative of the study area. The number of sites investigated and the total number of replicates are given for each species in Table 1.

Relationship between plant palatability and environmental factors

We looked for a relationship between mean RCR, used as a palatability index of each plant species, and environmental characteristics of its habitat. The average locations of each species i along the disturbance (Dis_i) and nutrient (Nut_i) gradients were assessed on the basis of species cover in each channel j (Cov_{ij}):

$$Dis_i = \frac{\sum_j (Cov_{ij} \times Dis_j)}{\sum_j Cov_{ij}}$$

$$Nut_i = \frac{\sum_j (Cov_{ij} \times Nut_j)}{\sum_j Cov_{ij}}$$

The interactive effects of Nut_i and Dis_i on RCR_i were assessed by means of multiple-regression analysis.

RESULTS

Environmental characteristics of the study sites

The first principal component of the analysis performed on the grain-size table explained 36% of its variation, and was positively correlated with silt/clay, sand, and coarse gravel ($r = 0.82, 0.67$, and 0.16 , respectively), and negatively correlated with mud and peat ($r = -0.61$ and -0.52 , respectively). This principal component therefore expressed the intensity of erosive processes, which validated its use in assessing disturbance level. The first principal component of the analysis performed on the disturbance table explained 41% of its variation, and was positively correlated with substrate grain size, overflow frequency, and slope ($r = 0.87, 0.73$, and 0.41 , respectively), and negatively correlated with normalized drainage capacity ($r = -0.44$). Hence, this component provided the location of the study sites along the disturbance gradient. The first principal component of the analysis performed on the nutrient-richness table explained 62% of its variation, and was positively correlated with both ammonium N water content, phosphate water content, and

phosphorus sediment content ($r = 0.91, 0.88$, and 0.51 , respectively). Hence, this component provided the location of the study sites along the nutrient gradient. The locations of the study sites along nutrient and disturbance gradients were not significantly correlated ($r = 0.11$, $n = 33$ sites, $P = 0.53$).

Plant palatability

The relative consumption rates recorded with *Lymnaea stagnalis* for the 40 plant species ranged from $3.9 \pm 1.2 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (mean ± 1 SE) for *Hottonia palustris*, to $137.9 \pm 9.9 \text{ mg} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for *Sagittaria sagittifolia* (Fig. 1). Interspecific differences in plant palatability were highly significant (ANOVA, $F_{39, 544} = 17.47$, $P < 0.001$).

Link between plant palatability and environmental factors

The palatability of each plant species was positively correlated with the disturbance level of its habitat, but unrelated to its nutrient richness (Fig. 2A). When tested sequentially after the effect of nutrient richness in multiple-regression analysis, the effect of disturbance level on plant palatability increased in significance (Table 2). Plant palatability was also significantly influenced by the interactive effect of nutrient richness and disturbance level (Table 2). Indeed, the slope of the linear relationship between relative consumption rate RCR and species location along the disturbance gradient was maximal in the most oligotrophic sites and decreased as nutrient richness increased (Fig. 2B). The interactive effects of site nutrient richness and disturbance level accounted for 31.7% of the interspecific variability in plant palatability.

DISCUSSION

As reported in previous studies (Chambers et al. 1991, Jacobsen 1994, Cronin 1998, Elger et al. 2002), our results revealed a wide interspecific variability in the palatability of freshwater macrophytes to a generalist invertebrate consumer. This trait is usually considered to depend primarily on plant morphology and on structural or chemical defenses, whereas the nutritive value of tissue would be of secondary importance (Chambers et al. 1991, Newman et al. 1996, Bolser et al. 1998, Lodge et al. 1998). However, the aim of the present work was not to identify the proximate causes of variation in plant palatability, but to focus on the ultimate causes of its variation. We therefore considered palatability as a global trait of each plant species, and attempted to relate it to environmental characteristics of its habitat.

We demonstrated a significant positive correlation between the palatability of macrophyte species and the disturbance level of their habitat, even when the effect of disturbance level was tested sequentially following that of nutrient richness in variance analysis. Jacobsen and Sand-Jensen (1995) showed that biomass losses

FIG. 1. Relative consumption rates recorded with *Lymnaea stagnalis* for 40 plant species through non-choice feeding experiments performed in the laboratory. Data are means $\pm$ 1 SE.

due to herbivory on *Potamogeton perfoliatus* in Danish streams and lakes were positively correlated with the biomass of some invertebrate grazers, especially Limnephilidae larvae, gastropods, and amphipods. The role of hydraulic disturbances (e.g., wave action in lakes or flood scouring in rivers) in the decrease of invertebrate biomass, especially herbivorous species, has been previously demonstrated (McGaha 1952, Newman 1991, Holomuzki and Biggs 1999, Nyström and McIntosh 2003). Therefore, high-palatability species should grow preferentially in disturbed sites, characterized by a low herbivore pressure. In contrast, high-palatability species are probably eliminated from stable habitats, likely because their susceptibility to grazing reduces their competitive ability (Van et al. 1998, Gross et al. 2001). This process of competitive exclusion does not explain why unpalatable species are less abundant in disturbed sites compared to others, but this pattern may be explained by the direct and ecological costs of anti-her-

bivore defenses (Strauss et al. 2002). Actually, the synthesis of such defenses may be incompatible with the short development time and high reproductive investment required for the long-term persistence of plants in disturbed habitats (Kautsky 1988, Grime 2001).

We did not find any relation between the palatability of macrophyte species and the nutrient richness of their habitat. This is consistent with previous results from wetland habitats showing that the defensive investment of emergent macrophytes is unrelated to their location along a fertility gradient (McCanny et al. 1990). However, our data indicate that the positive correlation between plant palatability and disturbance level decreases as nutrient richness increases, the different species tending to have an intermediate palatability in nutrient-rich habitats whatever the disturbance level. Invertebrate herbivory on macrophytes might be reduced in nutrient-rich habitats, even under low-disturbance regimes, due to the top-down effect of some predators

FIG. 2. Mean relative consumption rates (RCR) recorded with *Lymnaea stagnalis* for each of 40 plant species, used as a palatability index. (A) RCR plotted against species locations along the disturbance (left) and nutrient-richness (right) gradients. (B) RCR plotted against species locations along the disturbance gradient, for species located in nutrient-poor habitats (left) or in nutrient-rich habitats (right). This plot illustrates the interactive effect of disturbance level and nutrient richness on plant palatability, the slope of the linear relation between disturbance level and consumption rate decreasing as nutrient richness increases.

such as fish (Sheldon 1987), or due to the higher availability of alternative foods such as microbenthic algae (Sand-Jensen and Madsen 1989). Moreover, the ability of macrophytes to compensate for biomass losses is

obviously higher in nutrient-rich habitats (Jacobsen and Sand-Jensen 1992). Species with intermediate palatabilities can therefore develop in undisturbed nutrient-rich sites, thereby weakening the correlation between

TABLE 2. Variance analysis of the multiple regression between the mean relative consumption rate (RCR) calculated for each macrophyte species and its location along nutrient-richness and disturbance gradients.

Parameter	df	SS	MS	F	P
Nutrient richness	1	123.1	123.1	0.15	0.7051
Disturbance level	1	7057.4	7057.4	8.34	0.0065
Nutrient richness $\times$ disturbance level	1	6951.5	6951.5	8.22	0.0069
Residuals	36	30 447.3	845.8	...	...
Total	39	44 887.2	...	...	...

plant palatability and habitat disturbance level. The intermediate palatabilities of some species growing in disturbed habitats are more surprising, and the explanation of this pattern would require further investigations to determine the proximate factors involved in this decrease of palatability compared to species growing in disturbed nutrient-poor habitats.

The present work, combining field investigation and laboratory experiments, outlines the importance of spatial variation of flood disturbance in promoting plant diversity in fluvial corridors. Such variations in disturbance patterns may not only increase species richness on the floodplain scale (Pollock et al. 1998, Bornette et al. 2001), but may also promote functional diversity in riverine ecosystems, since low-palatability macrophyte species dominate stable communities, whereas high-palatability species tend to be eliminated from such communities, especially in nutrient-poor habitats. Although the exact role of herbivory in the exclusion of these species remains to be studied, perhaps via microcosm experiments or field manipulation, it is clear that palatable species are dependent on flood disturbances for their long-term persistence in fluvial corridors.

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LITERATURE CITED

- Bolser, R. C., M. E. Hay, N. Lindquist, W. Fenical, and D. Wilson. 1998. Chemical defenses of freshwater macrophytes against crayfish herbivory. *Journal of Chemical Ecology* **24**:1639–1658.
- Bornette, G., C. Amoros, H. Piegay, J. Tachet, and T. Hein. 1998. Ecological complexity of wetlands within a river landscape. *Biological Conservation* **85**:35–45.
- Bornette, G., H. Piegay, A. Citterio, C. Amoros, and V. Godreau. 2001. Aquatic plant diversity in four river floodplains: a comparison at two hierarchical levels. *Biodiversity and Conservation* **10**:1683–1701.
- Braun-Blanquet, J. 1932. *Plant sociology: the study of plant communities*. McGraw-Hill, New York, New York, USA.
- Bravard, J. P., and D. J. Gilvear. 1996. Hydrological and geomorphological structure of hydrosystems. Pages 98–116 in G. Petts and C. Amoros, editors. *Fluvial Hydrosystems*. Chapman and Hall, London, UK.
- Briner, T., and T. Frank. 1998. The palatability of 78 wildflower strip plants to the slug *Arion lusitanicus*. *Annals of Applied Biology* **133**:123–133.
- Bruehlheide, H., and U. Scheidel. 1999. Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *Journal of Ecology* **87**:839–848.
- Buckland, S. M., and J. P. Grime. 2000. The effects of trophic structure and soil fertility on the assembly of plant communities: a microcosm experiment. *Oikos* **91**:336–352.
- Calow, P., and L. J. Calow. 1975. Cellulase activity and niche separation in freshwater gastropods. *Nature* **255**:478–480.
- Carbrier, R., M. Trémolières, J. L. Mercier, and A. Ortscheit. 1990. Aquatic macrophyte communities as bioindicators of eutrophication in calcareous oligosaprobe stream waters (Upper Rhine plain, Alsace). *Vegetatio* **86**:71–88.
- Carriker, M. R. 1946. Observations on the functioning of the alimentary system of the snail *Lymnaea stagnalis appressa* Say. *Biological Bulletin of Woods Hole* **91**:88–111.
- Cates, R. G., and G. H. Orians. 1975. Successional status and the palatability of plants to generalized herbivores. *Ecology* **56**:410–418.
- Chambers, P. A., J. M. Hanson, and E. E. Prepas. 1991. The effect of aquatic plant chemistry and morphology on feeding selectivity by the crayfish *Orconectes virilis*. *Freshwater Biology* **25**:339–348.
- Coley, P. D., J. P. Bryant, and F. S. Chapin III. 1985. Resource availability and plant antiherbivore defense. *Science* **230**:895–899.
- Combroux, I., G. Bornette, N. J. Willby, and C. Amoros. 2001. Regenerative strategies of aquatic plants in disturbed habitats: the role of the propagule bank. *Archiv für Hydrobiologie* **152**:215–235.
- Corillon, R. 1975. *Flore et végétation du massif armoricain: tome IV. Flore des Charophytes (Characées) du massif armoricain et des contrées voisines d'Europe occidentale*. Jouve Editeurs, Paris, France.
- Cronin, G. 1998. Influence of macrophyte structure, nutritive value, and chemistry on the feeding choices of a generalist crayfish. Pages 307–317 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, New York, USA.
- Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. *Ecological Monographs* **70**:237–263.
- Elger, A., and M. H. Barrat-Segretain. 2002. Use of the pond snail *Lymnaea stagnalis* (L.) in laboratory experiments for evaluating macrophyte palatability. *Archiv für Hydrobiologie* **153**:669–683.
- Elger, A., M. H. Barrat-Segretain, and C. Amoros. 2002. Plant palatability and disturbance level in aquatic habitats: an experimental approach using the snail *Lymnaea stagnalis* (L.). *Freshwater Biology* **47**:931–940.
- Elger, A., and N. J. Willby. 2003. Leaf dry matter content as an integrative expression of plant palatability: the case of freshwater macrophytes. *Functional Ecology* **17**:58–65.
- Erneberg, M. 1999. Effects of herbivory and competition on an introduced plant in decline. *Oecologia* **118**:203–209.
- Feminella, J. W., and V. H. Resh. 1989. Submersed macrophytes and grazing crayfish: an experimental study of herbivory in a California freshwater marsh. *Holarctic Ecology* **12**:1–8.
- Fraser, L. H., and J. P. Grime. 1999. Interacting effects of herbivory and fertility on a synthesized plant community. *Journal of Ecology* **87**:514–525.
- Frömming, E. 1956. *Biologie der mitteleuropäischen Süßwasserschnecken*. Duncker and Humblot, Berlin, Germany.
- Gaevskaya, N. S. 1969. The role of higher aquatic plants in the nutrition of the animals of freshwater basins. (Translated from Russian by D. G. M. Muller, ed. K. H. Mann). Volumes I–III. National Lending Library of Science and Technology, Yorkshire, UK.
- Gilvear, D. J., and J. P. Bravard. 1996. Geomorphology of temperate rivers. Pages 68–97 in G. Petts and C. Amoros, editors. *Fluvial hydrosystems*. Chapman and Hall, London, UK.
- Grime, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley and Sons, Chichester, UK.
- Grime, J. P., S. F. MacPherson-Stewart, and R. S. Dearman. 1968. An investigation of leaf palatability using the snail *Cepaea nemoralis* L. *Journal of Ecology* **56**:405–420.

- Gross, E. M., R. L. Johnson, and N. G. Hairston, Jr. 2001. Experimental evidence for changes in submersed macrophyte species composition caused by the herbivore *Acentria ephemerella* (Lepidoptera). *Oecologia* **127**:105–114.
- Henry, C. P., C. Amoros, and G. Bornette. 1996. Species traits and recolonization processes after flood disturbances in riverine macrophytes. *Vegetatio* **122**:13–27.
- Henry, C. P., G. Bornette, and C. Amoros. 1994. Differential effects of floods on the aquatic vegetation of braided channels of the Rhône River. *Journal of the North American Benthological Society* **13**:439–467.
- Holomuzki, J. R., and B. J. F. Biggs. 1999. Distributional responses to flow disturbance by a stream-dwelling snail. *Oikos* **87**:36–47.
- House, W. A., T. D. Jickell, A. C. Edwards, K. E. Praska, and F. H. Denison. 1998. Reactions of phosphorus with sediments. *Soil Use and Management* **14**:147–153.
- Jacobsen, D. 1994. Food preference of the caddis larva *Anabolia nervosa* feeding on aquatic macrophytes. *Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen* **25**:2478–2481.
- Jacobsen, D., and K. Sand-Jensen. 1992. Herbivory of invertebrates on submerged macrophytes from Danish freshwaters. *Freshwater Biology* **28**:301–308.
- Jacobsen, D., and K. Sand-Jensen. 1995. Variability of invertebrate herbivory on the submerged macrophyte *Potamogeton perfoliatus*. *Freshwater Biology* **34**:357–365.
- Kautsky, L. 1988. Life strategies of aquatic soft bottom macrophytes. *Oikos* **53**:126–135.
- Kohler, A., R. Brinkmeier, and H. Vollrath. 1974. Verbreitung und Indikatorwert der submersen Makrophyten in den Fließgewässern der Friedberger Au. Bericht der Bayerischen Botanischen Gesellschaft zur Erforschung der Heimischen Flora **45**:5–36.
- Kubaneck, J., M. E. Hay, P. J. Brown, N. Lindquist, and W. Fenical. 2001. Lignoid chemical defenses in the freshwater macrophyte *Saururus cernuus*. *Chemoecology* **11**:1–8.
- Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and K. M. S. Moore. 1991. Stream water-body recovery following a catastrophic debris flow. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:196–207.
- Lodge, D. M., G. Cronin, E. van Donk, and A. J. Froelich. 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. Pages 149–174 in E. Jeppesen, M. Søndergaard, M. Søndergaard, and K. Christoffersen, editors. *The structuring role of submerged macrophytes in lakes*. Springer-Verlag, New York, New York, USA.
- Lodge, D. M., and J. G. Lorman. 1987. Reductions in submersed macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:591–597.
- McCanny, S. J., P. A. Keddy, T. J. Arnason, C. L. Gaudet, D. R. J. Moore, and B. Shipley. 1990. Fertility and the food quality of wetland plants: a test of the resource availability hypothesis. *Oikos* **59**:373–381.
- McGaha, Y. J. 1952. The limnological relations of insects to certain aquatic flowering plants. *Transactions of the American Microscopical Society* **71**:355–381.
- Newman, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. *Journal of the North American Benthological Society* **10**:89–114.
- Newman, R. M., W. C. Kerfoot, and Z. Hanscom. 1996. Watercress allelochemical defends high-nitrogen foliage against consumption: effects on freshwater invertebrate herbivores. *Ecology* **77**:2312–2323.
- Nyström, P., and A. R. McIntosh. 2003. Are impacts of an exotic predator on a stream food web influenced by disturbance history? *Oecologia* **136**:279–288.
- Pennings, S. C., T. H. Carefoot, E. L. Siska, M. E. Chase, and T. A. Page. 1998. Feeding preferences of a generalist salt-marsh crab: relative importance of multiple plant traits. *Ecology* **79**:1968–1979.
- Poff, L. N., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management* **14**:629–645.
- Pollock, M. M., R. J. Naiman, and T. A. Hanley. 1998. Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology* **79**:94–105.
- Rachich, J., and R. Reader. 1999. Interactive effects of herbivory and competition on blue vervain (*Verbena hastata* L.: Verbenaceae). *Wetlands* **19**:156–161.
- Reavell, P. E. 1980. A study of the diets of some British freshwater gastropods. *Journal of Conchology* **30**:253–271.
- Sand-Jensen, K., and T. V. Madsen. 1989. Invertebrates graze submerged rooted macrophytes in lowland streams. *Oikos* **55**:420–423.
- Sheldon, S. P. 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. *Ecology* **68**:1920–1931.
- Smits, A. J. M. 1994. Ecophysiological studies on nymphaeid water plants. Dissertation. University of Nijmegen, Nijmegen, The Netherlands.
- Strauss, S. Y., J. A. Rudgers, J. A. Lau, and R. E. Irwin. 2002. Direct and ecological costs of resistance to herbivory. *Trends in Ecology and Evolution* **17**:278–285.
- Tamelen, P. G. 1996. Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory and competition. *Journal of Experimental Marine Biology and Ecology* **201**:197–231.
- Tutin, E. D., V. H. Heywood, N. A. Burges, D. H. Valentine, S. M. Walters, and D. A. Webb. 1964–1980. *Flora Europaea*. Volumes 1–5. Cambridge University Press, Cambridge, UK.
- Van, T. K., G. S. Wheeler, and T. D. Center. 1998. Competitive interactions between *Hydrilla* (*Hydrilla verticillata*) and *Vallisneria* (*Vallisneria spiralis*) as influenced by insect herbivory. *Biological Control* **11**:185–192.
- Wardle, D. A., G. M. Barker, K. I. Bonner, and K. S. Nicholson. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology* **86**:405–420.