Regeneration and colonization abilities of aquatic plant fragments: effect of disturbance seasonality

Marie-Hélène Barrat-Segretain* & Gudrun Bornette
ESA CNRS 5023, Lab. Ecologie des Eaux Douces et des Grands Fleuves,
Université Claude Bernard Lyon I, F-69622 Villeurbanne Cedex, France
Tel: [+ 33] (0) 4 72 44 80 37. Fax: [+ 33] (0) 4 72 43 11 41.
E-mail: barrat@cismsun.univ-lyon1.fr

Abstract

The regeneration (regrowth into viable plants or production of propagules, such as turions or buds) and colonization (development of roots and establishment in the sediment) of fragments of six aquatic plant species (*Elodea canadensis* Michaux, *Hippuris vulgaris* L., *Luronium natans* (L.) Rafin., *Potamogeton pusillus* L., *Ranunculus trichophyllus* Chaix, *Sparganium emersum* Rehmann) occurring in habitats frequently disturbed by floods, were investigated through laboratory experiments conducted in two seasons, and compared to the recolonization patterns depicted after field experiments. Hypothesis was that differences observed between recolonization patterns after spring and autumn flood disturbances should be related to differences in recolonization (via rooting) and regeneration (via propagules) abilities of species fragments. In May and in August, five types of fragments were collected from the plants. Their development and/or rooting abilities were recorded over 10 weeks in the greenhouse. Fragments from *E. canadensis* and *H. vulgaris* had higher regeneration and lower colonization abilities in spring and conversely in autumn. Fragments from *R. trichophyllus* and *S. emersum* had high colonization and low regeneration abilities during both seasons. Fragments from *L. natans* developed new buds in spring, whereas root development occurred only in autumn. Fragments from *P. pusillus* never rooted into the sediment, but developed turions in autumn. Differences between recolonization patterns observed in the field at the two seasons can most often be related to differences in regeneration and colonization abilities of species fragments. Species that colonize disturbed areas rapidly whenever the disturbance by flooding occurs have at least one type of vegetative fragment with a high colonization potential; this is called the 'always-ready strategy' which appears to be an adaptation of aquatic plants to the unpredictability of flood disturbances.

Introduction

Many aquatic plants are known to propagate predominantly by vegetative means, i.e. via stolons, turions, tubers or unspecialized organs (Sculthorpe, 1967; Van der Valk, 1981; Barrat-Segretain, 1996). Several authors have reported the role of specialized organs in the propagation of species related to habitats frequently disturbed by floods (e.g. Sculthorpe, 1967; Aiken & Walz, 1979; Bartley & Spence, 1987; Kautsky, 1988;

Wiegleb & Brux, 1991). Recently, Barrat-Segretain et al. (1998) have demonstrated that fragmentation could also be efficient to cope with the unpredictability of flood disturbances. Depending on the plant fragment, two survival tactics (sensu Southwood, 1988) were exhibited: 1. the fragments develop roots and establish rapidly in the sediment (colonization) or 2. the fragments do not anchor themselves immediately but develop new propagules that can be dispersed (regeneration). For each species, a trade-off occurred between the two tactics.

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* Author for correspondence.

The influence of disturbance timing on species composition and structure of animal and plant communities has been reported in both terrestrial and aquatic ecosystems (e.g. Armesto & Pickett, 1985; Robinson & Minshall, 1986; Malanson & Trabaud, 1987; Barrat-Segretain & Amoros, 1995). The timing of disturbances relative to the stage of community development can determine community resistance and recovery (Pickett et al., 1987; Peterson et al., 1990; Peterson & Stevenson, 1992). It should also influence the resource availability, the replacement sequence of the species, depending on the availability of propagules, the species that are impacted and thus the early colonists following disturbance (Keever, 1979; Denslow, 1980; Noble & Slatyer, 1980; Pickett et al., 1987). Sousa (1985) assumed that the date of creation of a patch by a disturbance may influence the course of the post-disturbance succession because the propagules of certain species are only seasonally available. Barrat-Segretain & Amoros (1995, 1996a,b) have reported different recolonization rates of cleared patches by aquatic plant species according to the timing of disturbance: a few species recolonized cleared patches very rapidly at any season, whereas others presented a slower colonization rate after a summer disturbance than after a winter disturbance. In addition, different patterns of recolonization of cleared patches were depicted: some species invade bare areas by propagation from the adjacent vegetation (border effect= peripheral colonization), others randomly (i.e. apparently regardless of the position of nearby clumps) and others show intermediate recolonization patterns (Barrat-Segretain & Amoros, 1996a).

If fragmentation of aquatic plants is a major process in the recolonization of disturbed patches, then the different recolonization patterns observed for different seasonal timings of flood disturbances should be related to differences in the recolonization and regeneration abilities of the species fragments. We could thus expect that species exhibiting seasonal differences in their recolonization patterns should present the same seasonal differences in the recolonization and regeneration abilities of their fragments. In this frame, the hypothesis tested in the present paper was that species recolonizing patches rapidly at any season should have at least one type of vegetative fragment with high colonization abilities available at any season.

The regeneration and colonization abilities of six aquatic plant species (*Elodea canadensis* Michaux, *Hippuris vulgaris* L., *Luronium natans* (L.) Rafin., *Potamogeton pusillus* L., *Ranunculus trichophyllus*

Chaix, *Sparganium emersum* Rehmann) were investigated through laboratory experiments at two seasons. These species were selected because they co-occur in aquatic habitats frequently disturbed by floods (Bornette & Amoros, 1991; Bornette et al., 1994; Barrat-Segretain & Amoros, 1996a) and recolonize rapidly patches cleared by flood disturbances (Barrat-Segretain & Amoros, 1996b). Their fragments are frequently found in the field after floods have removed sediment and fragmented aquatic vegetation; therefore, they can be expected to be of ecological significance for the recolonization of species. The experiments were conducted, respectivelly, from May (date of fragmentation) to mid-August 1996, and from August to November 1996. The results from the two experiments were compared to the recolonization patterns of the species depicted through previous field experiments (Barrat-Segretain & Amoros, 1995, 1996a,b). This comparison allowed us to answer the following questions: 1. Do any differences exist between the survival, the regeneration and colonization abilities of the species during the two seasons? and 2. if such differences exist, are they related to the differences in the recovery patterns of the species after disturbances occurring at different seasons (colonization rate; peripheral or random colonization)?

Materials and methods

Plants were collected from a former channel of the Rhône River in France 30 km upstream from Lyon (45° 49′ N, 5° 10′ E) for both the spring experiment in May 1996 and the summer experiment in mid-August 1996. This former channel is patchily scoured by floods approximately 40–50 days a year. Field observations of the effects of floods showed that the sediments can be completely reworked by the current, and the plants fragmented and eliminated from the disturbed patches. However, rapid recolonization patterns were observed after each flood, as well as after experimental disturbances (Henry et al., 1994; Barrat-Segretain & Amoros, 1995, 1996b). Except during flood events, the water flow in the channel is almost nil. Plants were collected undamaged, stored in open plastic containers maintained wet with water collected at the site and immediatly brought to the greenhouse where the experiment was set up.

Five types of vegetative fragments were collected from the plants: 1. vegetative bud (B); 2. whole plant (above-ground and underground parts) (W); 3. above-

ground parts of the plant (A); 4. underground parts without any green vegetative part (U). 5. Fragments of shoots each with four internodes (S) were also collected from four species (*E. canadensis*, *H. vulgaris*, *P. pusillus*, *R. trichophyllus*). All types of fragments are frequently found in former channels after floods have removed sediment and caused fragmentation of aquatic vegetation; therefore, they can be expected to be of ecological significance for the recolonisation of the species. The fragments of each type and each species were arranged in plastic pans (24 × 18 × 10 cm) containing 1 cm of sand, overlaid with 1 cm of sediment (sandy silt) and 7 cm of water all collected in the area where the plants were collected. The fragments were merely placed on the water surface. For each species and each fragment type, three pans containing 10 fragments each (*n*=3) were placed randomly in the greenhouse.

Because these species grow in cold, stenothermous groundwater-supplied ecosystems (Kohler et al., 1974; Carbiener et al., 1990; Bornette & Large, 1995), greenhouse temperature was maintained at 10 °C during the night (from 6 p.m. to 10 a.m.) and at ambient temperature during the day (maximum 20 °C). Water temperature variation was, therefore, relatively close to field conditions. Light was provided simultaneously by natural light and fluorescent white tubes at a light intensity of 2000 lx from 8 a.m. to 10 p.m. These parameters are considered favourable for germination and growth of most species (Muenscher, 1936; Haag, 1983; Leck & Simpson, 1995). Groundwater collected on the site was regularly added to the pans to compensate for evaporation and to maintain a constant water level. Permanent oxygen supply was maintained in the pans (small air-pumps and plastic tubes) to simulate water renewal. Dead plant material was removed from the pans.

The experiment was monitored every week over 10 weeks, and several parameters were recorded for each fragment: its survival (dead or alive); its position in the pan (at the water surface, at the sediment surface or within the water layer); the growth and development of new buds and the number of these buds; the development of roots and its possible rooting into the sediment. Surviving fragments included fragments remaining floating in the pans and fragments that anchored themselves into the sediment and that were uprooted. Fragments that had successfully rooted themselves were counted and uprooted so that their development would not inhibit growth of other fragments by competition for light or nutrients. When

a new bud developed on a fragment and became detached from it, it was counted as a new individual, and its growth was recorded as for the other fragments.

Statistical comparisons of differences between the survival, the regeneration and the colonization abilities of fragments in spring and autumn were made using Student *t*-tests.

Results

The percentages used in the following results were calculated as mean for three samples of 10 original fragments.

Survival of the fragments

The survival of fragments depended on the season, the type of fragment and the species considered (Figure 1).

Vegetative buds (B) had very high survival for *E. canadensis* and *L. natans*, intermediate survival for *H. vulgaris* (about 30%) and very low survival for *P. pusillus*, *R. trichophyllus* and *S. emersum* (less than 20%). Survival of buds was significantly higher in spring compared to autumn for *E. canadensis*, *L. natans* and *P. pusillus*. For example, almost 90% of *E. canadensis* buds survived after 10 weeks when collected in spring, and only 35% survived when collected in autumn. All the buds of *P. pusillus*, *R. trichophyllus* and *S. emersum* died after only a few weeks the autumn experiment was started. Depending on the species, the surviving fragments either remained at the water surface (*L. natans*, *H. vulgaris*, *R. trichophyllus*, *S. emersum*, *P. pusillus*) or sank to the sediment surface (*E. canadensis*).

The survival of whole plants (W) was high for *E. canadensis*, *L. natans* and *S. emersum* in the spring experiment, intermediate for *H. vulgaris*, and low for *R. trichophyllus* and *P. pusillus*. It exceeded 100% for *E. canadensis*, because numerous fragments developed new buds that became detached and formed viable new plants. Survival was significantly lower in autumn than in spring for *H. vulgaris*, *S. emersum* and *P. pusillus*, while *L. natans* still had a high survival in autumn (about 90%).

The survival of above-ground parts (A) also differed according to the species. These fragments of *E. canadensis* and *R. trichophyllus* survived significantly better in autumn (about 50%) than in spring (5 – 30%), unlike those of *S. emersum* and *L. natans* (more
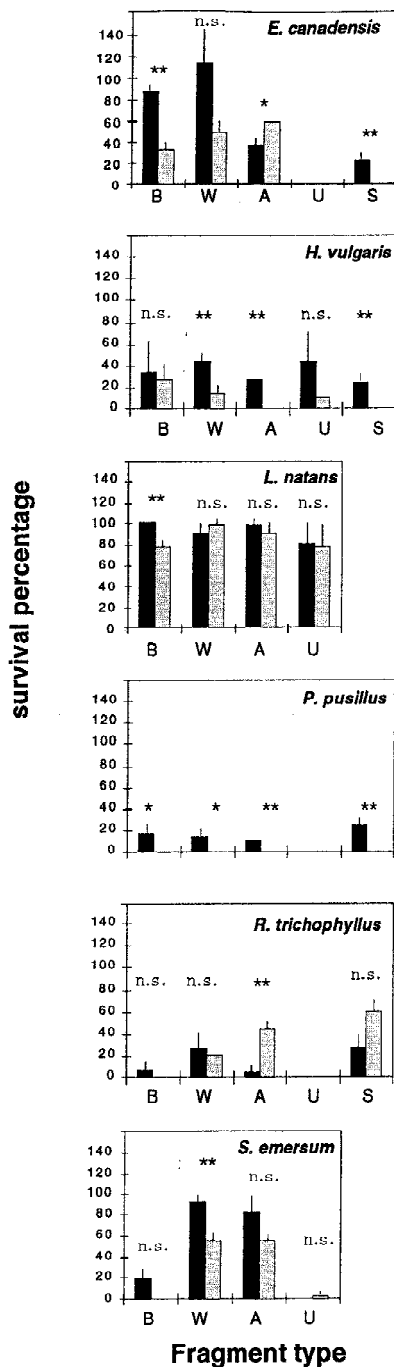
Figure 1. Mean survivorship (%± SD) of fragments of the six species after 10 weeks of spring experiment (in black) and autumn experiment (in grey). B: bud; W: whole plant; A: aboveground parts; U: underground parts; S: stem fragment of 4 internodes. Data are the mean of three replicates. Standard deviations using percentages were calculated after arc-sine transformation. Statistical comparisons of differences between the survival in spring and autumn respectively were made using Student t-tests. n.s.: not significant; *: $P < 0.05$; **: $P < 0.01$.

than 90% of above-ground parts of *L. natans* survived, both in spring and autumn).

Underground parts (U) from *E. canadensis*, *P. pusillus* and *R. trichophyllus* did not survive after 10 weeks in either experiment. Only 3% of those of *S. emersum* (autumn) survived. Those from *H. vulgaris* had a higher survival in spring (about 45%) than in autumn (10%), but the difference was not significant. In both spring and autumn, 80% of those of *L. natans* survived.

About 25% of stem fragments (S) of *E. canadensis*, *H. vulgaris* and *P. pusillus* survived in spring and 0% in autumn, while for *L. natans* and *R. trichophyllus*, there were no significant differences in the survival between the two seasons. In the case of *H. vulgaris* and *R. trichophyllus*, survival resulted from the anchorage of fragments after developing new roots, whereas fragments floating at the water surface rapidly died.

Colonization and regeneration

The mean percentages of fragments rooting in the sediment and forming new buds are given in Figures 2 and 3 for the six species.

All fragments of *E. canadensis* sank to the sediment only a few hours after the beginning of the experiments. Only whole plants (W) and above-ground parts (A) anchored themselves in the sediment, and this anchorage was significantly higher in autumn for above-ground parts (30%). All fragments (except underground parts (U)) developed new buds (from 23% up to 70% depending on the type of fragment) and this regeneration was higher in spring than in autumn except for buds (e.g. whole plants: 70% in spring, 10% in autumn).

Buds (B), whole plants (W) and underground parts (U) from *H. vulgaris* rooted only in autumn (from 10 up to 16%), whereas 23% of stem fragments (S) rooted only in spring. Above-ground parts (A) never rooted. Fragments systematically developed new buds, and regeneration was generally higher in spring (e.g. whole plants (W): 13% in autumn, 43% in spring).

In *L. natans*, anchorage occurred only in autumn for whole plants (W: 13%), above-ground parts (A: 26%) and underground parts (U: 13%). All fragments developed new buds in both seasons, but the percentages of regeneration were significantly higher in spring than in autumn. Fragments anchoring themselves were always the 'parent' fragments, with the new buds remaining at the water surface without developing roots.
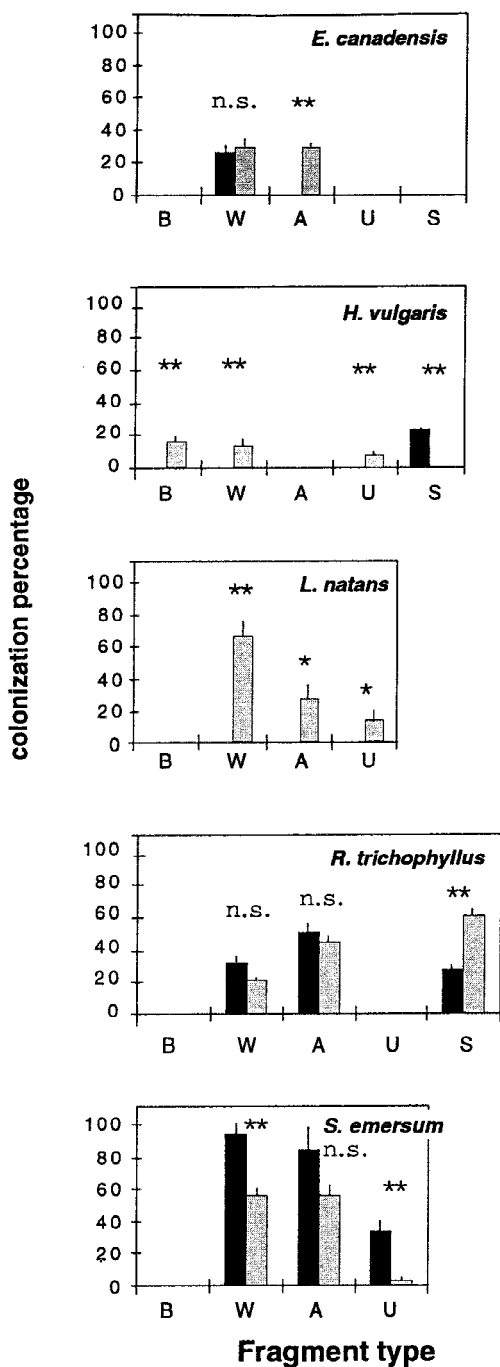
Figure 2. Colonization percentages (rooting in the sediment) of the different fragments of the six species after 10 weeks of growth in the spring (in black) and autumn (in grey). Scales have been adapted according to the species. B: bud; W: whole plant; A: aboveground parts; U: underground parts; S: fragment of 4 internodes. The graph from *P. pusillus* was omitted because this species exhibited no colonization abilities. Statistical test as in Figure 1.
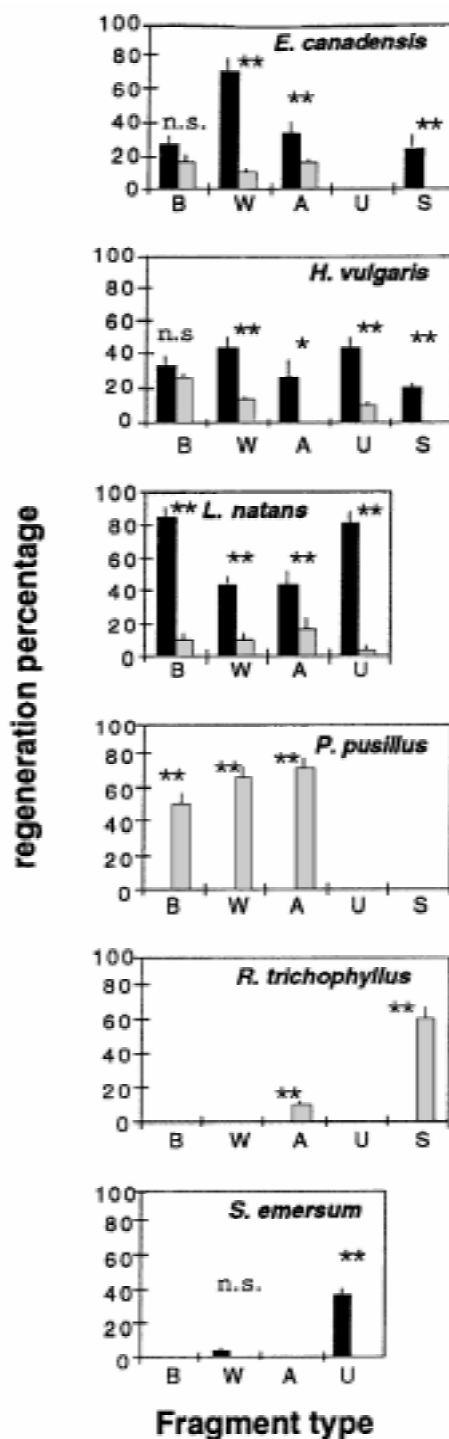
Figure 3. Regeneration percentages (fragments developing new buds detached from the parent) of the fragments of the six species after 10 weeks of spring experiment (in black) and autumn experiment (in grey). N.B.: scales are different according to the species. B: bud; W: whole plant; A: aboveground parts; U: underground parts; S: fragment of 4 internodes. Statistical test as in Figure 1.

Fragments of *P. pusillus* never developed roots. In autumn, most developed winter buds (i.e. turions) that appeared only on the fragments which already had buds (buds (B), whole plants (W) and above-ground parts (U)). Underground parts (U) and stem fragments (S) did not develop such buds. These turions became detached from the parent fragment that decayed at the water surface, and sank to the sediment surface. However, in spring fragments survived at the water surface but did not develop any perennating buds.

Some of the whole plants (W), above-ground parts (A) and stem fragments (S) from *R. trichophyllus* rooted in the sediment after a few weeks: this rooting was not significantly different between the two seasons for whole plants (30% *versus* 20%) and above-ground parts (50% *versus* 43%), but was higher in autumn (60%) than in spring (26%) for stem fragments. In autumn, 10% of above-ground parts (A) and 60% of stem fragments (S) developed new buds, which remained floating at the water surface.

In *S. emersum*, whole plants (W), above-ground (A) and underground parts (U) were able to root in the sediment and this colonization ability was significantly higher in spring than in autumn for whole plants and underground parts (e.g. whole plants: 93% *versus* 56%). Regeneration happened only in spring for whole plants and underground parts: new buds developed from the stolons and floated on the water surface without growing.

Discussion

Survival, regeneration and colonization abilities varied both within and between the species, depending on the type of fragment and the season of fragmentation. All six species exhibited two survival tactics that would be important following fragmentation after a disturbance. Barrat-Segretain et al. (1998) have proposed to rank species in two ways according to 1. their regeneration and dispersion abilities and 2. their colonization abilities. This study demonstrated a trade-off between the regeneration and the colonization abilities after the spring experiment. Comparison of greenhouse experiments with field experiments where recolonization patterns of macrophytes (colonization rate; peripheral or random colonization) on experimentally cleared patches of a few square-meters were determined allow us to analyse 1. the differences between the regeneration and colonization abilities of the species at the two seasons and 2. the relation between these differ-

ences and those observed in the field in the recovery processes of the species after disturbances occurring at two seasons (Table 1).

In the field, *E. canadensis* and *H. vulgaris* reappeared rapidly after flood disturbance, regardless of the season flooding occurred (Barrat-Segretain & Amoros, 1995). However, fragments of both species had a higher survival in spring than in autumn. Most vegetative parts (or fragments) decayed from late autumn until winter in relation with decreasing photoperiod and temperature (Cook & Urmi-König, 1985). This difference in the survival of fragments according to season did not seem to affect their recolonization ability in the field: either the percentage of fragments surviving is sufficient to ensure the colonization of bare patches, or fragments are not the only colonization means. *E. canadensis* and *H. vulgaris* had higher regeneration abilities than colonization abilities in spring, but the reverse in autumn. A few variations existed according to the type of fragment (for example, aboveground fragments (A) from *E. canadensis* developed roots only in autumn, four internodes-fragments (S) developed new buds only in spring). These results were consistent with the recolonization patterns depicted for the species after different disturbance timings (Barrat-Segretain & Amoros, 1995, 1996b): *E. canadensis* and *H. vulgaris* are both early colonizers (Bowmer et al., 1984; Bartley & Spence, 1987), *E. canadensis* colonizing cleared patches through both propagules and peripheral propagation (i.e. border effect, see Barrat-Segretain & Amoros, 1996a), and *H. vulgaris* predominantly through dispersed propagules (Table 1). In spring, most fragments developed propagules allowing the species to extent their distribution area; in summer and autumn most fragments anchored themselves, probably to increase survival during winter. But at each season, at least one fragment type of these species had a high regeneration and colonization potential, allowing rapid colonization, which is consistent with our hypothesis.

R. trichophyllus and *S. emersum* employ similar tactics, despite little differences in recolonization in the field: *R. trichophyllus* always re-appears in disturbed patches after the first colonizers. However, fragments of both species had high colonization and low regeneration abilities, and the plants recolonized patches predominantly through peripheral propagation. A few differences in the tactics appeared between the spring and the autumn experiment: colonization occurred during both seasons, whereas regeneration

Table 1. Relations between recolonization patterns observed in the field and regeneration and colonization abilities of the species fragments at the two seasons. Date of colonization (in the field): +++=early (< 1 month after the disturbance event); ++= intermediate (1–3 months); +=late (> 3 months); 0= no colonization. Regeneration and colonization abilities of the fragments in the greenhouse: +++=high; ++=intermediate ; +=slow; 0=absent. Establishment pattern (in the field): black= randomly; white= peripheral propagation. Field experiments (in the field) reported the recolonization patterns (rapidity of colonization; peripheral or random colonization) of macrophytes on experimental disturbed patches of a few square-meters. For more details about the field experiments, see Barrat-Segretain & Amoros (1995, 1996a,b).

	Colonization				Regeneration			
	Spring		Autumn		Spring		Autumn	
	Rapidity of colonization (in the field)	Fragment colonization (in the greenhouse)	Rapidity of colonization (in the field)	Fragment colonization (in the greenhouse)	Establishment pattern (in the field) 0 — 100%	Fragment regeneration (in the greenhouse)	Establishment pattern (in the field) 0 — 100%	Fragment regeneration (in the greenhouse)
Elodea canadensis	+++	+	+++	++	▉▉◻ (random ~half)	++	▉▉◻ (random ~half)	+
Hippuris vulgaris	+++	+	++	++	▉▉◻ (random ~half)	++	▉▉▉◻ (random)	+
Ranunculus trichophyllus	++	+++	++	++	▉◻ (small black)	0	◻ (white)	+
Sparganium emersum	+++	++	+++	+++	▉◻ (small black)	+	◻ (white)	0
Luronium natans	+	0	+	++	◻ (white)	+++	▉◻ (small black)	+
Potamogeton pusillus	+	0	+/0	0	▉▉▉▉ (black)	0	no colonization	+++

occurred only in spring for fragments of *S. emersum* having roots, and in autumn for above-ground parts and stem fragments of *R. trichophyllus*. Unlike *E. canadensis* and *H. vulgaris*, *S. emersum* and *R. trichophyllus* employed the same tactic regardless of season.

L. natans exhibited different patterns according to the season: fragments developed new buds in spring, whereas development of roots and rooting occurred only in autumn. In addition, it exhibited a trade-off between the two patterns that differ relative to season. In spring, because of their high survival and their ability to float for long periods, numerous fragments can be dispersed far from the parent plant. Later in the year, fragments that have reached a favourable site develop roots and establish themselves, whereas the others remain floating and will likely die during the winter. This tactic can explain why *L. natans* recolonized bare patches after a July-disturbance, but did not appear in places disturbed in December (Barrat-Segretain & Amoros, 1995).

P. pusillus also had different regeneration and colonization abilities depending on the season. Its fragments never developed roots and colonization did not occur, while its regeneration abilities were nil in spring and high in autumn. In the field, the species appeared to be a good colonizer in the spring after winter disturbance, but not following autumn

disturbance (Barrat-Segretain & Amoros, 1995). This is consistent with the formation of turions after autumn fragmentation, so that if a disturbance occurs in autumn or in winter, recolonization by the species is not affected because of the presence of turions which developed on the fragments in autumn, and are deposited on the sediment in autumn and winter. In contrast, a disturbance occurring in spring or in summer forms fragments that are unable to develop turions, and the species can disappear for a time from the disturbed zones, but should recolonise the following year from non-disturbed areas. These results are consistent with the random recolonization pattern depicted by Barrat-Segretain & Amoros (1996a).

Most results are in agreement with the hypothesis formulated, that species colonizing cleared patches rapidly, regardless of the timing of disturbance have, at least, one type of vegetative fragment with a high colonization potential (Table 1). Moreover, species with a low colonization rate in the field produce fragments with no or low regeneration abilities. In a few cases (*E. canadensis* and *H. vulgaris* in spring), the early colonization of cleared patches did not correspond to high colonization abilities of the fragments. This is because colonization by *E. canadensis* and *H. vulgaris* does not involve only vegetative fragments, but also peripheral propagation by rhizoms or stolons from undisturbed patches, that can also occur rapidly (Cook,

1990). In addition, in the case of *H. vulgaris*, rapid colonization of cleared patches in spring may also be due to germination of seeds (Arber, 1920).

At both seasons, there is no clear relation between the colonization abilities of one species (at random or peripheral) and the regeneration abilities of its fragments: for example species colonizing predominantly at random (*E. canadensis*, *H. vulgaris*, *P. pusillus*) and colonizing predominantly by peripheral propagation (*R. trichophyllus*, *S. emersum*, *L. natans*) can both exhibit high regeneration of their fragments. Therefore, high regeneration abilities of fragments can increase the potential dispersion of species and explain the extension rate of a species once it is established, but it is not sufficient to ensure the establishment in new areas.

In ecosystems frequently disturbed by floods, species usually have a high potential for vegetative reproduction and dispersal and a high ability to colonize bare substrates, that contributes to the high resilience of the communities (sensu Webster et al., 1983). Propagules of most species are vegetative fragments and/or specialized vegetative organs (stolons, tubers or turions). Unspecialized vegetative fragments should be able to recolonize disturbed patches at any time of the year, but the present study demonstrates that their ability to recolonize varies according to the season. Most species in the study are able to recolonize cleared patches through vegetative fragments whenever the disturbance occurs, and the recovery of vegetation in such ecosystems is rapid. Many species occurring in habitats frequently disturbed by floods exhibit an 'always-ready' strategy, which is an adaptation to the unpredictability of disturbances, that allows rapid colonization at any season. However, the seasonal timing of disturbance events affect the relative proportions of the species. Moreover, some species such as *P. pusillus* can maintain themselves in disturbed ecosystems despite their low regeneration abilities, probably using refuge areas.

The differences in the regeneration and colonization abilities of vegetative fragments of aquatic macrophytes explain very well the results obtained from field experiments on the recovery patterns investigated for different timings of disturbances. The comparison between greenhouse and field data (Table 1) confirms the hypothesis that fragmentation is an efficient way to recolonize disturbed areas for the six species investigated. Thus, the tolerance of the species to fragmentation and the survival of the fragments, their ability to float and their regeneration and colonization abilities are very useful for prediction in ecological management and restoration and for modelling ecosystem dynamics after disturbances.

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