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Effect of damage by the snail *Lymnaea* (*Lymnaea*) *stagnalis* (L.) on the growth of *Elodea canadensis* Michx.

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Abstract

The response of *Elodea canadensis* to grazing damage from the snail *Lymnaea* (*Lymnaea*) *stagnalis* was analysed in laboratory experiments. The type and degree of damage to *Elodea* as well as the post-damage growth of the plants were examined. *Lymnaea* (2–3 g fresh weight) consumed 35–260 mg fresh weight of *Elodea* daily. More than 90% of the plant material remaining after snail grazing bore clear signs of damage, with over 70% showing more than one kind of injury. Fragmentation of plants was noted most frequently, followed by damage to leaves and growing tips. Grazing scars on the surface of stems occurred more rarely.

Both naturally grazed plants and those damaged experimentally (with removed parts of leaves and/or growing tips) exhibited high survival and growth rates. Subsequent to damage, growth occurred mainly through the formation of new lateral shoots. Most (71%) plant fragments remaining after snail grazing were still alive after 35 days of exposure. Those that died without generating lateral shoots were mainly small pieces of the lower (hence oldest) parts of stems.

Keywords: Herbivory; Snails; *Elodea canadensis*; Plant damage

1. Introduction

Invertebrate herbivory on freshwater macrophytes has been assumed for many years to be rare and unimportant. It has been believed that macrophytes are rarely consumed alive, with the majority of invertebrates preferring to feed on the periphyton colonising their surface, as well as on senescing plants and detritus of plant origin. However, more recent papers show that invertebrate herbivory on freshwater macrophytes is more common than previously

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thought (Carpenter and Lodge, 1986; Lodge, 1991; Newman, 1991; Lodge et al., 1998). In the case of *Elodea*, Kornijow (1996) estimated that invertebrate herbivores consumed 2–23% of the plant biomass during the growing season in six European lakes.

Macrophytes can be eaten without being killed and often only part of the available plant biomass is consumed. As Lodge (1991) pointed out, many grazers destroy much more tissue than they eat. The extent of herbivore damage of freshwater macrophytes varies greatly among macrophyte species, as well as among and within sites, and it is also highly variable during the growing season (Soszka, 1975; Jacobsen and Sand-Jensen, 1992).

The damage done to macrophytes by invertebrate herbivores is usually attributed to the feeding by insects and crayfish. Snails are generally considered to feed on detritus and periphytic algae. However some snails, particularly the larger species can also be found feeding on macrophytes (Hutchinson, 1993). *Lymnaea* (*Lymnaea*) *stagnalis* (L.), generally considered to be omnivorous, is also known to consume and damage living macrophytes (Pip and Stewart, 1976; Lammens and van der Velde, 1978; Bijok, 1984; Kołodziejczyk, 1984; Elger and Barrat-Segretain, 2002).

Information about the post-damage growth of submerged macrophytes is scarce. However, it is known that some macrophyte species are able to regenerate new viable plants from their fragments and that fragmentation may be very important in plant propagation (Sculthorpe, 1967; Hutchinson, 1975; Barrat-Segretain et al., 1999).

In this study, laboratory experiments were designed (1) to determine the type and degree of damage to *Elodea canadensis* Michx. arising during feeding by the snail *L. stagnalis*, and (2) to evaluate the potential for post-damage growth of the plants.

2. Materials and methods

Two types of experiments were done. In the first type, the herbivory damage due to *Lymnaea* was surveyed, whilst the latter was concerned with the response to damage in *Elodea*. The post-damage growth of plants damaged by snails, as well as those damaged experimentally, was analysed.

The snails and macrophytes used in the experiments were collected during the growing season from small artificial pools (length 16 m and depth and width 1.5 m) at the Hydrobiological Station, Polish Academy of Sciences at Mikołajki (northern Poland), where they are abundant. Collected animals (adult *L. stagnalis*, 2–3 g fresh weight) and plants (floating shoots of *E. canadensis*) were carefully washed free of detritus, periphyton and calcium deposits before being weighed fresh after blotting of surface moisture. Glass chambers (600 ml, height 16 cm) filled with well water (the same as is used to supply the experimental pools) were used for the experiments. To avoid nutrient depletion in experimental chambers during plant growth, water was changed every 5 days. The water temperature in the experiments was 18–19 °C. Chambers were exposed to natural light in the laboratory. Light conditions were close to those in the artificial pool at the sampling site at 30 cm depth, i.e. corresponding to 50 μmol m^{-2} s^{-1} on a moderately cloudy day at noon (as measured by an LI-COR LI-189 underwater photometer). Chambers were arranged randomly with changes of position every day to avoid the possible effect of self-shading.

In order to determine grazing damage of *Elodea* by snails, 100 plants (branched shoots of *Elodea* of about 1 g of fresh weight and 15 cm in length) were placed individually in the chambers, each with two snails, for 24 h. Animals were starved for 24 h before the experiment. After exposure, for the remaining plant material, all types of damage (fragmentation, scars on stems, loss or damage of growing tips and leaves) were estimated.

To examine the response of *Elodea* to feeding damage from *Lymnaea* the growth of plants upon which snails had fed previously (hereafter referred as "damaged plants") was analysed. In order to obtain damaged *Elodea*, collected plants were exposed to *Lymnaea* (in the same proportion as used in previous grazing-damage experiment) for 24 h. In different experiments, snails reduced on average 25–50% of offered plant biomass. After exposure of plants with animals, all plant fragments were removed, weighed and measured for length of main and lateral shoots and then placed in another chamber without animals. The growth of plants subsequent to damage was estimated after various periods of exposure. Three preliminary, 10-day, experiments with 5–10 replicates were performed to estimate the ability of damaged *Elodea* to survive and grow. In the next (main) experiment, the growth of damaged and undamaged (control) plants was compared. Plants were monitored over 35 days with measurements after 10, 20 and 35 days. After each period of exposure, plants were carefully removed from experimental chambers, weighed, measured for lengths and then placed back in the chambers for the next period of observation. Sixteen replicates were run for the damaged plants and another sixteen for the undamaged (control) ones. The smallest fragments of plants which were analysed were pieces of stems having a minimum of one node of leaves. Single leaves or small stem fragments without leaves (usually senescing and lying on the bottom) were removed and omitted from the calculation. In the case of damaged plants, all fragments were measured separately and sum of their weight and length were calculated for each chamber.

The quantity of *Elodea* consumed by *Lymnaea* was estimated from the difference in the initial and final weights of plants exposed to snails in various experiments.

In order to obtain a more detailed estimation of the growth response of *Elodea* to various types of injury, an experiment with simulated herbivory was also run. The growth (in terms of increase of biomass) of undamaged plants and plants with five forms of damage caused experimentally was compared. Artificially damaged plants included 12 cm pieces of plants with loss of growing tips, part of leaves or both, and 2 cm pieces of upper and lower part of stems. Plants were grown for 20 days. Each treatment consisted of 10 replicates.

The significances of differences between initial and final weights and lengths of plants were estimated using paired Student's *t*-test ($P < 0.05$). Growth rate of plants was computed from exponential regressions. Differences in growth of plants exhibiting various types of damages were analysed using one way ANOVA with Tukey's post-hoc test ($P < 0.05$). The direct use of ANOVA was justified since variances were homogeneous.

3. Results

L. stagnalis fed intensively on *E. canadensis*. Consumption rates varied greatly with a snail of 2–3 g body fresh weight consuming 35–260 mg fresh weight of plants daily.

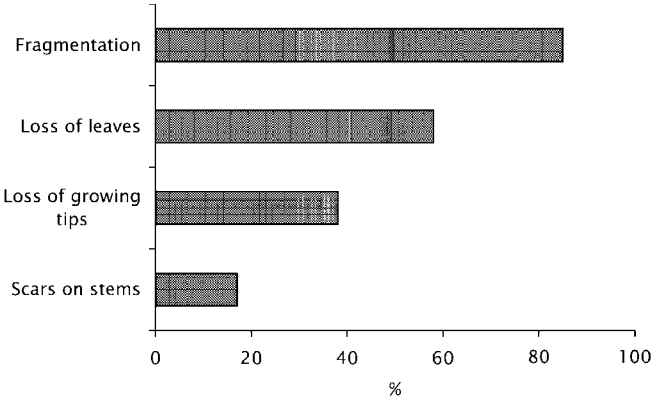

Fig. 1. Frequency of occurrence of various forms of injury of *E. canadensis* grazed by *L. stagnalis*. Expressed in percentage of experimental plants that show various signs of snail grazing ($N = 100$). Most plants showed several forms of injury.

In the experiment performed to determine the damage done to *Elodea* by *Lymnaea* more than 90% of the plant material remaining after snail grazing bore clear signs of damage, with 73% displaying more than one form of injury. Fragmentation of plants was noted most frequently (in 85% of the 100 plants analysed), followed by damage to leaves and growing tips. Grazing scars on the surface of stems occurred more rarely (Fig. 1).

In the post-herbivory growth experiments, plants upon which *Lymnaea* had fed previously became fragmented (with two–eight fragments noted), and other signs of damage were observed with a frequency similar to that presented in Fig. 1. In the three preliminary experimental runs, 10 days of exposure were in all cases followed by a significant increase in the length of damaged plants (by 12–35% over the initial length). The production of new, lateral shoots was noted in 30–80% of the fragments of plants in various experiments. The biomass of damaged plants increased significantly in two experiments, by 6 and 16%, respectively. No significant increase in biomass was observed in one experiment.

In the main post-herbivory experiment, length increase of the plants in terms of daily growth rates did not differ significantly ($P > 0.1$) in undamaged and damaged plants (1.26 and 1.16% per day, respectively; Fig. 2a). After 35 days of exposure, the length of plants had increased by 56 and 50% of initial values in control and damaged plants, respectively. Most (71% of a total of 89) plant fragments remaining after *Lymnaea* grazing were still alive after 35 days of exposure. Those that died before the end of exposure without generating lateral shoots, were mainly small fragments from the lower parts of stems. The new lateral shoots which appeared during exposure were significantly more numerous on damaged plants than on control ones (5.9 ± 0.6 versus 3.8 ± 0.6 per plant, mean $\pm$ 1S.E.).

In contrast to the situation with length, growth in terms of biomass differed greatly (Fig. 2b): the growth of damaged plants slowed down markedly after 20 days of exposure. After 35 days, the biomass had increased by 25 and 5% in undamaged and damaged plants, respectively. The daily growth rate differed significantly ($P < 0.05$) between

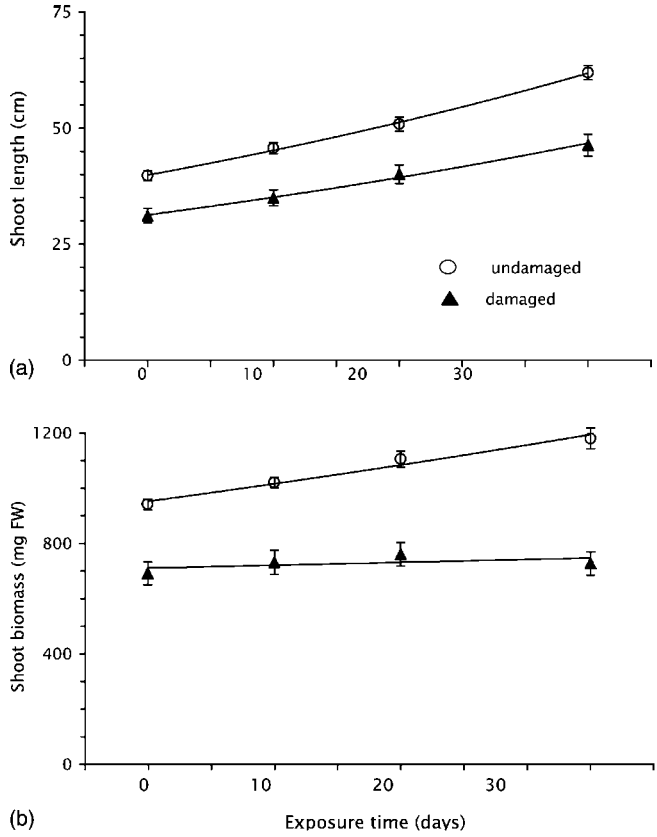

Fig. 2. Growth of undamaged and damaged *E. canadensis*. Presented are: (a) length (sum of length of main and lateral shoots) and (b) biomass development over 35 days of exposure (means and S.E.s of 16 replicates).

undamaged and damaged plants (0.63 and 0.14% per day, respectively). These limited changes in biomass of damaged plants occurred in spite of fact that new lateral shoots appeared and grew during the whole period of exposure, and a significant increase in plant length was noted. However, the new lateral shoots were very slender (delicate) and had low biomass. Simultaneously, from 10 days of exposure on, damaged leaves and lower (and hence the oldest) parts of fragmented stems began to die off, ensuring that total plant biomass is low with losses from decay not being compensated for by new growth yet. For undamaged control plants, mortality was almost absent (one piece of plant, no damaged growing tips and leaves).

When data on the growth of plants damaged by *Lymnaea* from all the experiments combined were considered, it was noted that plants exposed to grazing varied greatly in the extent of injury. There were no two plants having the same form and intensity of damage. No clear relation between intensity of damage and the growth of damaged plants was noticed. In some cases, percentage increases in total length and biomass (the sum of all fragments of a

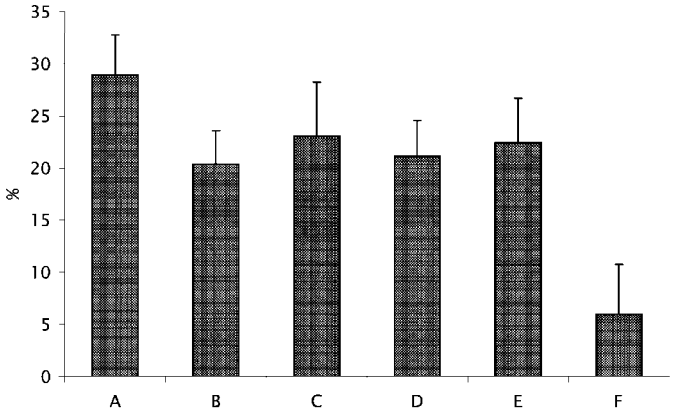

Fig. 3. Growth of *E. canadensis* damaged experimentally. Percentage increase of biomass after 20 days of exposure (means and S.E.s of 10 replicates per treatment): (A) control undamaged plants; (B) without growing tips; (C) 50% defoliation; (D) 50% defoliation and growing tips removed; (E) upper part of plant; (F) lower part of plant. (A–D) 12 cm pieces; (E, F) 2 cm pieces. Tukey's test showed that only treatment F led to significantly lower growth.

plant) were similar for different losses caused by grazing, whilst—vice versa—plants with similar types of damage could also differ greatly in growth rate.

The growth of plants with five forms of damages caused experimentally was compared with the growth of undamaged plants (Fig. 3). In spite of differences in injury, the relative increases in weight in treatments B–E) (12 cm plant fragments without growing tips, 50% defoliation or both types of damages as well as 2 cm apical plant fragments) were similar, ranging between 20 and 23% after 20 days of exposure, and not differing significantly from the control undamaged plants in treatment (A) (29%). Only the growth of the 2 cm lower fragments of shoot (F) was significantly lower (6%). The growth of individual plants in this treatment differed markedly—some plants died, others showed a decline in biomass, whilst just a small number generated lateral shoots.

4. Discussion and conclusions

The results of this paper sustain the opinion of several authors (Sheldon, 1987; Elger and Barrat-Segretain, 2002) who emphasize that living macrophytes can be eaten by snails. *L. stagnalis* fed intensively on *Elodea* and caused different forms of damage to this plant, amongst which fragmentation of the shoots was noticed most frequently. Various forms of injuries of submerged and floating-leafed macrophytes have been presented in the literature. Loss of leaf area (by holes and surface abrasion), defoliation and canals from mining animals have been reported for several localities or experimental studies (Soszka, 1975; Urban, 1975; Lammens and van der Velde, 1978; Wallace and O'Hop, 1985; Sheldon, 1987; Kouki, 1991; Jacobsen and Sand-Jensen, 1992, 1995; Cronin et al., 1998). In some cases, very specific injuries have been shown. Newman et al. (1996) reported that larvae of *Euhrychiopsis lecontei* (Curculionidae) damaged stems of *Myriophyllum spicatum* by

consuming the vascular cylinder and tissues within stem nodes and thus disrupting the translocation and storage of carbohydrate in plants. Johnson et al. (1998) and Gross et al. (2001) showed that the larvae of *Acentria ephemerella* (Lepidoptera) causes severe damage to the apical meristems of *M. spicatum*. When the density of grazers is high these forms of injuries can result in a significant watermilfoil decline.

In most cases, only one form of injury is reported as typical for the grazing of a defined species of invertebrate on a given plant species. However, the results of this paper demonstrate that grazing by *L. stagnalis* on *E. canadensis* results in various form of plant injury occurring simultaneously. The fragmentation which was most commonly found here is rarely reported in natural conditions. Even if plant fragments are observed in the habitat it is usually not possible to distinguish between their origin—mechanical damage (due to wave action) or damage through herbivory.

In contrast to the rich literature on terrestrial plants, there is only very scarce information on response to damage in freshwater macrophytes. However, the ability of damaged macrophytes to survive and grow has been observed in several cases.

Barrat-Segretain et al. (1999) studied experimentally the capacity for regeneration of different fragments of 16 aquatic plant species (*E. canadensis* among them). Fragments of *Elodea* exhibited a very high survival rate (which was independent of anchoring), as well as a high regeneration potential. The high survival and growth rates of plant fragments were also observed in a field experiment with *E. canadensis* and *Ceratophyllum demersum* (Pieczyñska unpublished data of 1999). Fragments of shoots (of 5–20 cm) were exposed in an experimental pool in mesh bags. After 100 days of exposure, most fragments introduced at the beginning of the experiment had died, while the new lateral shoots they had produced before dying were growing successfully, especially in the case of *Elodea*. Gross et al. (2001) observed that *E. canadensis* is able to develop new lateral shoots even when leaves are missing or when stems turn brown as a result of herbivory. Abernethy et al. (1996) found in glasshouse experiments that *E. canadensis* was less susceptible to shade stress and disturbance caused by cutting than *M. spicatum* (a smaller reduction in biomass and especially in length after cutting was noted).

In this study *E. canadensis* damaged by *Lymnaea* showed intensive regrowth. Most plant fragments remaining after snail grazing generated new shoots. Only a limited number of plant fragments were not able to survive. These were usually small pieces of lower (thus the oldest) parts of stems which were close to senescing. The growth in damaged *Elodea* most often occurs in the following way. In the initial period (the first 10 days), new lateral shoots appear and plant length and biomass increase. Then follows a period of further growth and the appearance of more lateral shoots, while at the same time (after about 20 days) some of the damaged leaves and stems die off. After some shoot fragments have died, the young ones arising from them become detached and form new viable plants.

In conclusion, the results obtained in this study suggest diverse influences of snail herbivory on macrophytes. *L. stagnalis* may cause a substantial reduction in biomass and severe damage to *E. canadensis*. But, at the same time, plant fragments remaining after snail grazing exhibited a high capacity to regenerate new plants. This could be of crucial importance in maintenance of a plant population in a water body, as well as in plant dispersion by vegetative means. This complex role of herbivory from snails as well as from other invertebrates seems to be underestimated.

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References

Abernethy, V.J., Sabbatini, M.R., Murphy, K.J., 1996. Response of *Elodea canadensis* Michx. and *Myriophyllum spicatum* L. to shade, cutting and competition in experimental culture, cutting and competition in experimental culture. Hydrobiologia 340, 219–224.

Barrat-Segretain, M.H., Henry, C.P., Bornette, G., 1999. Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats. Arch. Hydrobiol. 145, 111–127.

Bijok, P., 1984. Feeding and detritus formation by *Lymnaea stagnalis* (L.) under laboratory conditions. Pol. Arch. Hydrobiol. 31, 55–68.

Carpenter, S.R., Lodge, D.M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370.

Cronin, G., Wissing, K.D., Lodge, D.M., 1998. Comparative feeding selectivity of herbivorous insects on water lilies: aquatic vs. semi-terrestrial insects and submersed vs. floating leaves. Freshwater Biol. 39, 243–257.

Elger, A., Barrat-Segretain, M.H., 2002. Use of the pond snail *Lymnaea stagnalis* (L.) in laboratory experiments for evaluating macrophyte palatability. Arch. Hydrobiol. 153, 669–683.

Gross, E.M., Johnson, R.L., Hairston Jr., N.G., 2001. Experimental evidence for changes in submersed macrophyte species composition caused by the herbivore *Acentria ephemerella* (Lepidoptera). Oecologia 127, 105–114.

Hutchinson, G.E., 1975. A treatise on limnology. III. Limnological Botany. Wiley, New York, 660 pp.

Hutchinson, G.E., 1993. A treatise on Limnology. IV. The Zoobenthos. Wiley, New York, 944 pp.

Jacobsen, D., Sand-Jensen, K., 1992. Herbivory of invertebrates on submerged macrophytes from Danish freshwaters. Freshwater Biol. 28, 301–308.

Jacobsen, D., Sand-Jensen, K., 1995. Variability of invertebrate herbivory on the submerged macrophyte *Potamogeton perfoliatus*. Freshwater Biol. 34, 357–365.

Johnson, R.L., Gross, E.M., Hairston Jr., N.G., 1998. Decline of the invasive submersed macrophyte *Myriophyllum spicatum* (Haloragaceae) associated with herbivory by larvae of *Acentria ephemerella* (Lepidoptera). Aquat. Ecol. 31, 273–282.

Kołodziejczyk, A., 1984. Occurrence of Gastropoda in the lake littoral and their role in the production and transformation of detritus II. Ecological activity of snails. Ekol. Pol. 32, 469–492.

Kornijow, R., 1996. Cumulative consumption of the lake macrophyte *Elodea* by abundant generalist invertebrate herbivores. Hydrobiologia 319, 185–190.

Kouki, J., 1991. The effect of the water-lily beetle, *Galerucella nympaeae*, on leaf production and leaf longevity of yellow water-lily, *Nuphar lutea*. Freshwater Biol. 26, 347–353.

Lammens, E.H.R.R., van der Velde, G., 1978. Observations on the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae) with special regards to the leaves. Aquat. Bot. 4, 331–336.

Lodge, D.M., 1991. Herbivory on freshwater macrophytes. Aquat. Bot. 41, 195–244.

Lodge, D.M., Cronin, G., van Donk, E., Froelich, A.J., 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The Structuring Role of Submerged Macrophytes in Lakes. Ecol. Studies 131, 149–174.

Newman, R.M., 1991. Herbivory and detrivory on freshwater macrophytes by invertebrates: a review. J. N. Am. Benthol. Soc. 10, 89–114.

Newman, R.M., Holmberg, K.L., Biesboer, D.D., Penner, B.G., 1996. Effects of a potential biocontrol agent, *Euhrychiopsis lecontei*, on Eurasian watermilfoil in experimental tanks. Aquat. Bot. 53, 131–150.

Pip, E., Stewart, J.M., 1976. The dynamics of two aquatic plant-snail associations. Can. J. Zool. 54, 1192–1205.
Sculthorpe, C.D., 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, London, 610 pp.
Sheldon, S.P., 1987. The effects of herbivorous snails on submerged macrophyte communities in Minnesota lakes. Ecology 68, 1920–1931.
Soszka, G.J., 1975. Ecological relations between invertebrates and submerged macrophytes in the lake littoral. Ekol. Pol. 23, 393–415.
Urban, E., 1975. The mining fauna in four macrophyte species in Mikołajskie Lake. Ekol. Pol. 23, 417–435.
Wallace, J.B., O'Hop, J., 1985. Life on a fast pad: water-lily leaf beetle impact on water lilies. Ecology 66, 1534–1544.