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## THE INFLUENCE OF FRAGMENTATION ON THE GROWTH OF *ELODEA CANADENSIS* MICHX. IN DIFFERENT LIGHT CONDITIONS

**ABSTRACT:** Plant fragments are commonly noticed in a wide range of freshwater environments. However, data on their further growth remain very scarce. The post-fragmentation growth of *Elodea canadensis* was analysed in a laboratory experiment in which plants were exposed to different light conditions ranging from 3 to 30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . The growth of whole plants (12cm) and fragmented (cut) shoots (apical fragment of 3 cm and middle and lower fragments of 4 and 5 cm respectively) was analysed over 33 days (with measurements of weight and length after 11, 21 and 33 days).

In all light treatments both cut and whole plants grew. The growth rates were found to vary greatly over the exposure period. During the first 11 days, whole plants or the fragments thereof exhibited the greatest increases in biomass and length in all light treatments. Following further exposure under no shade and moderate shade, the growth of all plants, although still significant, was visibly more limited. Under conditions of a 90% shade level, 11 days of exposure left both whole and cut plants still alive, but incapable of any further significant increase in length or biomass. Generally, in high light levels cut plants grew more intensively, while in conditions of the most intensive (90%) shade, no differences in growth of these groups of plants were noted or the growth of cut plants was limited to a greater extent.

A greater number of new lateral shoots were noted in cut plants than in whole plants. Even in conditions of low light characterized by the poor growth of plant fragments the production of new shoots was still possible. In general, fragments of *Elodea canadensis* were found to be very efficient at surviving and regenerating under a wide range of light conditions.

**KEY WORDS:** *Elodea canadensis*, plant growth, fragmentation, light conditions

### 1. INTRODUCTION

Submerged macrophytes are subjected to various types of damage caused by herbivorous animals, both vertebrates and invertebrates (Prejs 1984, Lodge 1991, Newman 1991, Jacobsen and Sand-Jensen 1992, Pieczyńska 2002), as well as by water movement (Pieczyńska 1972, Barrat-Segretain *et al.* 1999). Also in the course of plant harvesting practices, large amounts of damaged plant material are retained in the environment (Nichols 1991).

Most grazers consume only a part of available macrophyte biomass, and in many cases they destroy much more plant tissue

than they eat. Fragmentation, defoliation, loss of leaf area (holes, surface abrasion), shoot breaking or clipping are observable in many sites (Soszka 1975, Urban 1975, Lodge and Lorman 1987, Jacobsen and Sand-Jensen 1992, Newman *et al.* 1996, Johnson *et al.* 1998, Bolser and Hay 1998, Cronin *et al.* 1998).

Secondary effects of grazing damage of plants are also of great importance. These include infection of grazing scars by microorganisms, which develop further decomposition (Wallace and O'Hop 1985, Kouki 1991, Cronin *et al.* 1998), or the influence of wave action, which may cause ripping of fragments of plants already weakened by grazers (Sheldon 1987).

Although damaged freshwater macrophytes are frequently noticed in a wide range of environments, data on their further growth remains scarce. However, it is known that fragments of some macrophyte species are able to grow successfully even when plants are severely damaged (Sculthorpe 1967, Hutchinson 1975, Barrat-Segretain *et al.* 1999).

Macrophyte fragments detached in the course of animal feeding, or due to water movement, can remain within the parental population or may float away, with some of them falling to the bottom at different depths, while others float in the water column. Thus the post-damage survival and growth of plants may be influenced markedly by differences in the intensity of light, water fertility and other environmental factors.

The aim of this study was to evaluate in a laboratory experiment the influence of fragmentation on the post-damage growth of *Elodea canadensis* Michx. in different light conditions. Plant growth in terms of length, biomass and the development of new lateral shoots was compared for whole and experimentally fragmented (cut) plants which were exposed to various shade levels.

## 2. MATERIALS AND METHODS

*Elodea canadensis* used in the experiment was collected during the growing season from the pond at the Botanical Garden of Warsaw University. Plants were kept in the

laboratory for one week prior to the experiment and then cleaned of algae and detritus. Plants were exposed to different light conditions. The experiment used artificial light of  $30 \mu\text{mol m}^{-2}\text{s}^{-1}$  (as measured with a LI-COR LI-189 photometer). Shading was achieved by putting several layers of tracing paper over chambers. Shading levels were 50% ( $15 \mu\text{mol m}^{-2}\text{s}^{-1}$ ), 75% ( $7.5 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) and 90% ( $3 \mu\text{mol m}^{-2}\text{s}^{-1}$ ) of full light. The light intensities used in the experiment were within the highly variable range of light conditions noted in habitats colonized by *Elodea canadensis* (for example in eutrophic Lake Mikołajskie, north-eastern Poland – Pieczyńska, unpublished data) reflecting light attenuation at different depths or the shading effect exerted by macrophytes themselves.

Well water enriched with the fertilizer AZOFOSKA up to a concentration of  $500 \mu\text{g P-PO}_4 \text{ l}^{-1}$  and  $1200 \mu\text{g N-NH}_4 \text{ l}^{-1}$  was used in the experiment. As found in the previous experiments (Mielecki unpublished data) these concentrations were found to be favourable for the growth of *Elodea canadensis*.

*E. canadensis* was grown in 1.5 l glass chambers. Apical, 12 cm sections of healthy plants without lateral shoots were selected. Their biomass ranged between 261–369 mg fresh weight. One plant was exposed as a whole and another cut into three fragments: the first – the 3 cm apical part of the shoot with growing tip, the second – the 4 cm middle part of the shoot with no growing tip, and the third – the lower 5 cm, without growing tip. In this way the sum of the three fragments of cut plant had initially the same length as the undivided plant, and both types of plants had one (apical) growing tip. Hereafter plants that were not cut were referred to as “whole plants” and those divided into three fragments as “cut plants”. The decision to cut plants into 3 fragments was made on the basis of previous experiments (Pieczyńska 2003, and unpublished data) in which 24 h feeding by the snail *Lymnaea (Lymnaea) stagnalis* (L.) and caddis larvae (*Limnephilus* sp.) on *Elodea canadensis* was found to have resulted (apart from damage to leaves, stems or growing tips) in fragmentation of plants (two to seven fragments were noted – three on average). Different lengths of pieces of cut plants (3,4, and 5 cm) were

employed to obtain fragments with a similar number of internodes, as intervals between nodes increase from the top to the bottom of a plant.

One whole plant and three fragments were placed in each chamber, with each light variant in the experiment comprising 7 such chambers. The experiment lasted for 33 days with measurements after 11, 21 and 33 days. With a view to nutrient depletion being avoided, the water in experimental chambers was changed after each exposure period, while plants were weighted and measured for length. The number of new lateral shoots was noted, and at the end of experiment these were detached and weighed separately. Plants were weighted fresh after blotting of surface moisture.

The significances of differences between initial and final weight and length of plants were estimated using paired Student's t-test ( $P < 0.05$ ). For comparison of growth of whole and cut plants Mann-Whitney U-test ( $P < 0.05$ ) was used.

### 3. RESULTS

After just the first 11 days of exposure, it was possible under all light conditions to note significant increases in the length of cut plants (by 15% to 54% over the initial value), as well as of whole plants (by 27–45%). The lowest values were noted for the greatest shade (Fig. 1). After 21 and 33 days, further increases in plant length were observed,

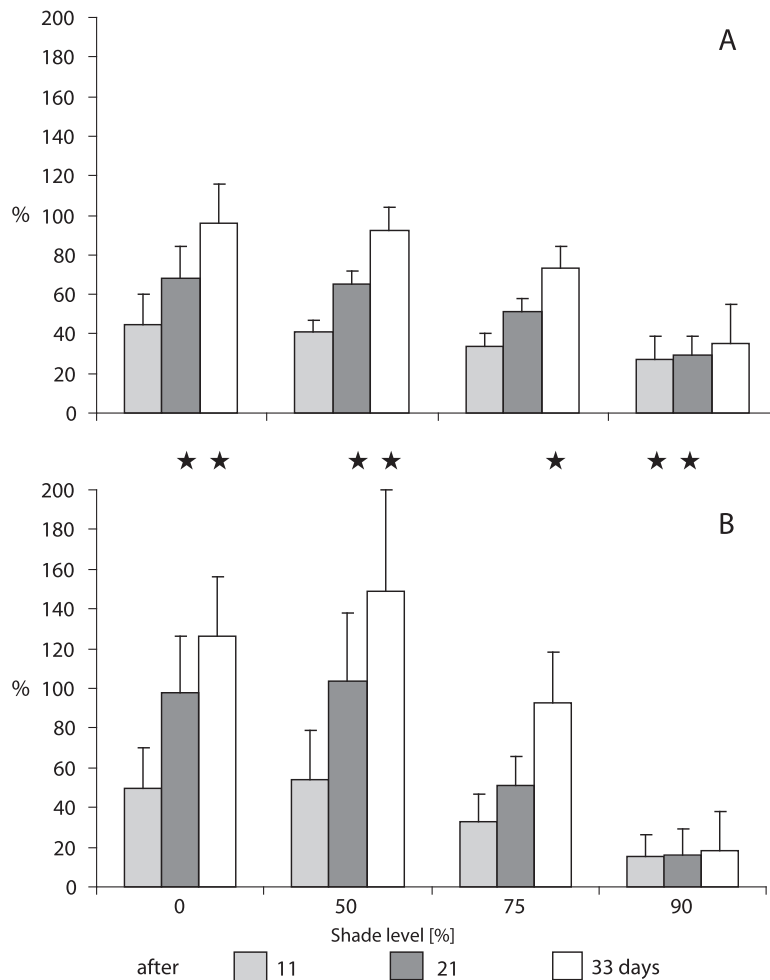


Fig. 1 Growth of whole plants and cut fragments of *Elodea canadensis* under different light conditions. Percentage increase in length above initial values after various periods of exposure. A – whole plants, B – cut plants. Data for cut plants are the sums of lengths for all three fragments. \* – significant differences between whole and cut plants.

with the growth of cut plants (as opposed to whole plants) being significantly greater in condition of high light intensity (no shade) or 50% shade. Under 75% shade such a difference was only to be observed at the end of the experiment (after 33 days). In turn, plant growth was poor under the most reduced light availability (90% shade), such that after 21 and 33 days the increase in length was significantly smaller in the case of cut plants (Fig. 1).

After the first 11 days, plant biomass had increased significantly above initial values at

all light levels by 19–64% (cut plants) and 17–44% (whole plants). Similarly as in the case of increases in length, the lowest values were noted under the highest level of shade. In full light, the cut plants displayed significantly greater percentage increases in biomass than whole plants throughout the experiment. Under conditions of 50% shade such a difference had only become apparent after 21 and 33 days of exposure. Finally, under 75% shade and 90% shade no significant differences had emerged between biomass increases of whole plants and cut plants after all exposure periods (Fig. 2).

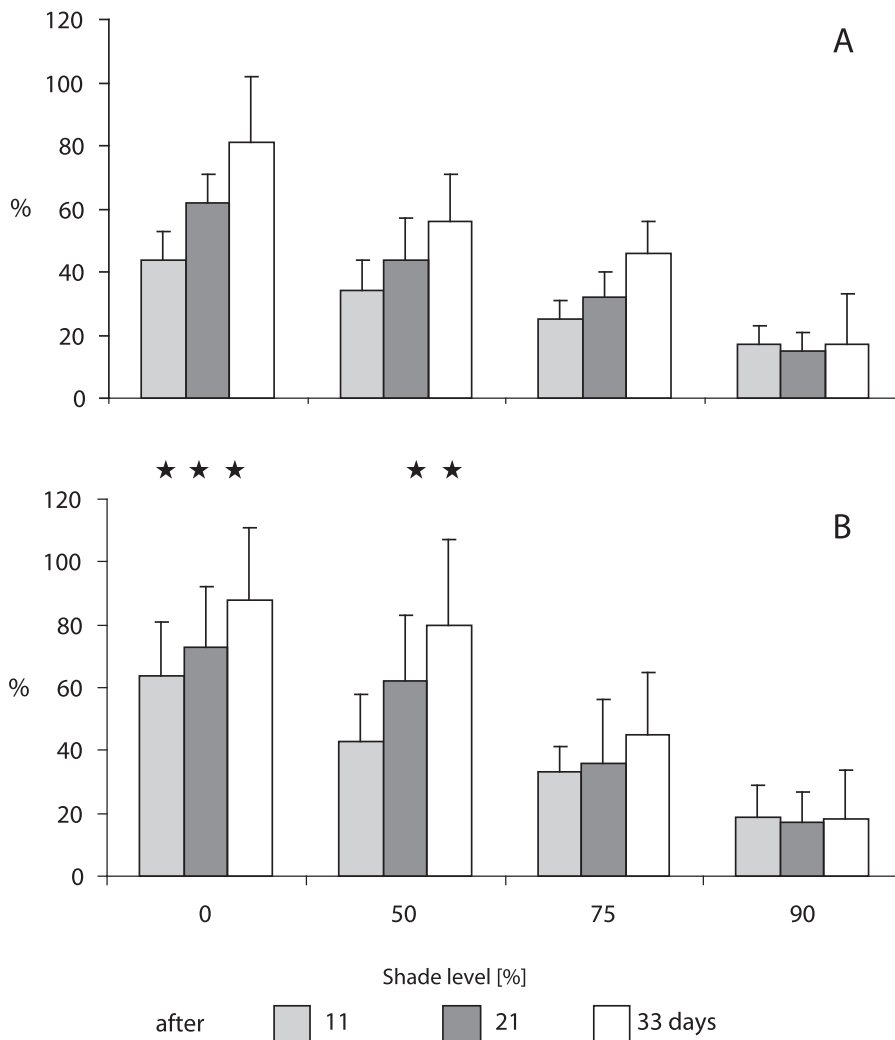


Fig. 2. Growth of whole plants and cut fragments of *Elodea canadensis* under different light conditions. Percentage increase in biomass above initial values after various periods of exposure. A – whole plants, B – cut plants. Data for cut plants are the sums of biomass for all three fragments. \* – significant differences between whole and cut plants.

The differences in the intensity of growth of plants during consecutive periods of exposure (0–11, 12–21 and 22–33 days) were estimated (Table 1). Plant length and biomass at the end of a particular period of exposure were taken as the initial values for the next stage (for the first period this was the initial value at the beginning of the experiment). In full light and 50% shade a marked increase in both the length and biomass of plants was noted in each period of exposure. However, the greatest growth rates for both whole and cut plants were characteristic of the first 11-day period of the experiment (Table 1). In subsequent stages (12–21 and 22–33 days), growth rates were visibly lower, especially in terms of biomass. Indeed, with a 90% level of shade, both whole and cut plants only showed a significant increase in length and biomass during the first 11 days, demonstrated a marked slackening off of growth after that (Table 1). In such reduced light conditions some plant fragments in fact begin to die off. It was possible to observe the detachment of some of the leaves and browning of lower parts of plant fragments with growing tips, and both ends of fragments without growing tips. Despite these symptoms of senescence, all plants placed in chambers at

the beginning of the experiment were still alive after 33 days of exposure.

Over the whole period of the experiment cut plants developed more lateral shoots than whole plants. Under no shade, all cut plants, as compared with only 14% of the whole plants, had new shoots by the time 11 days had elapsed (Fig. 3). Among the latter, new shoots on all plants had only appeared after 33 days of exposure. Under the highest (90%) level of shade, no whole plants had developed new shoots by the time 21 days, and it was only after 33 days that some (14%) had developed them. In contrast, in the cut plants under the same reduced light conditions new shoots had developed from the beginning of the experiment, if in smaller numbers than was the case with high light level (Fig 3). At the intermediate (50 and 75%) levels of shade (not presented on the figure) a higher number of new shoots was again observed on cut plants (which had two to ten times as many as the compared whole plants did).

The different fragments of cut plants developed different numbers of new lateral shoots (Fig 3). The apical fragments (I) having the growing tip grew mainly in terms of length increase of main shoot, developing relatively few new lateral shoots, with these only appearing after 21 days of exposure even

Table 1 Growth of whole plants and cut fragments of *Elodea canadensis* at various shade levels. Percentage increase in length (A) and biomass (B) over different periods of exposure (means  $\pm$  SD).

Shade level [%]	Type of plants	A			B		
		Exposure time [days]					
		0–11	12–21	22–33	0–11	12–21	22–33
0	whole	45* ( $\pm$ 15)	16* ( $\pm$ 3)	17* ( $\pm$ 9)	44* ( $\pm$ 9)	13* ( $\pm$ 7)	11* ( $\pm$ 8)
	cut	50* ( $\pm$ 20)	32* ( $\pm$ 12)	15* ( $\pm$ 6)	64* ( $\pm$ 17)	6* ( $\pm$ 5)	9* ( $\pm$ 5)
50	whole	41* ( $\pm$ 6)	17* ( $\pm$ 4)	16* ( $\pm$ 6)	34* ( $\pm$ 10)	8* ( $\pm$ 5)	8* ( $\pm$ 9)
	cut	54* ( $\pm$ 25)	33* ( $\pm$ 8)	22* ( $\pm$ 7)	43* ( $\pm$ 15)	14* ( $\pm$ 13)	11* ( $\pm$ 9)
90	whole	27* ( $\pm$ 12)	2 ( $\pm$ 3)	4 ( $\pm$ 12)	17* ( $\pm$ 6)	-1 ( $\pm$ 3)	2 ( $\pm$ 12)
	cut	15* ( $\pm$ 11)	1 ( $\pm$ 4)	2 ( $\pm$ 11)	19* ( $\pm$ 10)	-2 ( $\pm$ 5)	1 ( $\pm$ 9)

\* - significant increase.

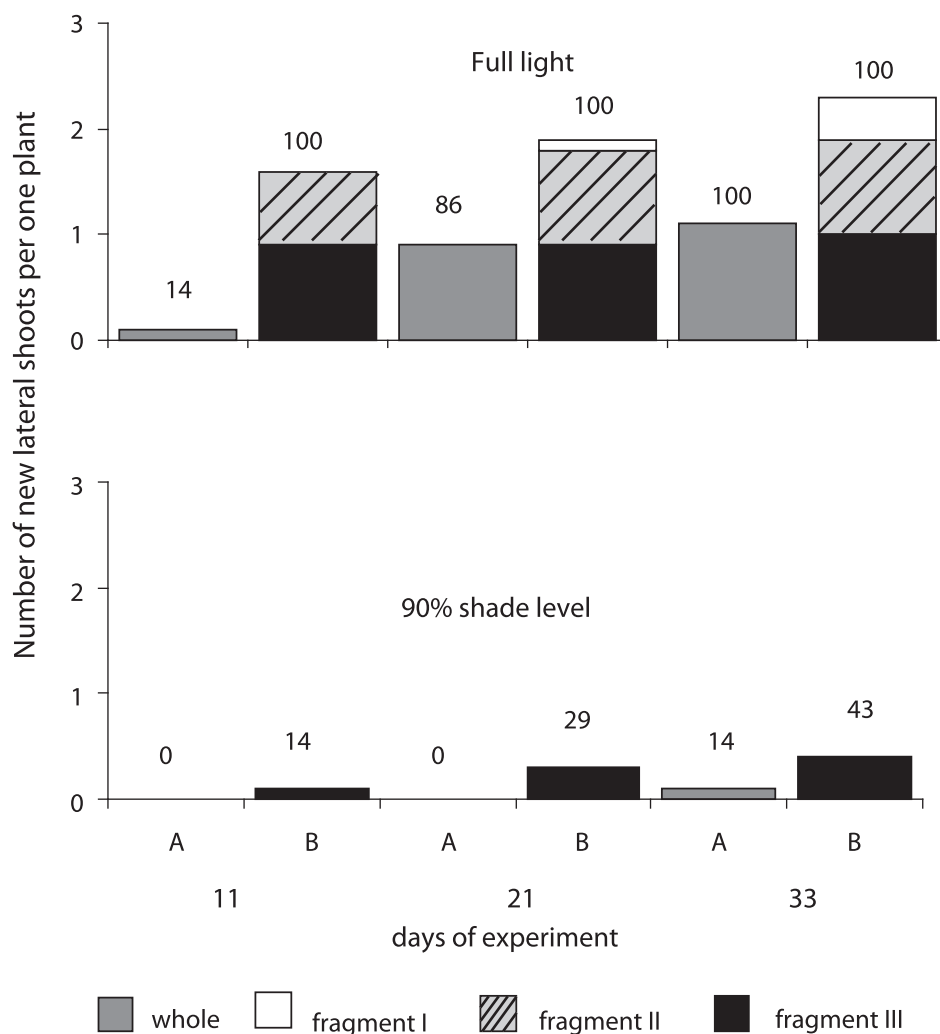


Fig 3. The number of new lateral shoots per plant and percentage of plants with new lateral shoots (numbers above columns) in whole plants (A) and cut fragments (B) of *Elodea canadensis* after various period of exposure under full light and a 90% shade level.

in full light. Middle (II) and lower (III) fragments accounted for greater numbers of new shoots. In full light the latter were observed in each periods of exposure in similar quantities. However, in conditions of 90% shade only lower fragments (III) developed new shoots albeit ones observed from the beginning of experiment (Fig. 3).

Calculated at the end of the experiment, the percentage contribution to total final biomass of plants accounted for by new shoots was visibly higher among cut plants than whole plants under all light conditions. In full light, new shoots come to account for

28% of the final biomass of cut plants, compared with only 15% in the case of whole plants. Under 90% shade, the contributions to biomass made by new shoots were low, albeit twice as high in cut (at 4%) as in whole plants (2%).

On the basis of the results of the experiment presented, theoretical calculations were made to evaluate whether, and if so, to what extent the possible loss of a fragment of shoot of *Elodea canadensis* could be compensated for by the growth of remaining plant fragments. In this calculation the sum of initial biomass of all three fragments of cut plants

was compared with the sum of biomass of two fragments after 33 days of exposure (fragment I, II, or III was in turn “eliminated”). The possibility to compensate for these losses depends on the type of “removed” fragment, as well as on light intensity. It was noted that, in full light, the “elimination” of the middle fragment (II) which would result in the lowering of the initial biomass of cut plants by 26%, could be fully compensated for after 33 days of exposure, as the biomass of the two remaining fragments increased by 38% above the initial biomass of all three fragments. The loss of plant biomass resulting from “removal” of two other fragments could be only partly compensated for during the same period, although in both cases plants grew. The loss of initial biomass (37% in the case of “elimination” of both fragments) was higher than biomass increases (19 and 20% in the cases of fragments I and III respectively). Under poor light conditions (90% shade) the growth of plants was so limited that “removal” of whichever fragment would not be compensated for. In this case, the final biomass of two fragments after 33 days was significantly lower than the initial biomass of the three fragments (by 12% to 28% depending on which of the different fragments was eliminated).

#### 4. DISCUSSION AND CONCLUSIONS

Large numbers of plant fragments are observed in various freshwater habitats, and particularly in those in which macrophytes became highly damaged by herbivory or physical factors. Although the further fate of macrophyte fragments has been poorly studied, there are evidences that fragments of *Elodea canadensis* and some other submerged macrophyte species can have high regenerative potential and are able to develop new viable plants. Barrat-Sergetain *et al.* (1999) demonstrated the regenerative capacity of fragments of different aquatic macrophytes collected from river habitats frequently disturbed by floods. They found that, among material from 16 plant species, fragments of *Elodea* demonstrated a relatively high survival rate and a high regeneration rate. Pieczyńska (2003) showed in

a laboratory experiment that *E. canadensis* is able to continue growing and generating new shoots from fragments following on from a very wide range of damage due to grazing by the snail *Lymnaea (Lymnaea) stagnalis*.

*Elodea canadensis* is reported from sites in lakes of a very wide range of depths, and the plant is generally considered relatively highly tolerant to low light conditions (Hutchinson 1975, Nichols and Shaw 1986). Abernethy *et al.* (1996) showed greater tolerance of *Elodea canadensis* than *Myriophyllum spicatum* to the cutting and stress caused by shading in experiments where growth of plants in terms of length and biomass was observed in different shade levels.

In the experiment presented in this paper, fragments of *Elodea canadensis* grew and produced new lateral shoots in light conditions ranging between 3 and 30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Such varying light intensities have been noted in various habitats, for example in Lake Mikołajskie at sites where *Elodea canadensis* grew, as well as where its fragments are noted abundantly (Pieczyńska unpublished data). The growth rate of *E. canadensis* was found to vary under different light treatments. In full light and moderate shade, plants grew during the whole period of exposure, albeit with the highest growth rate observed during the first 11 days. In these conditions, in most stages of the experiment, cut plants grew more intensively than whole plants. Under the highest (90%) shade, plants grew poorly and there were no differences in the growth of cut and control plants, or else the growth of cut plants was reduced to the greater extent. It is however important to point out that new shoots were produced by cut plants all the time in such conditions. The limited growth of plants in terms of total length and biomass in very low light conditions can be explained by the faster die off of plants (especially their cut edges), which could be only partially compensated for by new growth.

The growth of plants following fragmentation depends on kind and degree of damage, as well as on environmental factors. Mielecki (unpublished data) found a marked capacity of fragments of *E. canadensis* to grow at various level of water fertility ranging between 0.02 and 1.04 mg P-PO<sub>4</sub> l<sup>-1</sup> and 0.4–2.7 mg N-NH<sub>4</sub> l<sup>-1</sup>, but the intensity of growth

depended visibly on the level of fertilizer use. Barrat-Segretain *et al.* (1998) noted that different plant fragments remaining in the environment are of varying importance when it comes to the rebuilding of plant biomass. They show that above-ground and underground parts of plants, buds, or fragments with one or four internodes differed greatly in terms of both anchoring and regenerative potential. Moreover fragments from plants collected in different seasons (spring or summer) displayed different survival and regenerative abilities (Barrat-Segretain and Bornette 2000).

The possibility of compensation for the losses of shoot fragments of *E. canadensis* which both biological or physical factors may induce in nature depends on light conditions. As shown from the theoretical calculation presented in this paper, in full light, 33 days of exposure would be enough for, the lowering of plant biomass to be entirely or partly compensated for, depending on the kinds of fragments assumed to be lost. No compensation at all was noted when the response to the same level of assumed removal of successive plant fragments was calculated for 90% shade. Nevertheless, it is probable that, while biomass could not be rebuilt over 33 days of exposure, the new shoots produced in this period could in future generate new plants. Thus, even in such limited light conditions, compensation for biomass losses might well be possible over a longer period of time.

Presented experiment showed that the cutting of plants resulted in the production of a greater number of lateral shoots. In favourable light conditions all fragments of a cut plant (I- the top with growing tips, II- the middle and III- the lower section without growing tips) continued with growth and developed new lateral shoots, although the numbers of these differed greatly. While middle and lower fragments initially without growing tips grew only through the production of a large number of lateral shoots, the growth of the apical fragment resulted mainly from an increase in length from the retained apical meristem – this fragment produced a relatively limited number of lateral shoots.

The intensive production of new lateral shoots by plant fragments deprived of growing tips provided means by which these are

not predestined to die, but are rather able to rebuild lost tissues. Such fragments arise frequently in nature, as a result of plant harvesting or plant damage by grazing animals, especially when animals feed mostly on the apical tips of plants. Examples of such types of feeding include extensive damage of the apical meristem of *Myriophyllum spicatum* and *Potamogeton perfoliatus* by larvae of *Acentria ephemerella* (Johnson *et al.* 1998, Gross *et al.* 2002), or severe damage done to the growing tips of *Elodea canadensis* by *Lymnaea (Lymnaea) stagnalis* (Pieczyńska 2003).

The production of lateral shoots by highly damaged plants was noted by Gross *et al.* (2001) who pointed out that *Elodea canadensis* is able to form new side shoots, even when leaves are missing or stem turned brown as a result of herbivory. Similarly, Pieczyńska (2003) noted intensive production of new lateral shoots by damaged fragments of *Elodea canadensis* which remained after the feeding of snails. In another experiment (Pieczyńska unpublished data) it was possible to note a high regeneration capacity of fragments of *Elodea canadensis* and *Ceratophyllum demersum* exposed in an experimental pool in mesh bags. After 100 days of exposure, by which time most fragments introduced at the beginning of the experiment had died, the new lateral shoots they had produced beforehand dying were growing successfully, with *E. canadensis* producing more lateral shoots than *C. demersum*. All these observations support the opinion that fragments of *Elodea canadensis* have high regenerative capacities. This is important as in case of *E. canadensis* vegetative reproduction by fragmentation is the main way in which a population is rebuilt (as in most localities no generative reproduction of this plant is noted).

In conclusion, the experiment presented in this paper indicates that fragmentation does not restrict the growth of *Elodea canadensis* and can even stimulate it in favourable light conditions. Thus the intensive growth of cut plants offers a possibility for the biomass losses which may be caused by herbivores or physical factors to be compensated for. Fragments of *Elodea canadensis* grow in a wide range of light conditions and only a very marked reduction in light levels was

able to restrict the growth of the plants. In response to cutting, *E. canadensis* produced more lateral shoots. Of particular importance is the production of lateral shoots by plant fragments in very poor light conditions under which the main shoots begin to die off quickly. It can be expected that the death of a parent fragment will be followed by the continued growth of a young one detaching from it. This implies that fragmented *Elodea canadensis* is able to regrow into new individuals even when transported to the deeper part of the littoral characterized by low light levels.

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