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The Effect of Two Herbivorous Insect Larvae on Eurasian Watermilfoil[1]

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ABSTRACT

Larvae of the moth *Acentria ephemerella* (Denis and Schiffermüller) (=*Acentria nivea* (Olivier)) and the weevil *Euhrychiopsis lecontei* (Dietz) were associated with a population of Eurasian watermilfoil (*Myriophyllum spicatum* L.) that had declined. To determine if these herbivorous insect larvae played a role in the decline we conducted three experiments (*Acentria* alone, *Euhrychiopsis* alone, *Acentria* and *Euhrychiopsis* together) in outdoor pools which quantified their effects on watermilfoil growth. *Acentria* larvae significantly reduced watermilfoil growth in two experiments. *Acentria* damaged the plants by cutting the stem and removing leaves. Late instar *Euhrychiopsis* larvae significantly reduced watermilfoil growth in one experiment but not the other. Weevil larvae significantly reduced plant growth in the experiment in which watermilfoil exhibited a faster growth rate. Weevil larvae fed by burrowing through the stem and burrowed through approximately 6-8 mm of stem per day. These results suggest that these insect herbivores have potential as biological control agents for Eurasian watermilfoil in North America.

Key words: biological control, insect herbivory, submersed aquatic macrophytes, *Myriophyllum, Acentria, Euhrychiopsis.*

INTRODUCTION

Recent investigations of Eurasian watermilfoil (*Myriophyllum spicatum* L.) declines have found herbivorous insects associated with some of these watermilfoil populations (Kangasniemi 1983, Painter and McCabe 1988, MacRae et al. 1990, Creed and Sheldon 1991a, 1991b, 1992). The extent to which these herbivores may have contributed to these declines remains to be determined. However, experimental evidence documenting the ability of various aquatic insects to feed on and damage Eurasian watermilfoil in laboratory settings has been accumulating (e.g., Batra 1977, Buckingham and Bennett 1981, Buckingham and Ross 1981, Painter and McCabe 1988, MacRae et al. 1990, Creed and Sheldon 1992, 1993a, Creed et al. 1992). These observations and experimental results suggest that the potential for these insect herbivores to serve as biological control agents for nuisance Eurasian watermilfoil populations needs to be determined. Hereafter, Eurasian watermilfoil will be referred to as watermilfoil.

In Brownington Pond, Vermont, USA, we have found two insect herbivores associated with a watermilfoil population that has undergone a decline (Creed and Sheldon 1991a, 1991b, 1992). These are the caterpillar *Acentria ephemerella* (Denis and Schiffermüller) (=*Acentria nivea* (Olivier)) (Lepidoptera: Pyralidae), and the weevil *Euhrychiopsis lecontei* (Dietz) (Coleoptera: Curculionidae). *E. lecontei* is native to North America; *A. ephemerella* is a naturalized species. *Acentria* larvae and adult weevils feed primarily on stem and leaf tissue (Batra 1977, Buckingham and Ross 1981, Creed and Sheldon 1993a). First instar weevils feed on meristems and older larvae burrow through the stem. The number of *Euhrychiopsis* per stem in Brownington Pond was often 1 to 2 per stem; the number of *Acentria* was usually less than 1 but on occasion exceeded 2 per stem (Creed and Sheldon 1992, 1993b). We previously demonstrated that adults and first instar larvae of *Euhrychiopsis* significantly suppress watermilfoil growth (Creed and Sheldon 1993a). The objectives of these experiments were to determine the potential for *Acentria* larvae and late instar *Euhrychiopsis* larvae, separately and in combination, to suppress watermilfoil growth.

MATERIALS AND METHODS

The Effect of Acentria on Watermilfoil Growth. Several small, watermilfoil plants with intact roots were collected from Brownington Pond. Eighteen undamaged plants which were the most similar in length were selected and invertebrates and weevil eggs were removed from these plants. The plants were then weighed (blotted wet weight) and the length of the stem from a marker attached at the base to the tip of the apical meristem was measured. We also counted the number of leaf whorls on each stem above the marker. The initial lengths of the watermilfoil plants ranged from 160 to 203 mm; initial weights ranged from 0.33 to 0.75 g. Much of the variation in weight was attributable to differences in root biomass and not stem biomass.

Each watermilfoil plant was then planted in a chamber which consisted of a clear plastic cylinder (height 30 cm, inside diameter of tube 42 mm) set in a PVC pipe base. Plants were planted into sieved pond sediments taken from one of the watermilfoil beds in Brownington Pond. The top of the chamber was sealed with a tight-fitting cap covered with 500 μm, Nitex ™ mesh. The chambers were placed in a 750 l pool set out of doors in an unshaded area and aerated to prevent stagnation. Plants were allowed to acclimate to the chambers for one day before the *Acentria*

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larvae were added. The experimental design was a randomized complete block design with three treatments (0 (control), 2 or 4 *Acentria* larvae per chamber) and six replicates per treatment. The *Acentria* larvae came from a single batch of eggs collected from a watermilfoil plant in Brownington Pond. The larvae had hatched and had been feeding on watermilfoil in an aquarium for about two weeks. All larvae used in the experiment were very similar in their initial size (mean length ± 1 S.E. was 2.8 ± 0.13 mm, based on 8 extra, preserved larvae not used in the experiment). Water temperature in the pool was monitored using a max/min thermometer during the experiment.

After 22 days (19 July-10 August 1991) plants and *Acentria* larvae were removed from each chamber. The plants were measured (from marker to tip of rooted stem) and weighed (blotted wet weight). *Acentria* retreats, which are attached to the stem, were included in length and weight measurements. Any plant material not attached to the rooted stem was not included in the final plant length or weight. We also counted the number of whorls of leaves on each stem. Treatment effects were compared using an analysis of variance (ANOVA) with planned, orthogonal contrasts (Sokal and Rolhf 1981).

The Effect of Euhrychiopsis Larvae on Watermilfoil Growth. The design of this experiment, the collection of plants and the statistical analyses were the same as the *Acentria* experiment. The initial plant lengths ranged from 158 to 223 mm; initial weights ranged from 0.33 to 0.74 g. Late instar larvae (approximately 3-4 mm long) were collected from watermilfoil plants in Brownington Pond. Treatments consisted of a control, 1 and 2 late instar weevil larvae per plant. The experiment lasted 9 days (9-18 July 1991). We quantified change in plant length and weight, and measured the amount of stem that had been burrowed by the larvae. As weevil larvae do not appear to feed extensively on leaves, we did not quantify changes in the number of leaves or leaf whorls. Weevil larvae died in both the one and two larvae treatments in one row so n = 5 for these two treatments; n = 6 for the control.

The Combined Effect of Acentria and Euhrychiopsis Larvae on Watermilfoil Growth. The collection and processing of the plants and the experimental chambers were the same for this experiment as for the previous two. The initial lengths of the twenty four watermilfoil plants ranged from 206-230 mm; initial weights ranged from 0.23-0.88 g. Much of the variation in weight was attributable to differences in root biomass and not stem biomass.

The experimental design was a randomized complete block design with four treatments and six replicates per treatment. The treatments were as follows: control (no larvae), weevil (1 *Euhrychiopsis* larva per chamber), *Acentria* (1 *Acentria* larva per chamber) and the combination treatment (1 larva of each species in a chamber). Late instar *Euhrychiopsis* larvae and *Acentria* larvae (approximately 5-6 mm long) were collected in Brownington Pond and were paired by size for each row.

The experiment lasted for 13 days (5-18 August 1992). Plants and larvae were then removed from each chamber. After removing the larvae, the watermilfoil plants were measured, weighed (blotted wet weight) and the number of leaf whorls was counted. Any plant material not attached to the rooted stem was not included in the final plant length or weight. Weevil larvae in the single weevil treatment died in rows 1 and 6 and an *Acentria* larva died in the single *Acentria* treatment in row 6. These two rows were removed from the analysis so n=4 for all treatments. Treatment effects were compared using an ANOVA with planned, orthogonal contrasts (Sokal and Rolhf 1981).

RESULTS

The Effect of Acentria on Watermilfoil Growth. Acentria larvae alone significantly reduced watermilfoil length (Figure 1A). The mean change in length of the control plants was 68.5 mm compared to -7.5 mm for the 2-*Acentria* treatment and -37.5 mm for the 4-*Acentria* treatment. The contrast between the 0-*Acentria* treatment (control) versus the *Acentria* treatments was highly significant. There was no significant difference between the 2- and 4-*Acentria* treatments.

The change in the number of leaf whorls on the stems was similar to the change in length response (Figure 1B). Control plants added an average of 10 new leaf whorls whereas plants with *Acentria* showed either little change in the number of leaf whorls (2-*Acentria* treatment) or a loss of leaf whorls (4-*Acentria* treatment). The contrast between the controls and the *Acentria* treatments was highly significant. The two treatments with *Acentria* were not significantly different from one another.

Acentria larvae also significantly reduced plant weight (Figure 1C). Control plants gained the most weight and were significantly different from the *Acentria* treatments. There was no significant difference between the two *Acentria* treatments. The observed increase in weight in the *Acentria* treatments appears to have been due to increases in root biomass as length of these plants either did not change or decreased. More unattached plant material was found in the chambers containing *Acentria* larvae which suggested that the loss of watermilfoil biomass in the presence of the caterpillars was not entirely a result of consumption. Mean (± 1 S.E.) wet weights of unattached material in the 0-, 2- and 4-*Acentria* treatments were 0.03 (± 0.01), 0.14 ± 0.04 g and 0.11 ± 0.04 g, respectively. The mean (± 1 S.E.) amount of unattached plant material expressed as a percentage of the total plant weight (all plant material in a chamber) for the three treatments was as follows: 0- *Acentria* treatment 3.4 ± 1.6%; 2- *Acentria* treatment 15.0 ± 3.9%; 4- *Acentria* treatment 17.4 ± 8.6%. During the experiment the mean minimum water temperature was 18.8C and the mean maximum temperature was 25.8C (range 16.1-32.2C).

The Effect of Euhrychiopsis Larvae on Watermilfoil Growth. Euhrychiopsis larvae did not have a consistent effect on watermilfoil growth in this experiment (Figures 2AandB). The presence of one larva reduced stem length compared to the control but there was no difference between the two larva treatment and the control. Due to this varied response, the contrast between the control and the weevil treatments was not significant. However, the contrast between the one larva and the two larvae treatment was marginally ($p<0.10$) significant (Figure 2A). Weevil larvae did have a consistent effect on plant weight (Figure 2B). Control plants gained about twice as much weight as either of

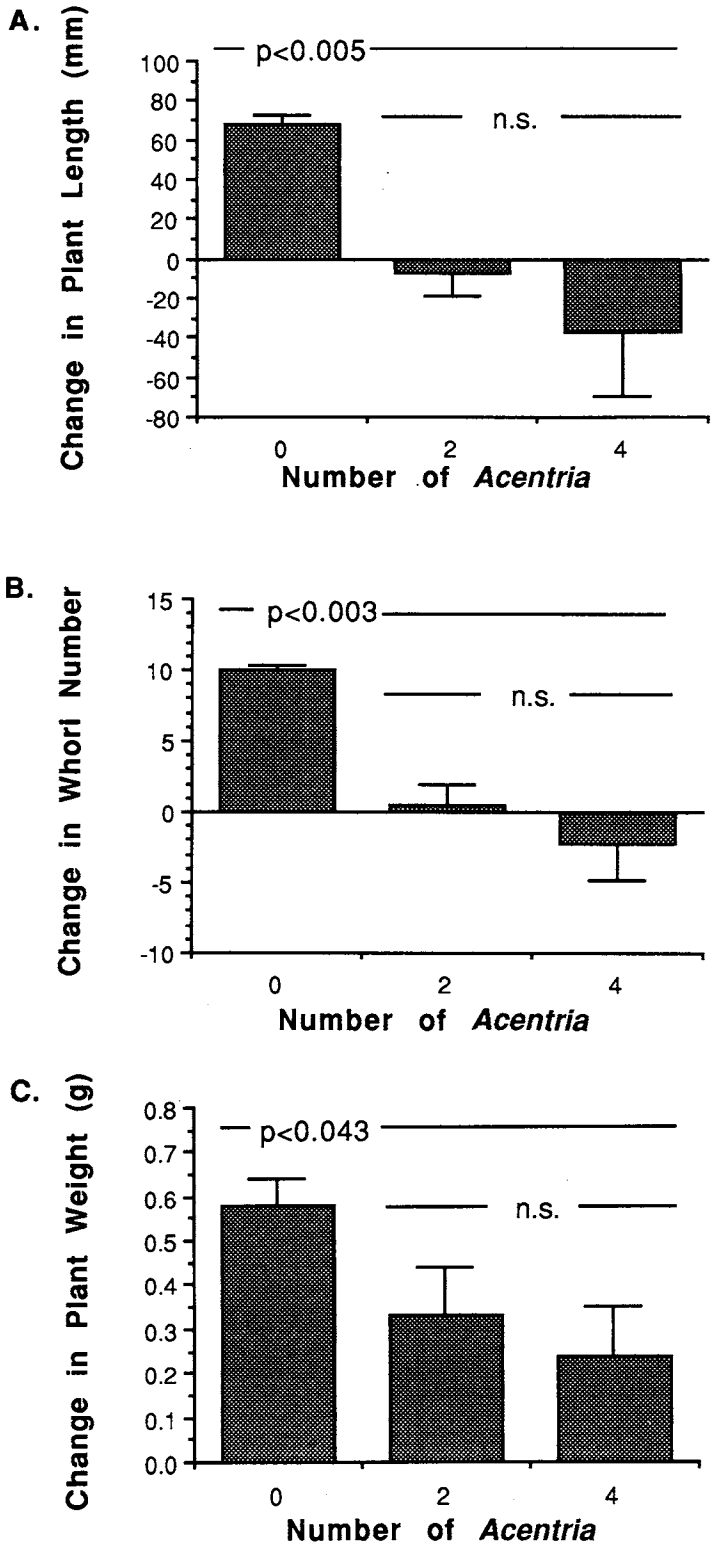

Figure 1. A - C. The effect of feeding by *Acentria* larvae on watermilfoil plants. The bars in the histogram represent the mean change in a response variable (± 1 S.E.) for each treatment. The lines with significance values above the histograms show the results of ANOVA comparisons with orthogonal contrasts. In each figure, the upper line represents the comparison of the control vs the *Acentria* treatments; the lower line represents the comparison of the two vs the four *Acentria treatment*. A. Change in plant length (in millimeters). B. Change in the number of whorls per plant. C. Change in plant weight (in grams).

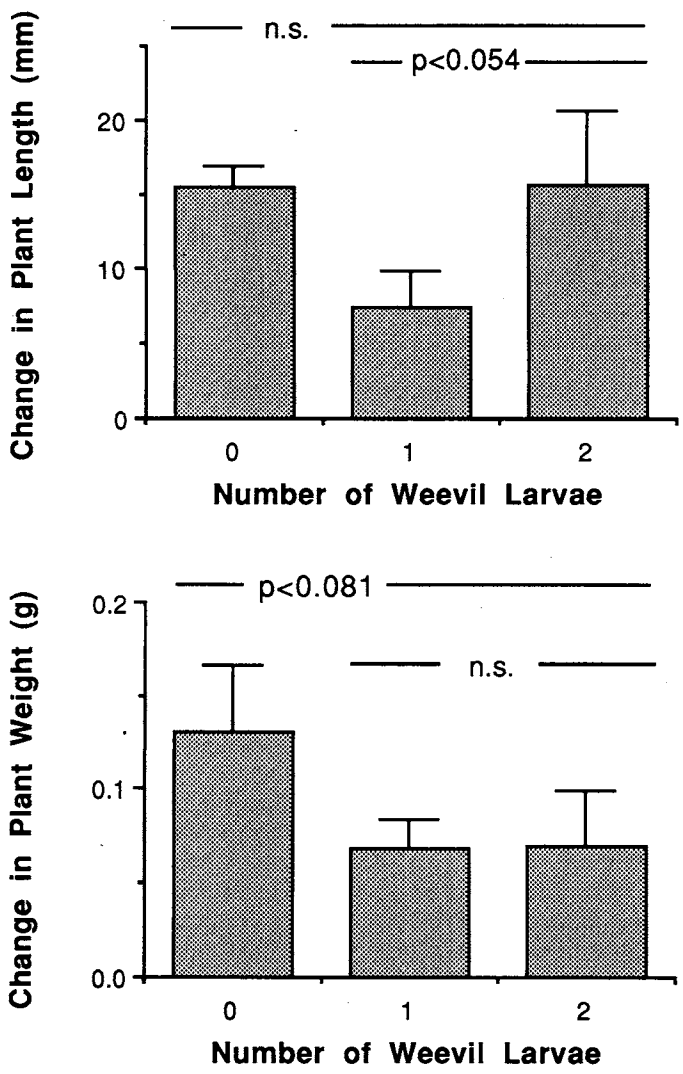

Figure 2. A and B. The effect of feeding by *Euhrychiopsis* larvae on the watermilfoil plants. The bars in the histogram represent the mean change in a response variable (± 1 S.E.) for each treatment. The lines with significance values above the histograms show the results of ANOVA comparisons with orthogonal contrasts. In each figure, the upper line represents the comparison of the control vs the weevil treatments; the lower line represents the comparison of the one vs the two weevil treatment. A. Change in plant length (in millimeters). B. Change in plant weight (in grams).

the weevil treatments; the greater weight of the control plants appears to be due to increased root production as there was no significant difference in length. The contrast between the control and the two weevil treatments was marginally significant. The contrast between the two weevil treatments was not significant. The mean (± 1 S.E.) length of stem hollowed by weevil larvae in the two treatments was as follows: one larva treatment, 75.4 ± 6.7 mm (range 59 to 98 mm); two larvae, 106.2 ± 18.6 mm (range 59 to 160 mm). These values translate into burrowing rates of 8.4 mm/day for single larvae and 11.8 mm/day for two larvae. No burrowing damage was observed in internodes 1 (just beneath the meristem) to 5. Weevil larvae burrowed

through internodes 6 and greater. Watermilfoil stems often lost their structural integrity and buckled in the regions where they were burrowed by weevil larvae. During the experiment the mean minimum water temperature was 15.6C and mean maximum water temperature was 22.5C (range 11 to 27C).

The Combined Effect of Acentria and Euhrychiopsis Larvae on Watermilfoil Growth. Acentria and *Euhrychiopsis* larvae, both alone and in combination, significantly suppressed increases in length, weight and the number of whorls (Figure 3 A-C). Watermilfoil plants with just one weevil larva were shorter, had fewer whorls and weighed less than control plants. The mean (± 1 S.E.) amount of stem hollowed out by weevil larvae was 93.5 ± 24.9 mm (range 50 to 147 mm) which translates into a mean burrowing rate of 7.8 mm/day. As in the previous experiment, watermilfoil stems often buckled in the regions where they were burrowed by weevil larvae. Only 0.01 ± 0.006 g of unattached plant material was found in the weevil treatment. Plants with *Acentria* larvae, either alone or in combination with a weevil larva, exhibited even more damage than plants with just a weevil larva. The means for all three measurements of plant growth were negative for plants with *Acentria* larvae. The mean amount of unattached plant material found in the chambers containing only *Acentria* was 0.08 ± 0.03 g wet weight. The damage to plants with both *Acentria* and *Euhrychiopsis* larvae was slightly less than that exhibited by plants that had a single *Acentria*. A similar amount of unattached plant material was found in this treatment (0.09 ± 0.03 g). No unattached plant material was found in the controls. During the experiment the mean minimum water temperature was 16.6C and mean maximum water temperature was 22.7C (range 12.8-26.1C).

DISCUSSION

Acentria larvae significantly reduced watermilfoil growth in both the first and third experiments and much of their effect appeared to have been attributable to cutting the stem while feeding and for retreat construction. Early instar larvae usually construct retreats by folding over a single leaf and attaching it to the stem with silk (Batra 1977). While late instar larvae may also dwell in such retreats (Batra 1977) they may also cut the stem, slide the upper portion of the stem down and construct a silk retreat between the two stem pieces. Seven out of twelve stems with *Acentria* were cut in the first experiment which used smaller larvae. All of the stems were cut in the treatments with *Acentria* in the third experiment which used late instar larvae. The difference in the weight response in the two experiments with *Acentria* (weight gain in the first experiment and weight loss in the third experiment) may have been due to when the stems were cut by the larvae. Many of the larger larvae used in the third experiment had cut the stem of their plants within the first two or three days of the experiment. Cut stems were not observed in the first experiment for 1 1/2 to 2 wk which may have been sufficient time for some root production to occur. While *Acentria* larvae consumed watermilfoil in the chambers, it was not possible to determine the amount consumed as the difference between *Acentria* treatments and controls could

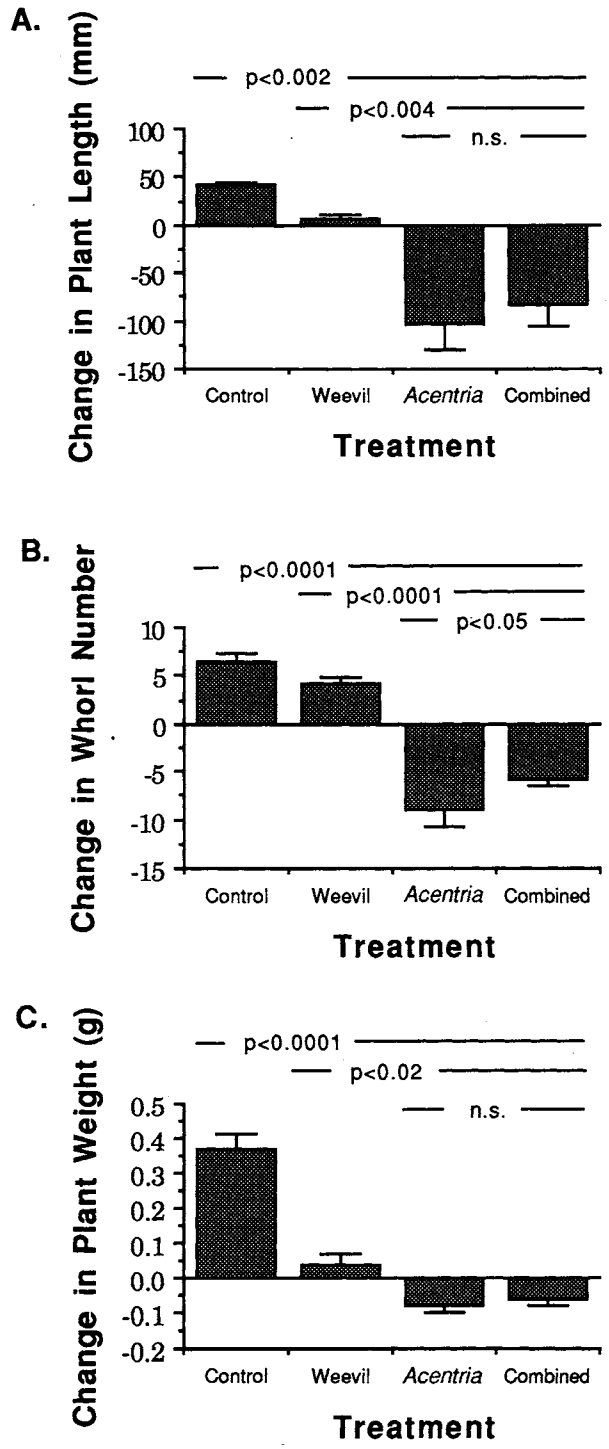

Figure 3 A - C. The effect of feeding by *Euhrychiopsis* and *Acentria* larvae on watermilfoil plants. The bars in the histogram represent the mean change in a response variable (± 1 S.E.) for each treatment. The lines with significance values above the histograms show the results of ANOVA comparisons with orthogonal contrasts. In each figure, the upper line represents the comparison of the control vs the three herbivore treatments; the middle line represents the comparison of the weevil treatment versus the two treatments containing *Acentria* larvae; the lowest line represents the comparison of the *Acentria* alone treatment versus the treatment with both the *Acentria* and the *Euhrychiopsis* larvae (combined). A. Change in plant length (in millimeters). B. Change in the number of whorls per plant. C. Change in plant weight (in grams).

have been due to consumption of tissue, inhibition of growth and decay of some of the unattached material. Our results with rooted stems confirm those of Painter and McCabe (1988) who examined the effects of *Acentria* on floating watermilfoil fragments. They noted that watermilfoil continued to grow when *Acentria* densities were less than one per stem. When *Acentria* densities exceeded one per stem a dramatic reduction in watermilfoil weight was observed (Painter and McCabe 1988).

The effect of *Eurhychiopsis* larvae on watermilfoil length and weight varied between experiments. This variation in response appears to be due in part to differences in watermilfoil growth rates in the two experiments. In the experiment with only *Eurhychiopsis* larvae (the second experiment), mean change in stem length for control plants was only 15 mm and mean change in weight was only 0.13 g. In the third experiment (*Acentria* and *Eurhychiopsis* larvae combined), mean changes in stem length and stem weight for control plants were three times that of the first experiment (mean change in length was 43 mm and mean change in weight was 0.38 g). Changes in plant length and weight in the one weevil treatment in both experiments were fairly similar. Thus, while weevil larvae can suppress the growth of slow-growing plants the inhibition of watermilfoil growth by weevil larvae is more pronounced when watermilfoil plants have the potential to grow at faster rates. We do not know the cause of the difference in growth rates in the two experiments. Water temperatures were similar for both experiments and the same water source was used to fill the pools. Possible explanations include either differences in sediment nutrient concentrations or plant condition.

Late instar *Euhrychiopsis* larvae burrowing through the stem destroy the lacunal system and the vascular tissue. The lacunal system in watermilfoil can act as a gas reservoir for respired CO_2 (Nichols and Shaw 1986) and also permits diffusive gas exchange between the roots and shoots (Grace and Wetzel 1978, Nichols and Shaw 1986). Destruction of the lacunal system by weevil larvae may have adverse effects on watermilfoil physiology if the accumulated CO_2 is lost and if oxygen exchange between the shoots and the roots, where respiratory demand is high (Wetzel 1983), is disrupted. Removal of stem vascular tissue could also influence growth as a result of reduced or halted translocation of nutrients from roots to actively growing portions of shoots. If adequate quantities of nutrients can be removed directly from the water by the plant then this effect should be negligible. When our results are considered in conjunction with the results of previous studies on nutrient uptake in watermilfoil (Nichols and Keeney 1976, Best and Mantai 1978, Carignan and Kalff 1980, see also review by Smith and Barko 1990), they suggest that larval weevil burrowing might have a more pronounced effect on watermilfoil growth in nutrient-poor water bodies if the growing portion of the stems can not obtain sediment nutrients.

While *Acentria* consistently reduced watermilfoil growth compared to *Euhrychiopsis* in these experiments, our field observations suggest that the weevil may do more damage in natural environments. When one of the watermilfoil beds (the West Bed) in Brownington Pond collapsed in mid-July of 1991 mean weevil abundance in this bed ranged from 2.0-3.2 weevils per stem. Mean weevil abundance in the second bed (the South Bed) which did not collapse ranged from 0.2-1.0 weevils per stem. There was no difference in the average abundance of *Acentria* between the two beds: South Bed 0.0-0.6 larvae per stem; West Bed 0.2-0.4 larvae per stem (Creed and Sheldon 1992). Weevil burrowing also causes watermilfoil to lose its buoyancy (Creed et al. 1992) and may have other adverse effects on watermilfoil biology such as those mentioned above. While *Acentria* can damage the stem, especially during construction of the late instar retreat/puparium (see above), retreat construction does not appear to have any long term effect on stem buoyancy. We have frequently seen watermilfoil plants with one or two late instar *Acentria* retreats that did not appear to have suffered any loss of buoyancy. While we have occasionally encountered *Acentria* larvae in meristems, *Acentria* appear to concentrate their feeding on leaves below the meristem (but see Painter and McCabe 1988). Thus apical elongation may continue despite the *Acentria* feeding. First instar *Euhrychiopsis* larvae, on the other hand, destroy meristems which can result in a suppression of stem elongation (Creed and Sheldon 1993a). We have also demonstrated in a pond enclosure experiment that weevil feeding suppressed the production of lateral stems and root tissue (Creed and Sheldon 1993b). The pool experiments suggest that *Acentria* can have a strong, negative effect on watermilfoil as a result of cutting the stem and biomass consumption. Our field observations, on the other hand, suggest that *Acentria* may not be as important in producing declines as *Euhrychiopsis*. *Euhrychiopsis* larvae and adults may suppress watermilfoil growth to a greater extent than *Acentria* by affecting the physiology of the entire plant.

Feeding by *Acentria* and *Eurhychiopsis* larvae on watermilfoil may result in stem fragmentation. This effect was clearly seen in the treatments containing *Acentria* in both experiments but not in the *Euhrychiopsis* treatments. Larval weevil burrowing does weaken the watermilfoil stem and burrowed stems are easily broken. While we have commonly encountered such broken stems in lakes and ponds, this effect was not observed in treatments with weevil larvae as the stems were protected from physical disturbance by the chambers. It is possible that this herbivore-induced fragmentation could promote the spread of watermilfoil. However, the amount of spread, if any, would depend on the viability of the herbivore-damaged fragments. Recently, we have demonstrated that stem fragments (stem tissue plus meristem) damaged by weevil larvae were still viable but produced significantly less stem and root tissue than undamaged control fragments (Creed et al. 1993). We have not determined the viability of stem fragments produced by *Acentria* larvae.

To date, herbivorous insects have been found associated with declining watermilfoil populations in British Columbia (Kangasniemi 1983, MacRae et al. 1990), Ontario (Painter and McCabe 1988) and Vermont (Creed and Sheldon 1991a, 1991b, Creed et al. 1992, Creed and Sheldon 1993b). These field observations, considered in conjunction with the results of laboratory experiments (Painter and McCabe 1988, MacRae et al. 1990, Creed et al. 1992, Creed and Sheldon 1993a) suggest that herbi-

vores might be playing important roles in watermilfoil declines and maintaining populations at reduced levels. The results of recent field experiments support the hypothesis that weevils are involved in producing watermilfoil declines (Creed and Sheldon 1993b). Continued effort should be focused on determining the mechanisms by which these herbivores affect watermilfoil and their role in producing declines.

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