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Plant–herbivore interactions in streams near Mount St Helens

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SUMMARY

1. In four separate field experiments near Mount St Helens (Washington, U.S.A.) during 1986, the grazing effects of two large benthic herbivores, tadpoles of the tailed frog *Ascaphus truei* and larvae of the caddisfly *Dicosmoecus gilvipes*, were investigated using streamside channels and in-stream manipulations. In the experimental channels, abundances of periphyton and small benthic invertebrates declined significantly with increasing density of these larger herbivores.

2. In eleven small, high-gradient streams affected to varying degrees by the May 1980 eruption, in-stream platforms were used to reduce grazing by *A. truei* tadpoles on tile substrates. Single platforms erected in each tributary and compared to grazed controls revealed only minor grazing effects, and no significant differences among streams varying in disturbance intensity (and, consequently, tadpole density). However, results probably were confounded by high variability among streams in factors other than tadpole abundance.

3. Grazing effects were further examined in two unshaded streams with different tadpole densities, using five platforms per stream. In the stream with five tadpoles m^{-2}, grazing reduced periphyton biomass by 98% and chlorophyll *a* by 82%. In the stream lacking tadpoles, no significant grazing effects were revealed. Low algal abundance on both platforms and controls, and high invertebrate density in that stream (*c.* 30 000 m^{-2}) suggests that grazing by small, vagile invertebrates was approximately equivalent to that of tadpoles.

4. The influence of large benthic herbivores on algal and invertebrate communities in streams of Mount St Helens can be important, but reponses vary spatially in relation to stream disturbance history, local environmental factors, and herbivore distributional patterns and abundance.

Introduction

The cataclysmic eruption of Mount St Helens on 18 May 1980 devastated over 500 km^2 of forested landscape in south-west Washington, U.S.A. The lateral volcanic blast triggered debris avalanches, pyroclastic flows, severe windstorms, and mud-flows, which destroyed the coniferous forests within the blast zone and greatly altered aquatic habitats (Franklin *et al.*, 1985). For over 200 km of streams and rivers, riparian vegetation was burned or buried, sediments were severely scoured by debris flows or ash, and most aquatic plants and animals were killed. Streams near the perimeter of the blast zone,

however, were less severely disturbed and many aquatic organisms survived in protected habitats (Hawkins & Sedell, 1990).

Even in severely disturbed streams close to the volcano, benthic plants (primarily algae) recolonized stream beds within days and weeks after the eruption (Ward *et al.*, 1983; Rushforth, Squires & Cushing, 1986). Early in the recolonization process, conditions were favourable for primary production because of higher solar radiation due to removal of riparian canopy (Franklin *et al.*, 1985), increased inorganic nutrient concentrations (Klein, 1984), and reduced densities of grazing invertebrates (Wilzbach, Dudley & Hall, 1983). Consequently, benthic algae have flourished in many habitats (Ward *et al.*, 1983; Steinman & Lamberti, 1988). Small, vagile insects such as chironomid midges and baetid mayflies rapidly recolonized even the most severely disturbed streams (Fuste', 1981; Wilzbach *et al.*, 1983; Hawkins, 1988), but recolonization by larger invertebrates (e.g. trichopterans, molluscs) and vertebrates (e.g. amphibians, fish) has been slower (Anderson & Wisseman, 1987; Hawkins & Sedell, 1990).

Herbivory, the consumption of living plants or their parts by animals, is an important process in stream ecosystems (Gregory, 1983; Lamberti & Moore, 1984), particularly in systems with high autotrophic production (Minshall, 1978). Some environmental features (e.g. solar radiation, nutrients, temperature) of disturbed streams near Mount St Helens favoured high algal production, yet in many streams periphyton standing crop is low (Steinman & Lamberti, 1988). We postulated that herbivory could be an important process regulating algal accrual in those streams.

Disturbance intensity at Mount St Helens produced differences in the abundance of larger benthic herbivores in natural streams, thereby providing a basis for examining whether these organisms can influence lotic periphyton. Our study was designed to (i) evaluate the potential impact of large benthic herbivores on periphyton in these streams and (ii) determine whether the intensity of herbivory was related to disturbance history.

Study animals

Our studies concentrated on two lotic herbivores: tadpoles of the tailed frog *Ascaphus truei* Stejneger and larvae of the limnephilid caddisfly *Dicosmoecus gilvipes* (Hagen). We selected these two species because they were abundant and conspicuous members of the herbivore guild in or near the study area.

The rheophilic tadpoles of *A. truei* are abundant ($>3\,m^{-2}$) in some high-gradient streams near Mount St Helens (Hawkins, Gottschalk & Brown, 1988). Tadpoles use a strong, toothed oral disc to cling to rocks in swift current and to scrape attached algae from submerged surfaces. The tadpoles are long-lived (2 years from egg to adult) and large (*c.* 1 g wet mass at metamorphosis) compared to most invertebrate herbivores.

Dicosmoecus gilvipes larvae are uncommon in small, high-gradient streams near Mount St Helens but densities can exceed $30\,m^{-2}$ in undisturbed, lower-gradient streams. Larvae avoid swift current and prefer pools where they can use their robust mandibles and tarsal claws to gather periphyton (Lamberti *et al.*, 1987). *Dicosmoecus gilvipes* is univoltine at Mount St Helens with relatively synchronous development of the larvae, which attain large size in the final instar (*c.* 0.3 g wet mass).

Study area

Mount St Helens is part of the Cascade Mountains of south-western Washington, U.S.A. We studied eleven small streams located 15–20 km NE of the volcano. Of these, ten unnamed streams were perennial tributaries within the upper Clearwater Creek drainage, located at the perimeter of the volcanic blast zone (see map in Hawkins, 1988). Most vegetation in the upper Clearwater Creek area was destroyed by the eruption, where the coniferous forest was blown down or killed and the understory vegetation was burned or buried by ashfall. However, some forest along the eastern ridgetops and in the lower part of the basin survived relatively intact. This included the headwaters of some tributaries and some complete lower tributaries of Clearwater Creek. The eleventh tributary, Wakepish Creek, was in the adjacent Iron Creek drainage (5 km NE of Clearwater Creek; see map in Steinman & Lamberti, 1988). This drainage received volcanic ashfall but was otherwise undisturbed.

The eleven, second-order catchments were similar with respect to average gradient (15–20%), drainage area (5–10 km^2), channel substrate composition (cobble dominated) and discharge (summer baseflow

c. 0.1 $m^3 s^{-1}$) (Hawkins, 1988). They differed in degree of volcanic disturbance, varying from minimal disturbance to complete forest destruction. Five streams (NF1–NF5) drained completely deforested sub-basins, three streams (F1–F3) drained catchments with entirely intact forest, and three streams (HWF1–HWF3) had intact forest only in the headwaters (upper 20–40% of the catchment) with deforested lower sub-basins.

Ascaphus truei densities also varied with forest condition (Hawkins *et al.*, 1988). NF streams had few tadpoles (*c.* 0.6 tadpoles m^{-2}, on average), F streams had moderate tadpole densities (*c.* 2.7 tadpoles m^{-2}), and HWF streams had high densities (*c.* 4.4 tadpoles m^{-2}).

Materials and Methods

Experimental design

Four experiments were conducted during June–September 1986. In Experiments I and II, we manipulated densities of *D. gilvipes* and *A. truei*, respectively, in streamside experimental channels to determine if these larger herbivores had the capacity to affect algal abundance. In Experiments III and IV, we conducted *in-situ* manipulations in the eleven streams with varying *A. truei* density to determine whether tadpoles affected algal assemblages in natural streams.

Experiments I and II. Densities of *D. gilvipes* larvae (Experiment I) and *A. truei* tadpoles (Experiment II) were manipulated in nine parallel experimental channels placed on the floodplain of HWF2. Each wooden channel was 1.80 m long by 0.28 m wide (*c.* 0.5 m^2) and 0.13 m deep. Eighteen unglazed 7.4 × 7.4 cm clay tiles (55 cm^2) were placed in each channel on 3 cm of clean gravel. A set of eighteen tiles was also placed directly in HWF2 at the water-intake site (termed 'in-stream' plot) during Experiment I. Tiles were spaced about 3 cm apart. Water from HWF2 was transported through PVC pipes by gravity, filtered through an inclined, self-cleaning 250-μm-mesh screen into a header box, and delivered to the channels. The screen removed large particulate matter and macroinvertebrates, but allowed passage of algae and small invertebrates. In each channel, flow was maintained at 16 l min^{-1}, water depth at 5 cm using a standpipe, and current velocity at 2 cm s^{-1}. Current velocity at the in-stream plot was somewhat higher (5 cm s^{-1}) than in the channels but other features were similar. Bird netting was placed over the channels to discourage avian predation.

Fourth-instar *D. gilvipes* larvae were collected from Yellowjacket Creek, a stream just outside the blast zone. One-year-old *A. truei* tadpoles were collected from HWF2. Herbivores were stocked at densities of 0, 4, 8, 16, 24, 32, 48, 64, and 96 m^{-2} (=0–48 animals per 0.5-m^2 channel). A 5-mm-mesh screen on the standpipes kept large herbivores in the channels but allowed invertebrate drift out of the streams. Experiment I (*D. gilvipes*) was run for 32 days (26 June–28 July 1986); Experiment II (*A. truei*) lasted 26 days (7 August–2 September 1986). We recovered 90% of the *D. gilvipes* larvae at the end of Experiment I; density did not decline by over 15% in any single channel. We recovered 85% of the *A. truei* tadpoles; density declined by no more than 25% in any channel.

All sampling occurred at the end of the experiment. For analysis of benthic algae, six tiles were removed at random from each channel and from the in-stream plot, placed in separate plastic containers on ice, and frozen within 4 h. In the laboratory, three tiles from each channel were analysed separately for algal biomass and for chlorophyll *a* abundance (Lamberti & Resh, 1985).

For analysis of benthic invertebrates, three tiles from each channel and from the in-stream plot were removed at random and placed into a 250-μm-mesh net located directly downstream. The three tiles were then pooled and preserved in 90% ethanol.

Experiments III and IV. In-situ stream platforms were used to reduce grazing by benthic herbivores (Lamberti & Resh, 1983; Feminella, Power & Resh, 1989). Each platform was a metal plate (625 cm^2), raised 10 cm above the stream bed, but still submerged, and supporting nine 55-cm^2 clay tiles. Colonization and grazing by less mobile benthic herbivores was reduced with this design, but that of more mobile (drifting or swimming) herbivores was less affected (Lamberti & Resh, 1983). An identical control plate with nine tiles was placed directly on the stream bed next to the platform and was accessible to all herbivores.

In Experiment III, we used the eleven individual streams for replication of catchment type (i.e. forest condition and thereby *A. truei* density). We placed

one platform and control set in a pool within each stream during 24–26 June 1986. About 35 days later, two sets of three tiles from each platform and control plate were sampled at random, each set pooled, and later analysed for algal biomass or chlorophyll *a*.

In Experiment IV, we placed platforms in two streams, one with high tadpole densities (HWF3; 5.5 tadpoles m^{-2}) and one with low densities (NF1; <0.5 tadpoles m^{-2}). Five replicate platform and control sets were placed in separate pools in NF1 and in the unshaded section of HWF3, all within a 200-m reach of each stream. Platforms were erected 1 August 1986 and sampled 33 days later. All benthic animals were collected from each platform and control by gently washing each tile and both sides of the metal plate with water through a 250-μm-mesh net and then manually removing any remaining invertebrates. From each platform and control, three tiles were sampled at random and pooled for each of three analyses: algal biomass, chlorophyll *a*, and algal taxonomic composition.

Laboratory analyses

Algae. In the laboratory, algae were scraped from the upper surface of each tile with a razor blade, transferred to water, and collected on a preweighed Millipore filter (0.45-μm pore size). To determine algal biomass, each filter was dried at 55°C for 24 h, weighed, combusted at 500°C for 24 h, and reweighed to estimate ash-free dry mass by loss on ignition. For chlorophyll *a* analysis, each filter was ground and the pigments extracted in buffered 90% acetone for 4 h. The scraped tile was also soaked in 90% acetone for 24 h to extract any residual pigment. Chlorophyll *a* was measured by absorbance on a spectrophotometer using both the trichromatic and acidification methods (APHA, AWWA & WPCF, 1985). Phaeophytin generally was a small proportion (<10%) of chlorophyll *a* and hence no correction was made.

Taxonomic structure of the algal assemblages was determined quantitatively following the method of Steinman & McIntire (1986). Algae were scraped from three tiles, preserved in Lugol's solution, pooled, and settled in a 50-ml chamber. From each sample, 500 algal units were counted at ×400 with a Nikon MS inverted microscope. An algal unit was defined as an individual cell if the taxon was unicellular, or as a filament or colony if multicellular. All algae were identified to species at this step except diatoms, which were cleaned, mounted, and identified at ×1250 with a Zeiss RA microscope.

Invertebrates. In the laboratory, invertebrates were sorted and identified to the lowest taxonomic level possible (usually genus) and counted. General feeding habit (herbivorous or non-herbivorous) for each taxon was determined using the classification of Merritt & Cummins (1984).

Data analysis

For Experiments I and II, regression analysis was used to examine effects of large herbivore density on algal biomass, chlorophyll *a*, and small invertebrate density. Data were fitted to logarithmic models. Pearson product–moment correlation was used to examine the relationship between algal biomass and small invertebrate density.

In Experiments III and IV, we used ANOVA to determine if the difference between platforms and controls varied among catchment type (III) or individual stream (IV); *F*-values and significance of these difference tests are reported. When Bartlett's test detected unequal variances among groups, logarithmic transformations were applied to the data. Non-transformed means and errors are presented in the text and figures.

Similarity in taxonomic composition of algal or invertebrate communities was determined using the SIMI measure (McIntire & Moore, 1977). SIMI compares two samples and is calculated as:

$$\text{SIMI} = \sum_{i=1}^{n} P_{ih}P_{ik} / \sqrt{\sum_{i=1}^{n} P_{ih}^2} \sqrt{\sum_{i=1}^{n} P_{ik}^2}$$

where P is the proportion of species i of the entire sample, h is the first sample, k is the second sample, and n is the number of species. SIMI values can range from 0 to 1.0, where 0 indicates that two communities have no species in common, and 1.0 indicates that they are identical in both species composition and relative abundance.

Results

Channel experiments

Experiment I. The abundance of benthic algae was inversely related to *Dicosmoecus gilvipes* density after

32 days in the streamside channels (Fig. 1). Regression analysis showed that both algal biomass ($R^2 = 0.58$; $n = 27$; $P < 0.001$) and chlorophyll *a* ($R^2 = 0.18$; $n = 27$; $P < 0.05$) declined significantly with increasing caddisfly density. At caddisfly densities exceeding 24 m^{-2}, there was little additional reduction in algal standing crop.

The density of other benthic invertebrates also declined with increasing *D. gilvipes* density ($R^2 = 0.58$; $n = 9$; $P < 0.05$) (Fig. 1a). Invertebrate density was positively correlated with periphyton biomass in the channels ($r = 0.76$; $n = 9$; $P < 0.05$). Invertebrate densities ranged from about 500 to 7000 m^{-2} and assemblages were dominated by chironomid larvae and, secondarily, by baetid mayflies. These were mostly small individuals that either passed through the inflow screen or developed from eggs laid in the channels.

The abundance of chlorophyll *a* in the channel with no *D. gilvipes* larvae (Fig. 1b) was similar to that in the natural stream (7.30 ± 0.87 mg m^{-2}; $\bar{x} \pm$ SE, $n = 3$). However, biomass in all experimental channels (Fig. 1a) was higher than that observed on the instream tiles (0.29 ± 0.17 g m^{-2}; $\bar{x} \pm$ SE, $n = 3$), probably because the slower current in the channels resulted in greater deposition of fine organic matter than in the stream. Invertebrate density on the instream tiles (4091 m^{-2}; $n = 3$ pooled) was within the range found in the experimental channels, and the natural assemblage also was dominated by small dipterans.

Experiment II. After 26 days in channels stocked with *Ascaphus truei*, algal biomass generally declined with increasing tadpole density ($R^2 = 0.56$; $n = 27$; $P < 0.001$) (Fig. 2a). Benthic chlorophyll *a* also was inversely related to tadpole density ($R^2 = 0.59$; $n = 27$; $P < 0.001$) (Fig. 2b). The decline in algal standing crop was more gradual and variable than for *D. gilvipes*, perhaps indicating patchy feeding by the tadpoles.

As in Experiment I, the density of benthic invertebrates declined significantly with increasing *A. truei* density ($R^2 = 0.50$; $n = 9$; $P < 0.05$) (Fig. 2a).

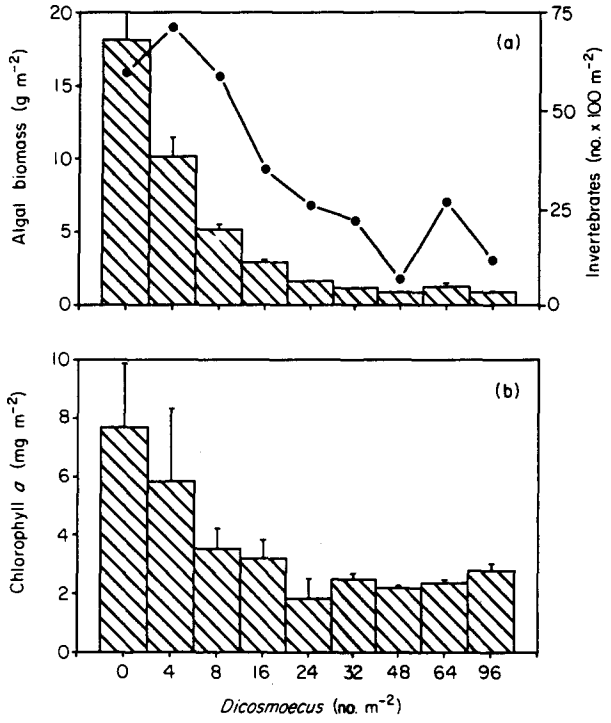

Fig. 1 Results of channel Experiment I. Effects of *Dicosmoecus gilvipes* density on (a) algal biomass as ash-free dry mass ($\bar{x} \pm$ SE; $n = 3$) and total invertebrate numbers ($n = 3$ pooled), and (b) benthic chlorophyll *a* ($\bar{x} \pm$ SE; $n = 3$). If *D. gilvipes* density = *X*, regression equations are: ln AFDM = 2.03 − 0.02*X*; ln Chl *a* = 1.599 − 0.006*X*; ln Inverts = 8.53 − 0.02*X*. ▨, algal biomass or chlorophyll *a*; ●——●, invertebrates.

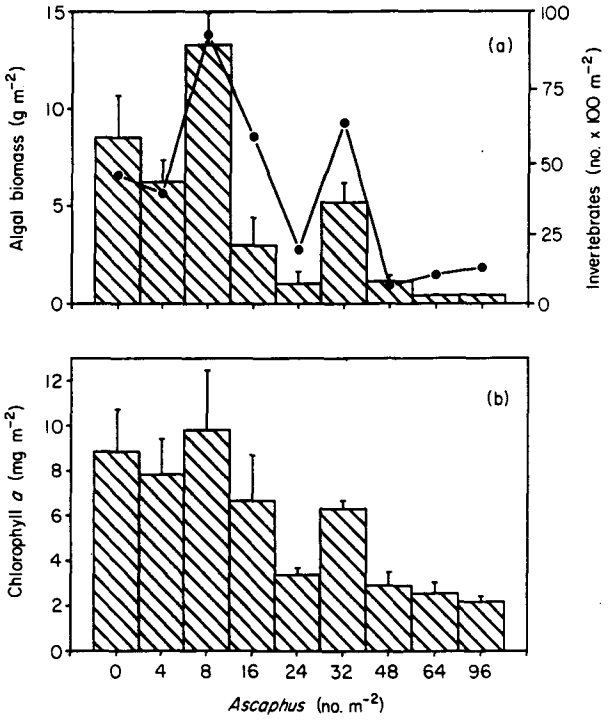

Fig. 2 Results of channel Experiment II. Effects of *Ascaphus truei* density on (a) algal biomass ($\bar{x} \pm$ SE; $n = 3$) and total invertebrate numbers ($n = 3$ pooled), and (b) benthic chlorophyll *a* ($\bar{x} \pm$ SE; $n = 3$). If *A. truei* density = *X*, regression equations are: ln AFDM = 2.02 − 0.02*X*; ln Chl *a* = 2.177 − 0.013*X*; ln Inverts = 8.58 − 0.02*X*. ▨, algal biomass or chlorophyll *a* ●——●, invertebrates.

Invertebrate density was highly correlated with algal biomass ($r = 0.86$; $n = 9$; $P < 0.01$). Invertebrate assemblages also mostly consisted of chironomids and small mayflies.

In-situ experiments

Experiment III. We postulated that algal abundance in the eleven study streams should be negatively related to *A. truei* density. Therefore, differences between platforms (reduced tadpole grazing) and controls (ambient grazing) should be greatest in HWF streams (higher tadpole densities), intermediate in F streams (moderate numbers of tadpoles), and least in NF streams (fewer tadpoles). However, catchment type did not significantly affect platform-control differences for either algal biomass ($F_{2,8} = 1.00$; $P = 0.41$) or chlorophyll *a* ($F_{2,8} = 3.79$; $P = 0.07$) (Fig. 3). High variability was observed among streams within any single catchment type, although forested basins in general had lower algal standing crop than did the other catchments.

Experiment IV. We replicated platforms ($n = 5$) within two streams: one with high average densities of *A. truei* (HWF3) and one with low tadpole densities (NF1). Platform-control differences were significantly different between HWF3 and NF1 for both algal biomass ($F_{1,8} = 6.2$; $P < 0.05$) and chlorophyll *a* ($F_{1,8} = 13.3$; $P < 0.01$). Platforms in HWF3 had about fifty times higher mean algal biomass and about six times greater chlorophyll *a* than did controls after 33 days (Fig. 4). In contrast, platform-control differences for algal biomass and chlorophyll *a* were small in NF1. In general, algal standing crop was about the same on control tiles in the two streams but differed markedly on platforms.

Algal community structure in HWF3 was similar on platform and control tiles (SIMI = 0.74) but not identical. Non-adnate diatoms dominated algal

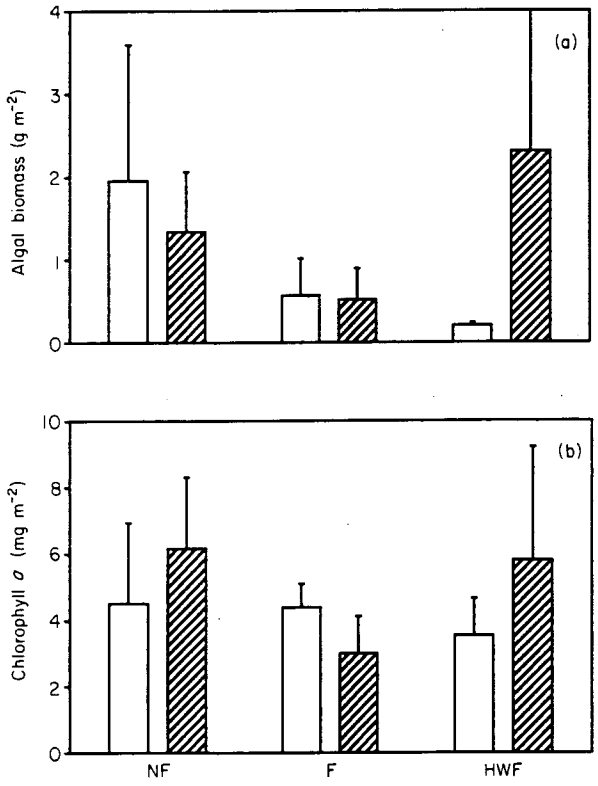

Fig. 3 Results of *in-situ* Experiment III in eleven study streams of the Clearwater Creek drainage having either low *Ascaphus truei* densities (NF; $n = 5$), moderate densities (F; $n = 3$), or high densities (HWF; $n = 3$). Effects of herbivore exclusion are shown on (a) algal biomass ($\bar{x} \pm$ SE; n as above) and (b) benthic chlorophyll *a* ($\bar{x} \pm$ SE; n as above). □, control; ▨, platform.

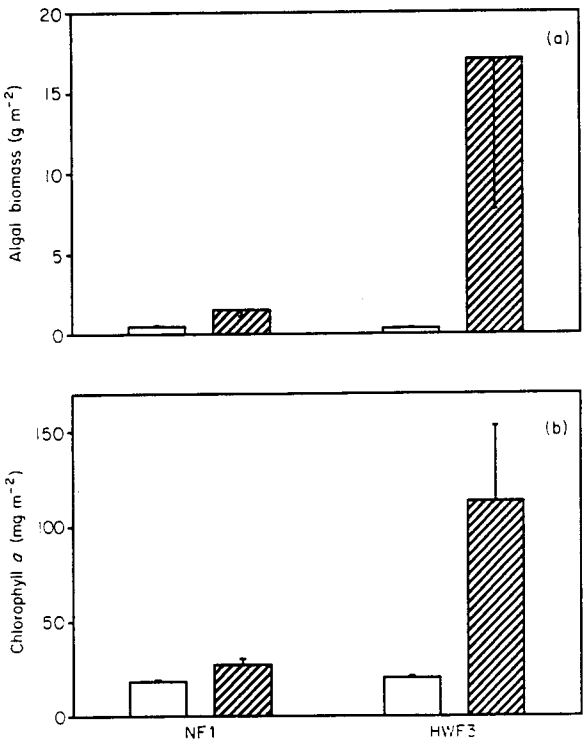

Fig. 4 Results of *in-situ* Experiment IV in two streams having either low (NF1) or high (HWF3) *Ascaphus truei* densities. Effects of herbivore exclusion are shown on (a) algal biomass ($\bar{x} \pm$ SE; $n = 5$) and (b) benthic chlorophyll *a* ($\bar{x} \pm$ SE; $n = 5$). □, control; ▨, platform.

assemblages on both platforms and controls, but platforms supported higher proportions of filamentous green algae, especially *Ulothrix zonata* (Weber & Mohr) Kütz. and *U. tenerrima* Kütz. (Fig. 5a). Algal community structure in NF1 was nearly identical on platform and control tiles (SIMI = 0.99). Small adnate diatoms, particularly *Achnanthes minutissima* Kutz., dominated algal assemblages (>70% of cell numbers), with the remainder consisting of non-adnate diatoms (20%) and small amounts of filamentous green and blue–green algae (Fig. 5b). In comparing the two streams, adnate diatoms were relatively more abundant in NF1, whereas HWF3 had higher proportions of non-adnate diatoms and filamentous green algae.

Platform-control differences in invertebrate density were not significantly different between NF1 and HWF3 ($F_{1,8} = 0.32$; $P = 0.59$). The platforms had little overall effect on the density of smaller invertebrates, although mean invertebrate densities appeared to be higher in NF1 than in HWF3 (Fig. 6). More than fifty invertebrate taxa were collected from each stream but assemblages were dominated (>80%) by chironomid larvae and mayfly nymphs. Herbivores constituted about 40% of the invertebrate assemblage by density in both streams (Fig. 6). In NF1, invertebrate assemblages on platforms were similar to control plots (SIMI = 0.95), whereas in HWF3 assemblages were moderately dissimilar (SIMI = 0.62).

Discussion

Interpretation of experimental results

In combination, results from our four experiments in streams near Mount St Helens demonstrated that large lotic herbivores (*Ascaphus truei* and *Dicosmoecus gilvipes*) can directly affect the local abundance of benthic algae through consumption. Although not conclusive in this study, the large herbivores also may have indirect effects on (i) smaller invertebrates by reducing algal standing crop and (ii) periphyton by reducing the abundances of smaller invertebrates that also use the resource.

The *in-situ* experiments revealed substantial spatial variability in herbivory in natural streams. The results of Experiment III comparing catchments, in particular, were equivocal, apparently due to patchiness in tadpole distribution (Hawkins *et al.*, 1988), experimental limitations (see below), and variation in factors other than tadpole abundance. These factors could include catchment differences in channel stability, substrate composition, hydrology, and water

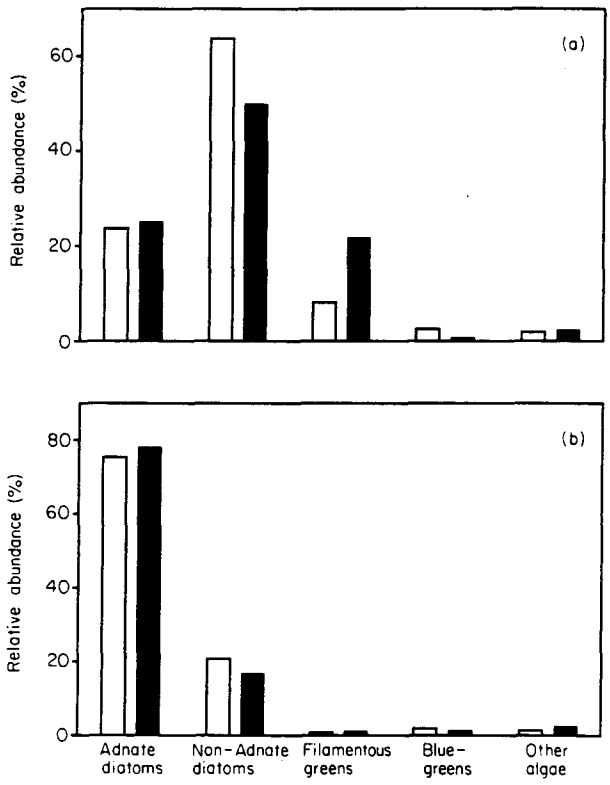

Fig. 5 Relative abundance of algal physiognomic groups, as per cent of total cell numbers, on control and platform tiles from (a) HWF3 and (b) NF1 at the end of *in-situ* Experiment IV. □, control; ■, platform.

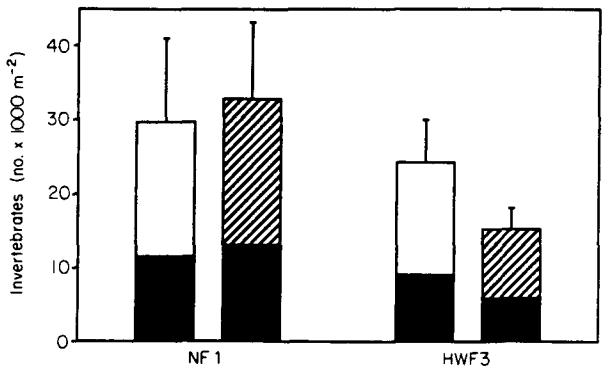

Fig. 6 Invertebrate abundance ($\bar{x} \pm$ SE; $n = 3$) on control and platform tiles from NF1 and HWF3 at the end of *in-situ* Experiment IV. Herbivore proportion of total is indicated by filled bars. □, control; ▨, platform; ■, herbivores.

chemistry that were not measured in this study but can affect plant–herbivore interactions.

Experiment IV was more conclusive, and revealed that at higher densities in HWF3, tadpole grazing was intense enough to significantly reduce algal abundance and possibly invertebrate density. Although algal biomass was also low in NF1, we were unable to detect a grazing effect in that stream. This may be related to differences in herbivore guild composition between NF1 and HWF3. The platform design, while effective for excluding crawling herbivores, does not exclude herbivores that swim or drift readily. Thus, in streams such as NF1 that have high densities of small, mobile invertebrates, platforms can be readily colonized by small herbivores. In these cases, manipulation of grazers with platforms may not be possible, and grazing effects will not be revealed.

Control tiles in HWF3 and NF1 had similar standing crops of periphyton, despite marked differences in herbivore guild composition. This suggests that in the absence of large dominant herbivore, small, less-conspicuous grazers may be equally effective herbivores.

Effectiveness of herbivore exclusions

We assumed that control tiles in the streams received ambient levels of tadpole grazing, whereas the platforms prevented grazing by *Ascaphus truei*. However, no tadpoles were ever collected from either controls or platforms in any stream (including HWF3), nor were tadpoles observed foraging during daylight. Previous observations indicate that *A. truei* tadpoles forage at night on the upper surfaces of rocks (Altig & Brodie, 1972) and inhabit interstitial spaces and rock undersides during the day (Hawkins *et al.*, 1988). On 2 September 1986, we observed 1-m^2 areas surrounding each platform/control set in HWF3 from 1800 to 2400 h using flashlights. Tadpoles were first seen foraging about 1 h after sunset, with activity (and apparent density) further increasing until midnight. Fifty tadpoles in total were observed, of which two were seen on the platforms and forty-eight were observed grazing on control tiles or nearby rock surfaces. The following day, grazing scars left by tadpoles (distinct bands of *c.* 7 mm width) were abundant on control tiles.

There was considerable variation in algal biomass among replicate platforms (note error bars in Fig. 4a). For example, three of the five platforms in HWF3 displayed a strong response to tadpole exclusion (i.e. high algal biomass), whereas two platforms showed a weak response. This disparity may be related to differences in current velocity near the platforms. The two platforms with low algal biomass also had the lowest current velocity (9–12 cm s^{-1}), whereas the three platforms with high algal biomass had higher velocity (25–35 cm s^{-1}). Because *A. truei* tadpoles are not strong swimmers (Altig & Brodie, 1972), it is unlikely they could reach platforms at swifter velocities, but may have reached platforms in slower current. The two tadpoles observed on platforms at night were at lower velocities. Differences in algal biomass probably were not due to velocity alone, as the range in velocity was similar for platforms (7–35 cm s^{-1}) and controls (5–25 cm s^{-1}) in both streams. Thus, tadpole grazing may more strongly affect algal biomass than our results suggest, due to limitations in our ability to exclude tadpoles.

Role of large herbivores in stream succession

In some ecosystems, the activities of dominant consumers ('strong interactors') can strongly influence community structure and ecological succession (Paine, 1980). Stream herbivores, as a guild (*sensu* Root, 1967), can influence the biomass, metabolism, physiognomy, and taxonomic composition of periphyton (see reviews by Gregory 1983; Lamberti & Moore, 1984). Some investigators have suggested that, within guilds, large lotic herbivores most strongly influence benthic structure (Hawkins & Furnish, 1987; Power & Matthews, 1983), whereas others postulate that frequent disturbance by floods may prevent the establishment of dominant populations (Minshall, 1988; Townsend, 1989).

Our research at Mount St Helens suggests that *A. truei*, and possibly *D. gilvipes*, can alter the abundance of benthic algae and potentially compete with other herbivores. Tadpoles are generally not regarded as ecologically important organisms in streams, even though they are known to influence the abundance and composition of attached algae in ponds and lakes (Dickman, 1968; Osborne & McLachlan, 1985). In some Mount St Helens streams, *A. truei* tadpoles may function as dominant herbivores. They appear particularly important in small streams that retained patches of headwater forest, which may have served

as refugia after the eruption and as sources for downstream dispersal of tadpoles.

D. gilvipes larvae typically inhabit larger, lower-gradient streams than do *A. truei* tadpoles (Lamberti & Resh, 1979; Hart, 1981). Although larvae presently are not abundant in the main stem of Clearwater Creek, we suspect they will eventually become important herbivores in that stream. Anderson & Wisseman (1987) speculate that continued stream bed instability may be responsible for low overall caddisfly densities in Clearwater Creek. If *D. gilvipes* densities increase in Clearwater Creek, we predict they will exert considerable grazing pressure during spring and early summer (see Lamberti *et al.*, 1987).

Stream ecosystem recovery at Mount St Helens

Most natural disturbances in streams (e.g. floods, drought) are non-catastrophic (Resh *et al.*, 1988), and their effects are usually short-lived (Gray & Fisher, 1981; Fisher *et al.*, 1982; McElravy, Lamberti & Resh, 1989). In contrast, we known relatively little about biotic responses to natural catastrophic disturbance, particularly where basin-wide patterns of geomorphology and vegetation are altered substantially. At Mount St Helens, streams were part of an abrupt, cataclysmic landscape disturbance. Current ecological processes must be viewed within the context of an actively recovering landscape.

Undisturbed habitats at Mount St Helens potentially served as refugia for lotic organisms, providing colonists for disturbed habitats. Organisms with high mobility (e.g. sloughed algal cells, drifting macroinvertebrates, aerial adults, swimming vertebrates) were probably favoured in succession. Of these, herbivores may have been particularly important in stream succession because of other trophic responses (e.g. high primary production) that favoured their recovery.

As streams recover from the volcanic eruption, large lotic herbivores that survived the eruption (e.g. *A. truei*) and small invertebrates that dispersed readily (e.g. drifting insects, ovipositing adults) both potentially have been important in regulating the accumulation of benthic algae. Where abundant, large herbivores such as *A. truei* tadpoles may reduce the standing crop of algae and density of small invertebrates. However, the influence of large herbivores on benthic communities appears to vary spatially in relation to stream disturbance history, local environmental factors, and abundances of those herbivores. The eruption of Mount St Helens is providing unique opportunities to examine attributes of herbivory and other stream ecosystem processes in a naturally disturbed landscape.

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