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Source: *Oikos*, Vol. 80, No. 3, (Dec., 1997), pp. 499-508

Published by: Blackwell Publishing on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.org/stable/3546623>

Accessed: 16/06/2008 18:30

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Primary productivity and trophic dynamics investigated in a North Derbyshire, UK, dale

Lauchlan H. Fraser and J. Philip Grime

Fraser, L. H. and Grime, J. P. 1997. Primary productivity and trophic dynamics investigated in a North Derbyshire, UK, dale. – *Oikos* 80: 499–508.

Trophic interactions were investigated on herbaceous communities in a limestone dale in Northern England. Manipulative experiments involved the application of molluscicides and foliar and soil insecticides along natural productivity gradients. The results supported the theories of Fretwell and Oksanen in which trophic dynamics are predicted to be dependent upon primary productivity. Furthermore, the results extend the Fretwell–Oksanen model by the inclusion of invertebrates, and the applicability of the model to the small, individual habitat scale. At very low productivity, the vegetation was dominated by slow-growing, unpalatable species and did not experience a detectable amount of herbivory. In circumstances of high productivity, ‘top-down’ control of herbivores by carnivores appeared to protect the resident fast-growing and relatively palatable perennials from herbivory. Vegetation of intermediate productivity responded strongly to the removal of herbivores; here we conclude that herbivore pressure is high because productivity is insufficient to sustain a high intensity of ‘top-down’ control from carnivores.

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Until recently the two dominant theories on trophic interactions have been based on whether the primary control is by resources (‘bottom-up’ forces) or predators (‘top-down’ forces). The proponents of the ‘bottom-up’ view believe that organisms at each trophic level are food-limited (White 1978). The ‘top-down’ view counters that organisms at the top of food chains are food limited, while at successive lower levels, they are alternately predator-, then food-limited (Hairston et al. 1960, Menge and Sutherland 1976). Early discussions weighing the merits of ‘top-down’ and ‘bottom-up’ explanations of trophic interactions in ecosystems have been modified by the recognition that, first, both mechanisms occur in nature (Power 1992) and, second, they vary in relative importance from place to place (White 1993). A crucial further step has been the proposal that the importance of top-down control increases in direct proportion to primary productivity

(Fretwell 1977, 1987, Oksanen et al. 1981, Oksanen 1990a, b). The work described in this paper seeks to re-examine this revised hypothesis by conducting an experiment along a productivity gradient in one of the Derbyshire Dales of Northern England.

A conspicuous feature of many of the limestone dales (valleys) of North Derbyshire is a mosaic of herbaceous communities varying in productivity from sparsely vegetated rock outcrops to tall herb communities on deep colluvial soils (Balme 1953, Pigott and Taylor 1964, Grime and Blythe 1969, Lloyd et al. 1971, Grime and Curtis 1976). Laboratory screening experiments have revealed that these local gradients of increasing productivity coincide with increasing vegetation height and potential growth rates in component plant species (Grime and Hunt 1975). They are also associated with a marked decline in the effectiveness of plant defences against generalist invertebrate herbivores (Grime et al.

Accepted 21 May 1997

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ISSN 0030-1299

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1968, 1996). These results suggest that different mechanisms may be involved in the persistence of the plant communities at opposite ends of the productivity gradients. A manipulative field experiment was therefore conducted to test the hypothesis of Fretwell and Ok-
sanen that with increasing productivity there is a shift from direct plant defence (low palatability) to indirect facilitation of plants by carnivores (top-down control).

Methods

Experimental site

The experiment was undertaken in Tideswell Dale, an unmanaged limestone dale typical of a kind found widely on the carboniferous limestone of North Derbyshire (Balme 1953, Pigott and Taylor 1964, Grime and Blythe 1969, Lloyd et al. 1971, Grime and Curtis 1976). Six different sites described in Table 1 were selected ranging from low to high productivity ecosystems. Table 1 also provides detailed species lists and abundances for the sites. All were no further than 500 m from each other and with the exception of the *Petasites hybridus* community, which was separated from the other sites by a footpath, formed elements of the same complex mosaic. Consistent with theories on the relation between diversity and productivity (Grime 1973a, b, Connell 1978) species richness reached a maximum in the middle of the productivity gradient, at sites 3 and 4. The proximity of each of the experimental sites suggested that animals could move readily between them.

Experimental design

With the exception of the *Sedum acre* communities, sampled areas of which were 0.2 m², each experimental plot comprised 0.5 m². Within each of the six sites, ten pairs of experimental plots were established, thus creating a total of 120 plots. In each of the pairings, one of the plots was left undisturbed as a control while the other was treated with pesticides. Every two weeks beginning May 1995, 5 g of systemic below-ground insecticide (Bio Chlorophos; active ingredients chlorpyrifos and diazinon) and 100 ml of a systemic above-ground insecticide (Bio Long-Last; active ingredients dimethoate and permethrin) were applied to each of the ten 0.5-m² plots within each site until the final harvest in September 1995. The pesticides were applied between 0400 h and 0600 h when winds were low. The pesticides were tested independently for possible stimulatory or phytotoxic effects on five of the dominant plants occurring within the study sites (Fraser 1996). It was found that the pesticides were lightly phytotoxic, but this result was only significant for one plant species (*Urtica dioica*).

The experiment commenced in May 1995 and ran for four months, ending in September. From each of the 0.5-m² experimental plots, a 0.2-m² area was harvested, except for site 1, the *Sedum acre* community, where only 0.05-m² samples of vegetation were removed. The above-ground vegetation was sorted into species, dried at 80°C, and weighed.

In August, two probes were placed in each of the control plots to estimate, respectively, herbivore and carnivore activity within the six sites. The first probe consisted of organically grown leaves of lettuce cut into discs with a diameter of 20 mm. One wet lettuce disc in a shallow-sided Petri dish was placed in each of the 60 control plots in the late afternoon and collected the next morning. The percentage of each disc consumed was recorded. The second probe involved ten blow-fly maggots occupying an open Petri dish; these were also placed in each of the 60 control plots and collected the next morning. The numbers of maggots missing, presumed eaten, were recorded. Independent tests showed that the maggots were not able to escape from the Petri dishes.

Analysis

In order to determine the overall effect of herbivore removal in each site, an analysis of variance was conducted using the total above-ground plant biomass recorded in each plot. The analysis examined the importance of both pesticide treatment and site productivity. The variance was tested and found to be normal and homogeneous using Bartlett's test (Wilkinson 1990). Tukey's Honestly Significant Difference test was used to separate treatment means and the 95% confidence limits were calculated for each mean. For each plant species the change in biomass mediated by the removal of herbivores was calculated and for each site the species were ranked in order of decreasing benefit from pesticide treatment. This allowed a determination of which species profited and which suffered by the removal of herbivores.

For many of the species, especially those in the low-nutrient grassland communities in the middle of the productivity gradient, laboratory measurements of maximum relative growth rate were available (Grime and Hunt 1975); these were used in a linear regression model to determine the extent to which this parameter can be a predictor of response to the removal of herbivores. The final analysis regarding the above-ground vegetation involved, for all six sites, plotting the percentage change in total biomass against a productivity index. The percentage change in biomass resulting from the removal of herbivores was calculated for each pairing of plots and 95% confidence limits were calculated for each site. Specific leaf area and canopy height were the characteristics used as indicators of productiv-

Table 1. Lists of species in each site and their percentage abundance, which was measured as the mean dry shoot biomass harvested from ten 0.2-m² control plots. Canopy height (can ht) and specific leaf area (sla) taken from FIBS.

site 1	% abundance	can ht	sla	site 2	% abundance	can ht	sla
<i>Sedum acre</i>	100	1	11.9	<i>Festuca ovina</i>	90.3	2	10.4
				<i>Solidago virgaurea</i>	8.1	3	14.4
				<i>Achillea millefolium</i>	0.1	2	11.2
				<i>Heiracium</i> sp.	0.1	–	–
site 3	% abundance	can ht	sla	site 4	% abundance	can ht	sla
<i>Centaurea nigra</i>	23.4	3	21.9	<i>Brachypodium sylvaticum</i>	19.7	3	–
<i>Betonica officinalis</i>	20.6	1	16.1	<i>Arrhenatherum elatius</i>	15.6	5	31.3
<i>Arrhenatherum elatius</i>	14	5	31.3	<i>Plantago major</i>	11	2	18.4
<i>Potentilla erecta</i>	8.8	2	22.7	<i>Origanum vulgare</i>	8.2	4	15.7
<i>Serratula tinctoria</i>	5.5	3	14.2	<i>Centaurea nigra</i>	7.6	3	21.9
<i>Brachypodium sylvaticum</i>	5.0	3	–	<i>Stachys officinalis</i>	6.7	1	16.1
<i>Plantago major</i>	3.7	2	18.4	<i>Dactylis glomerata</i>	6.1	3	24.0
<i>Achillea millefolium</i>	2.6	2	11.2	<i>Galium verum</i>	5.3	2	13.4
<i>Teucrium scorodonia</i>	2.6	3	13.5	<i>Lotus corniculatus</i>	4.8	2	19.7
<i>Festuca ovina</i>	2.6	2	10.4	<i>Agrostis capillaris</i>	4.6	2	28.7
<i>Viola riviniana</i>	2.3	2	–	<i>Hypericum hirsutum</i>	2.7	4	–
<i>Valeriana officinalis</i>	1.6	3	–	<i>Mercurialis perennis</i>	2.1	3	–
<i>Agrostis capillaris</i>	1.3	2	28.7	<i>Carex flacca</i>	1.8	2	15.6
<i>Mercurialis perennis</i>	1.1	3	–	<i>Viola riviniana</i>	1.4	2	–
<i>Hypericum perforatum</i>	1.0	3	16.4	<i>Valeriana officinalis</i>	0.9	3	–
<i>Hypericum hirsutum</i>	0.8	4	–	<i>Angelica sylvestris</i>	0.6	3	–
<i>Lathyrus pratensis</i>	0.7	4	19.6	<i>Hypericum perforatum</i>	0.4	3	16.4
<i>Luzula pilosa</i>	0.5	1	–	<i>Anthoxanthum odoratum</i>	0.3	2	23.4
<i>Helictotrichon pratense</i>	0.4	2	9.8	<i>Festuca rubra</i>	0.2	2	37.2
<i>Briza media</i>	0.4	1	19.9	<i>Achillea millefolium</i>	0.1	2	11.2
<i>Plantago lanceolata</i>	0.3	2	19.9	<i>Leontodon hispidus</i>	0.1	2	23.9
<i>Lotus corniculatus</i>	0.2	2	19.7	<i>Festuca ovina</i>	0.1	2	10.4
<i>Trisetum flavescens</i>	0.2	2	21.0				
<i>Campanula rotundifolia</i>	0.2	2	20.2				
<i>Hieracium</i> sp.	0.1	–	–				
<i>Carex flacca</i>	0.1	2	15.6				
<i>Leontodon hispidus</i>	0.1	2	23.9				
site 5	% abundance	can ht	sla	site 6	% abundance	can ht	sla
<i>Urtica dioica</i>	100	5	21.3	<i>Petasites hybridus</i>	100	5	24.5

ity and were taken from FIBS (Functional Interpretation of Botanical Surveys), a comprehensive, unpublished database assembled by the Unit of Comparative Plant Ecology (UCPE), Sheffield, England. Specific leaf area was chosen because it is the most easily measured of a number of important structural and functional characteristics including net photosynthetic capacity, growth rate, leaf life-span and toughness which are strongly correlated with habitat productivity and the capacity for rapid growth (Reich et al. 1992, Reich 1993, van Arendonk and Poorter 1994). It is argued that in productive ecosystems plants can maximise their photosynthetic potential by rapidly producing thin, short-lived leaves with high nitrogen concentration and high specific leaf area, while in unproductive habitats leaves tend to be tough and long-lived with a low specific leaf area (Coley et al. 1985, Reich et al. 1991, 1992). Specific leaf area does show some variation in

response to habitat conditions, but despite this plasticity it can be effectively used to distinguish between productive and unproductive habitats (Reich et al. 1992, Reich 1993). Specific leaf area as an indicator of growth rate combined with canopy height gives a useful index of above-ground competitive ability and habitat productivity. The approach to define a ready index of competitive ability has been employed before but with the addition of lateral spread (Grime 1973a, b, 1974). The mean specific leaf area and mean canopy height were calculated for each site and corrected so that they were equally weighted. The corrected mean specific leaf area and canopy height were added and divided by two to provide a value intended to reflect the productivity of each site. Table 1 lists the known canopy height and specific leaf area measurements for each species whilst Table 2 provides the productivity indices calculated for each site.

Table 2. Productivity index = corrected mean specific leaf area (sla) + corrected mean canopy height (can ht)/2. See Table 1 for the composition of species in each site.

	mean sla	corr sla	mean can ht	corr can ht	productivity index
Site 1	11.9	48.6	1.0	20	34.3
Site 2	10.4	42.4	2.0	40	41.2
Site 3	19.2	78.4	2.4	48	63.2
Site 4	20.4	83.3	2.6	52	67.7
Site 5	21.3	86.9	5.0	100	93.5
Site 6	24.5	100.0	5.0	100	100.0

Results

Plant community response to treatments

The pesticide treatment brought about changes in shoot biomass and species relative abundance (Table 3) but these were confined to two of the experimental sites. Site 3 and site 4, the two grassland communities, were the only sites that showed statistically significant change in total above-ground vegetation as a consequence of the application of pesticides (Fig. 1). The mean total above-ground biomass of site 3 was virtually doubled (5.10 g to 9.90 g) and that of site 4, increased from 9.21 g to 14.12 g with the addition of pesticides. Sites 1, 2, 5 and 6 showed no consistent change in above-ground biomass between pesticide treatment and the control. Three of these unresponsive sites (1, 5 and 6) were monospecific stands (Table 1) and even in site 2 which contained four species, *Festuca ovina* contributed the vast majority (90.3%) of the shoot biomass.

Sites 3 and 4 were relatively diverse plant communities, allowing calculations to be made of individual species responses to the addition of pesticides (Fig. 2). In both sites, most species became more abundant in the pesticide treated plots. However, some species were suppressed and in certain cases, e.g. *Brachypodium sylvaticum* and *Mercurialis perennis*, the species responded differently at the two sites. *Brachypodium sylvaticum* increased in mean shoot biomass in site 3 when herbivores were removed but decreased in site 4. *Mercurialis perennis* had the opposite response to *B. sylvaticum*, decreasing in site 3 and increasing in site 4.

The species for which maximum relative growth rates (R_{\max}) were known (Grime and Hunt 1975) were plotted against the change in biomass mediated by the removal of herbivores in sites 3 and 4 (Fig. 3). A linear regression analysis for site 3 showed that for this population 46.6% of the variation in the change in biomass could be accounted for by R_{\max} (Table 4). Those species that have a high R_{\max} (e.g. *Plantago major* and *Arrhenatherum elatius*) became relatively more abundant when herbivores were removed. Site 4 did not show a significant relationship between the R_{\max} values and the change in biomass in component species (Table 4).

For each site, the mean percentage change in total shoot biomass resulting from removal of herbivores was calculated and plotted against the productivity index (Fig. 4). The two sites with the lowest productivity indices (sites 1 and 2), and the two sites with the highest productivity indices (sites 5 and 6) showed no statistically significant change in total biomass with the addition of pesticides. The sites with intermediate productivity indices (sites 3 and 4) exhibited relatively large changes. In consequence, the resulting plotted curve has a characteristic humped-back shape.

Herbivore and carnivore activity in each site

Consumption of lettuce discs and maggots showed a positive correlation with increasing productivity in the part of the gradient corresponding to sites 1, 2, 3 and 4 (Fig. 5). As productivity increased further, the amount of maggots eaten continued to increase, and at sites 5 and 6, approximately 9 out of 10 maggots disappeared overnight. However, this pattern was not observed with respect to the lettuce discs; here there was a dramatic decrease in consumption at the two sites with the highest productivity.

Discussion

Fretwell and Oksanen suggest that the dynamics of trophic interactions are dependent on the productivity of the plant community through its controlling effect on the length of food chains (Fretwell 1977, 1988, Oksanen et al. 1981, Oksanen 1990a, b). At extremely low productivity levels these authors contend that there is not enough food to sustain a second or a third trophic level. Under these conditions plant growth and nutritional quality are limited and regulation of animal biomass is severe and 'bottom-up'. Environments with intermediate productivity levels are predicted to contain sufficient palatable material to sustain herbivores but these are not so abundant that a large third trophic level of carnivores or parasitoids can be supported; here again, therefore, the control of the trophic structure and dynamics is resource driven (bottom-up) from the point of view of the herbivores. At higher productivity, how-

Table 3. Results of 2-way ANOVA examining the effects of the pesticide treatments (PESTS) within the site treatments (SITE) on the mean above-ground plant biomass. This table presents the sum of squares (SS), degrees of freedom (d.f.), mean squares (MS), *F*-ratios, and *p*-values (*p*).

Source of variation	SS	d.f.	MS	<i>F</i> -ratio	<i>p</i>
SITE	8477.85	5	1695.57	241.78	<0.001
PEST	92.48	1	92.48	13.19	<0.001
SITE × PEST	146.23	5	29.25	4.17	0.002
ERROR	757.40	108	7.01		

ever, it is proposed that plant production can sustain and support at least three trophic levels; this brings in train the possibility for 'top-down' control of herbivores and restriction of their impact on primary productivity and vegetation composition.

To accept that the evidence presented in this paper supports Fretwell and Oksanen's theory of trophic interactions, we would expect five specific results from our herbivore removal experiment.

1. Little change in total above-ground biomass in sites of low productivity following the removal of herbivores.
2. A significant increase in total above-ground biomass in sites of intermediate productivity following the removal of herbivores.
3. Little change in total above-ground biomass in sites of high productivity following the removal of herbivores.
4. Increasing herbivore activity, estimated by lettuce disc bioassay, from low to intermediate productivity sites, but very little herbivore activity at the high productivity sites.
5. Little carnivore activity at the low and intermediate productivity sites, but high carnivore activity at high productivity.

The results of the experiment meet all five of these conditions and thus provide strong support for Fretwell

and Oksanen's theory. Although we do not know which herbivores, carnivores and parasitoids were important in each site, the lettuce disc and maggot bioassays provide further evidence of differences in the intensity of herbivory and carnivory along the productivity gradient. Furthermore the patterns in the activity of herbivores and carnivores conformed to those predicted by the Fretwell and Oksanen theory. At low productivity there was little activity, presumably because plant communities at low productivity have low and unpalatable biomass and cannot sustain the second and third trophic levels. The herbivore activity that was recorded may well have been caused by foraging herbivores exported from higher to lower productivity communities (Pimm 1982, Holt 1985, Pimm and Kitching 1987, Oksanen 1990c, Wootton and Power 1993). At intermediate productivity it appears that there was an increase in the activities of herbivores and carnivores compared to those occurring at the low productivity sites. The increase was minimal for carnivores, but herbivore activity increased considerably as productivity increased. This result agrees with the phenomenon termed the 'Paradox of Enrichment' by Rosenzweig (1971) where increased primary productivity only increases the densities of herbivores until primary productivity is high enough to support carnivores. At high productivity positions on the Tideswell Dale gradient carnivore activity, as reflected in the removal of maggots, was very high and herbivore activity was minimal, again suggesting 'top-down' control. Caution must be used before claiming that lettuce disc and maggot bioassays unlock the complex workings of an ecosystem, but their use has provided a tentative basis for inferring changing activities of both herbivores and carnivores along the productivity gradient.

Interestingly, Oksanen (see Oksanen 1990a, Oksanen et al. 1992) restricted the model to mammals only, not invertebrates. Since invertebrates were probably the main herbivores in Tideswell Dale, and possibly the main carnivores, the Fretwell–Oksanen model can be extended to invertebrates as well. A further extension of the original Fretwell–Oksanen model is the scale in which trophic dynamics operate. Spatial scale has been explored in other studies related to the Fretwell–Oksanen model (Oksanen 1990c, Oksanen et al. 1992) but there has been no experimental evidence to support the 'exploitation model'. In these papers, the 'spill-over'

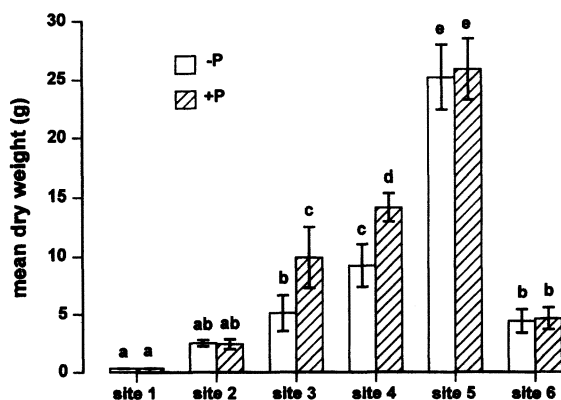


Fig. 1. Effect of pesticide (P) treatment (– absent, + present) on the mean total shoot biomass (g) at each of the six sites. See Table 1 for the composition of species in each site. Error bars represent 95% confidence limits. Bars sharing the same letter are not significantly different (Tukey's HSD).

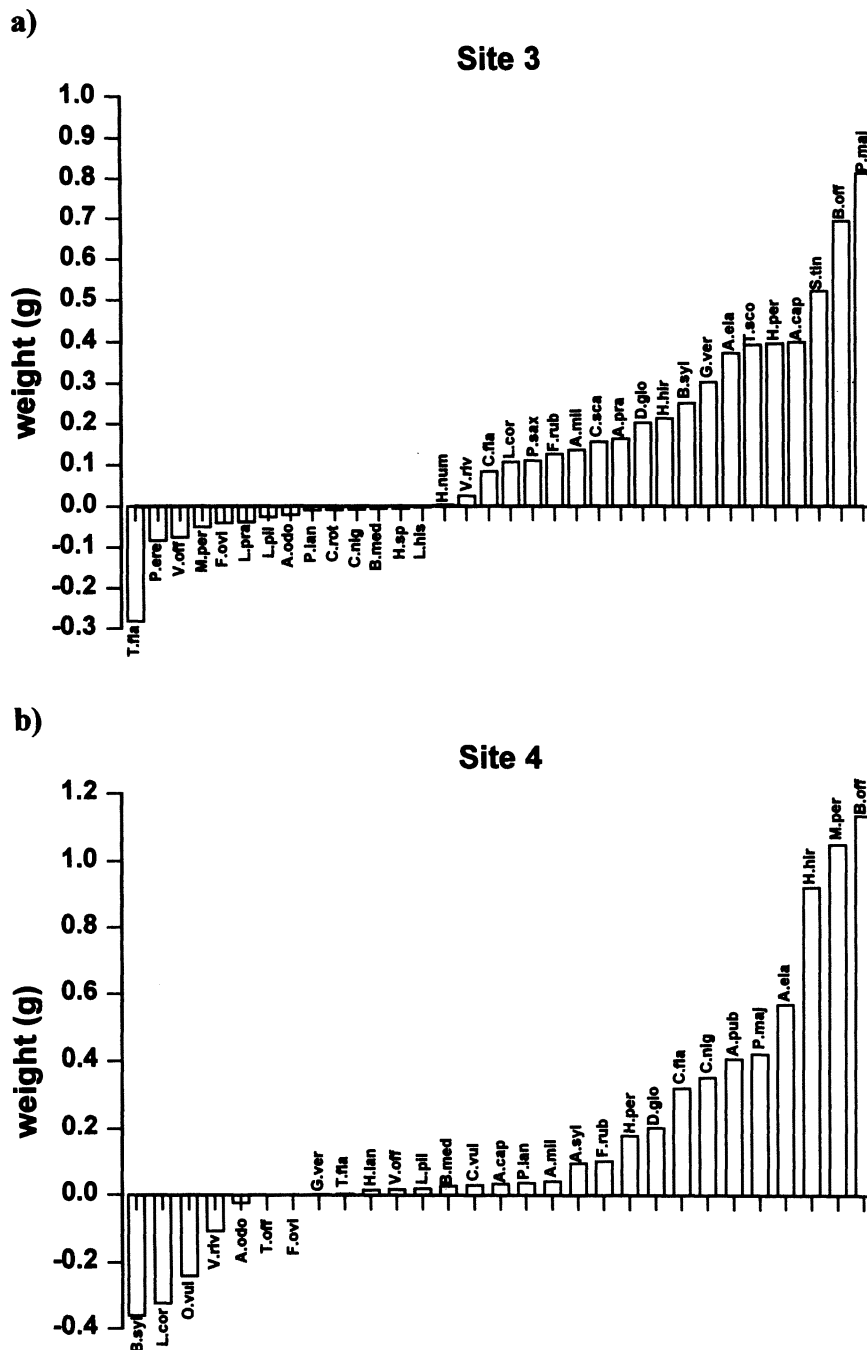


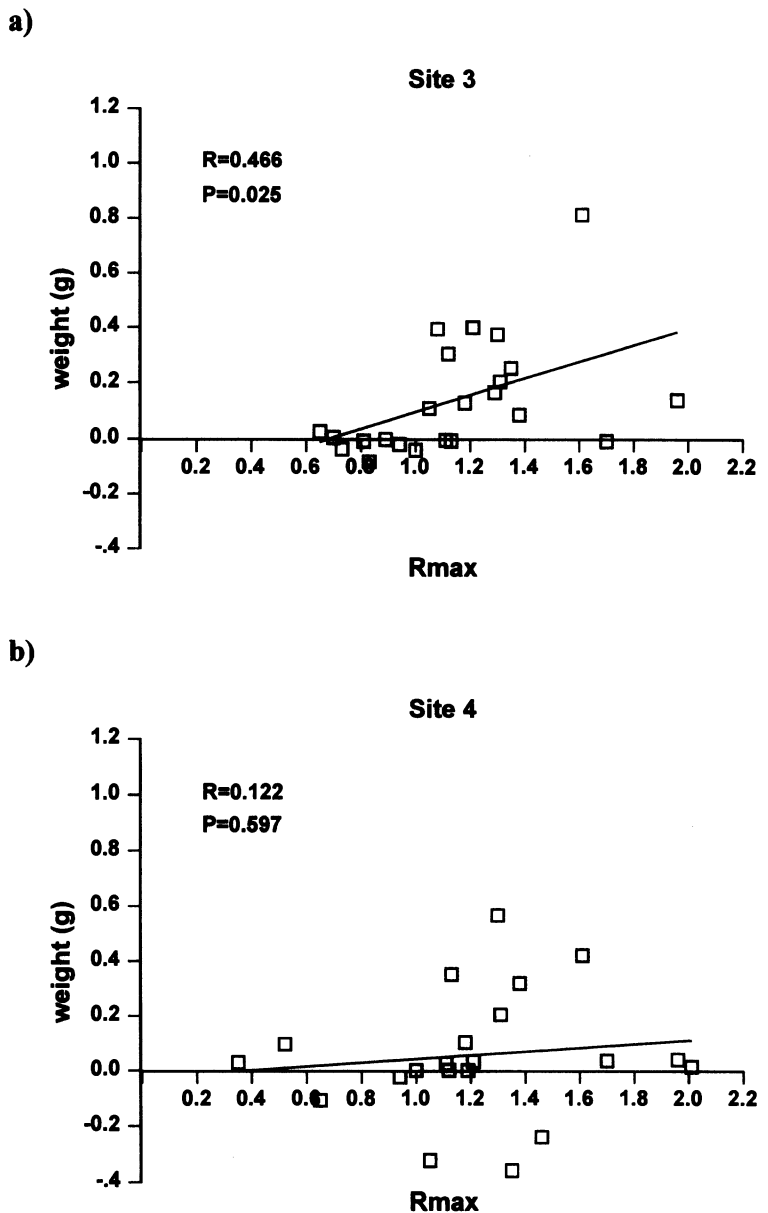
Fig. 2. Ranking of the mean change in shoot biomass (g) mediated by the pesticide treatment for each species found in, (a) site 3 and (b) site 4.

effect of predators (herbivores and carnivores) from productive sites exploiting less productive, barren sites was explored. It was found that patch size and configuration have a significant influence on trophic dynamics. For example, where productive habitats are dominant in a landscape consisting of productive and unproductive habitats, predators tend to 'spill-over' from productive habitats and exploit the less productive habitats

(Oksanen 1990c, Oksanen et al. 1992). However, they conclude that this model is mainly applicable only at the landscape scale (Oksanen et al. 1992). Our experimental study suggests that 'spill-over' may also occur at the smaller scale that is associated with the individual habitats.

The results from the Tideswell Dale experiment are summarised as a simple model (Fig. 6) predicting the

Fig. 3. Relationship between the mean change in shoot biomass and the maximum relative growth rate (R_{max}) for, (a) site 3 and (b) site 4. See Table 1 for the species composition in each site.



changing densities of herbivores and carnivores along a gradient in productivity. Numbers of herbivores increases from low productivity (I) and reaches a peak at intermediate productivity (II). It is proposed that at high productivity (III) herbivore numbers are small and limited by a relatively large number of carnivores and parasitoids (i.e. top-down control); here detritivores are included with the herbivores as a possible extra food source increasing at high productivity and sustaining the carnivore population.

In view of the evidence of the restricted activity of herbivores it is necessary to consider how the carnivores are supported in the high productivity sites. At least two possible answers can be proposed. These are not necessarily independent or mutually exclusive. The first

is that the herbivores present in the productive vegetation have high turnover rates. According to this theory the total numbers of herbivores detected at any one time may be low because of carnivory, but the gross output of herbivores is high and therefore able to sustain the carnivores. A similar situation was reported off the south-west coast of South Africa (Bosman and Hockey 1986, 1988a, b). Here guano-enriched rocky shores provide an ideal environment for profuse algal growth, and, consequently, the herbivorous limpets (*Patella granularis*) that feed on the algae also achieve high rates of growth. However, the limpets never reach a large population size because they are controlled by, and support, large colonies of African black oystercatchers (*Haematopus moquini*). On neighbouring im-

Table 4. Results of linear regression models examining the interaction between the response of plant species change to pesticide treatments and the maximum relative growth rate for sites 3 and 4. This table presents the sum of squares (SS), degrees of freedom (d.f.), mean squares (MS), *F*-ratios, and *p*-values (*p*).

Source of variation	Dependent variable Site 3					Site 4				
	SS	d.f.	MS	<i>F</i> -ratio	<i>p</i>	SS	d.f.	MS	<i>F</i> -ratio	<i>p</i>
regression	0.21	1	0.21	5.83	0.025	0.02	1	0.02	0.29	0.597
residual	0.75	21	0.04			1.02	19	0.05		

poverished mainland shores the growth of algae is slow and sparse, yet there are more limpets. In marked contrast the limpets found on the enriched island shores grow larger and faster and have many more offspring. A problem in drawing a parallel between the alga–limpet–oystercatcher system and that prevailing at the high productivity sites in Tideswell Dale arises from the failure to detect significant evidence of herbivory on the dominant plant species *Urtica dioica* and *Petasites hybridus*. These plants achieved a large size and showed little evidence of damage by herbivores. However, the possibility must be considered that the herbivores relied upon methods of feeding (e.g. sap-sucking above or below ground) which were cryptic and were continuously compensated by increased resource capture by the host plants. If this were the case, herbivore numbers could conceivably be no lower than herbivore numbers found in low productive environments that were free from top-down control. The difference between the plants growing in the high and low productive environments is their response to herbivory: plants adapted to high productive communities have high growth rates which allow them to quickly recover from herbivore damage; while plants adapted to low productive envi-

ronments are slow-growers and are therefore more sensitive to the effects of herbivory (Grime 1979, Coley et al. 1985).

The alternative explanation is that the carnivores are supported by a detritivore community large enough to sustain high numbers of carnivores which in turn would suppress the herbivores. A dramatic example of detritivores sustaining carnivores is found on small, poorly vegetated islands in the Gulf of California (Polis and Hurd 1995). Polis and Hurd (1995) found remarkably high spider densities, which they related directly to high rates of carrion drifting in from the ocean, and the subsequent large populations of detritivores associated with the carrion. A similar scenario is feasible in Tideswell Dale. Plants adapted to growing in highly fertile soils have palatable, easily decomposable litter compared to plants adapted to less fertile soils (Cornelissen 1996). It has been suggested that palatable litter is an inevitable consequence of the weak defences of the living leaves of plants exploiting fertile soils (Grime and Anderson 1986, Grime et al. 1997a). However, it remains possible that such a relationship could arise also from an evolutionary feedback in which plants growing in highly fertile sites have responded to

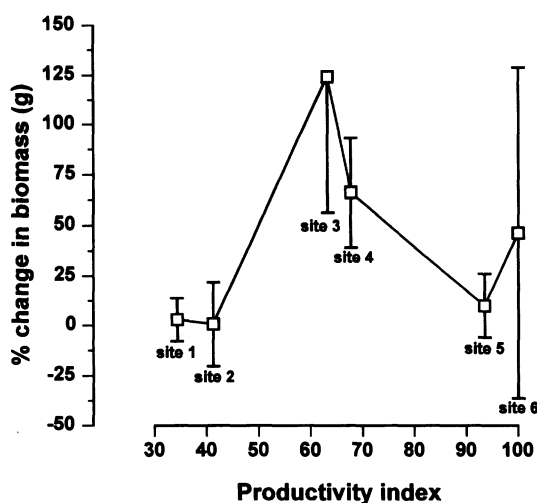


Fig. 4. Effects of the pesticide treatment on the mean percentage change in shoot biomass (g) for all six sites investigated at Tideswell Dale. Table 1 lists the composition of species in each site. Error bars represent 95% confidence limits.

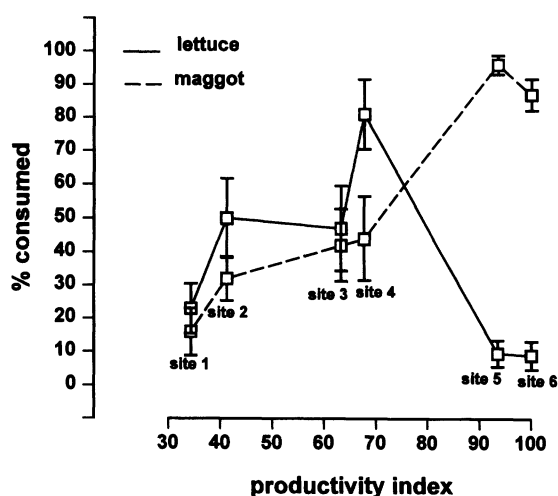


Fig. 5. Mean percentage of lettuce and maggots consumed at each of the six sites at Tideswell Dale. Table 1 lists the composition of species in each site. Error bars represent 95% confidence limits.

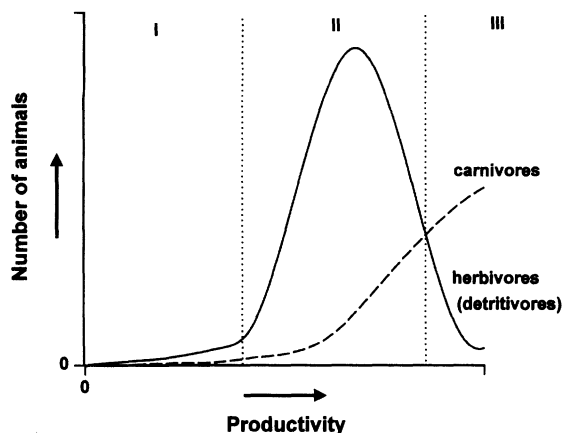


Fig. 6. Tideswell Dale trophic dynamic model illustrating the Fretwell–Oksanen theory on the interaction between trophic dynamics and primary productivity. In the figure I, II, and III represent, respectively, areas of low, intermediate and high productivity.

selection by producing copious palatable and easily decomposable litter which in turn would encourage a large detritivore population capable of supporting carnivores. In effect, this would then protect those plants by providing a large food source for a high number of carnivores, assuming of course, that the carnivores feeding on detritivores also feed on herbivores.

Acknowledgements – We wish to thank L. Oksanen, M. J. Crawley and J. G. Hodgson for their helpful comments. This research was supported by the National Environment Research Council, and a Univ. of Sheffield post-graduate scholarship to L.H.F.

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