

Short communication

The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: evidence from decomposer food-webs

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Received: 31 August 1992 / Accepted: 2 November 1992

Abstract. The relative importance of predation and competition (resource limitation) in influencing the components of a below-ground food-web consisting of three trophic levels (bacteria and fungi; bacterial-feeding and fungal-feeding nematodes; and top predatory nematodes) was estimated using microbial biomass and nematode frequency data collected throughout a 1-year period in two agro-ecosystems. The study suggested that bacterial and fungal biomass were likely to be regulated by grazing and competition respectively, and that these differences were likely to be attributed to the biological (probably morphological) differences between bacteria and fungi, in contrast to the predictions of the hypothesis of Hairston et al. (1960). Top predatory nematodes were sometimes strongly related to the microbial but not microbial-feeding trophic levels, indicating that microbial biomass may directly influence top predator numbers, and that the intermediate level may simply serve as a conduit by which resources pass from the bottom to top trophic levels. This study also suggests that the detritus food-web acts as two distinct (bacterial- and fungal-based) compartments.

Key words: Competition – Detritus food web – Microbial biomass – Nematode – Predation

The relative importance of predation and competition as regulatory forces in above-ground (plant-based) food-webs has been intensively studied (Schoener 1989). The Hairston, Smith and Slobodkin (HSS) hypothesis (Hairston et al. 1960) maintains that in plant-based food-webs with three trophic levels the top (predator) and bottom (producer) trophic levels are competition (resource) regulated while the intermediate (herbivore) level is predator-regulated. Alternative theories predict that predation becomes more important at lower trophic levels (Menge and Sutherland 1976; Menge et al. 1986) or that con-

sumers of plants may typically have very small populations as a consequence of poor food quality rather than predation (Murdoch 1966; White 1978).

Although the below-ground (detritus-based) food web is a critical component of most terrestrial ecosystems through regulating nutrient cycling, energy flow and decomposition processes, studies on below-ground ecosystems have had only a negligible impact on the development of food-web theory (Lawton 1989; Wardle 1991). However, the detritus food-web may behave differently to above-ground food-webs, because it contains longer food-chains, distinct (bacterial and fungal-based) within-habitat compartments, a higher incidence of omnivory, and much greater species richness (Moore and Hunt 1988; Polis 1991; Wardle 1991). Our purpose was to estimate the relative importance of competition and predation in regulating the various components of a detritus-based food-web consisting of three trophic levels (bacteria and fungi; bacterial-feeding and fungal-feeding nematodes; and top predatory nematodes) by using microbial biomass and nematode frequency data from two New Zealand agro-ecosystems.

Methods

Two agro-ecosystems, cropped to asparagus and maize respectively, and located 5 km from Hamilton, New Zealand were selected for this study. For each system, five weed management strategies (sawdust mulching, inter-row cultivation, hand-hoeing of weeds, and two herbicide treatments: bromacil and terbutylazine in asparagus; atrazine and rimsulfuron in maize) were applied to each of five replicate plots (each plot approximately 7 × 3 m) beginning in September 1990 (asparagus) or November 1990 (maize); details of these sites and treatments are given elsewhere (Wardle et al. 1993). At each of four sampling times during the following 12 months, fifteen 5-cm diameter soil cores were taken from each plot, bulked within each plot, and separated into 0–5 cm and 5–10 cm depth layers. The nematodes present in 250-ml subsamples of each of the 50 samples from each site were extracted using a tray variant of the Baermann method. Total nematode numbers were counted, then nematodes were fixed and killed with boiling fixative (100 ml 40% formaldehyde: 10 ml glacial acetic

acid: 390 ml distilled water). Subsequently around 125 specimens per sample were identified to genus level and assigned to trophic groups (Yeates 1971; Yeates et al. 1992). Selective inhibition of substrate-induced respiration was used to quantify relative bacterial and fungal biomass (according to West 1986) on 15-g subsamples at 55% moisture (dry weight basis) and using a non-continuous flow method of measuring CO₂-C production (Wardle 1993). While this method is difficult to calibrate for providing absolute microbial biomass values, it usually provides consistent relative values across gradients and in response to treatments (Wardle and Parkinson 1990).

Correlation coefficients were calculated (following appropriate data transformation prior to analysis where necessary) between the microbial and nematode trophic groups for the 50 samples for each site and sampling date. This approach, which enables assessment of the response of various trophic groups to a gradient of microbial biomass, is analogous to approaches which have been used in relating herbivore or predator biomass to gradients of primary productivity in plant-based systems (McNaughton et al. 1989; Power 1992).

Results and discussion

At all sampling dates in the asparagus site, total numbers of bacterial-feeding nematodes were only weakly correlated with soil bacterial biomass but tended to be much more strongly correlated with soil fungal biomass (Fig. 1). These trends were also apparent in the maize system, but due to greater variability these trends were not as strong (data not presented). It therefore appears that bacterial-feeding nematode numbers and fungal biomass are closely related and a possible explanation is that grazing pressure by bacterial-feeding nematodes reduces bacterial biomass, giving fungi a potential advantage (through reduced competitive pressure from

Table 1. Ratio of microbial feeding nematodes to microbial biomass (mean \pm SE) for each of four sampling times (mean of $n=50$ samples) in an asparagus ecosystem

Sampling date	Bacterial-feeding nematode numbers: bacterial biomass	Fungal-feeding nematode numbers: fungal biomass
16 November 1990	7.5 \pm 0.7	1.1 \pm 0.2
28 February 1991	6.3 \pm 0.5	1.3 \pm 0.2
23 May 1991	20.0 \pm 2.8	2.7 \pm 0.3
26 August 1991	15.5 \pm 1.4	1.8 \pm 0.2

Only relative figures are presented because calibration of methods for estimating absolute values for microbial biomass are frequently unreliable (Wardle and Parkinson 1990)

bacteria) and causing an increase in fungal biomass. If this explanation holds then bacteria would be more limited than fungi by grazing. The ratio of bacterial-feeding nematode numbers of bacterial biomass is also substantially higher than the ratio to fungal-feeding nematode numbers to fungal biomass, providing further evidence that bacteria are subjected to considerably more grazing pressure than are fungi (Table 1), and this may be accompanied by a higher turnover rate and level of productivity of bacteria relative to fungi (Schnürer et al. 1986). This is consistent with data presented in other studies (Ingham et al. 1985, 1989). Because fungi are not restricted by grazing to the same extent that bacteria are, fungal biomass is likely to be constrained more by resource limitation, and competition is most likely to be the dominant interaction occurring.

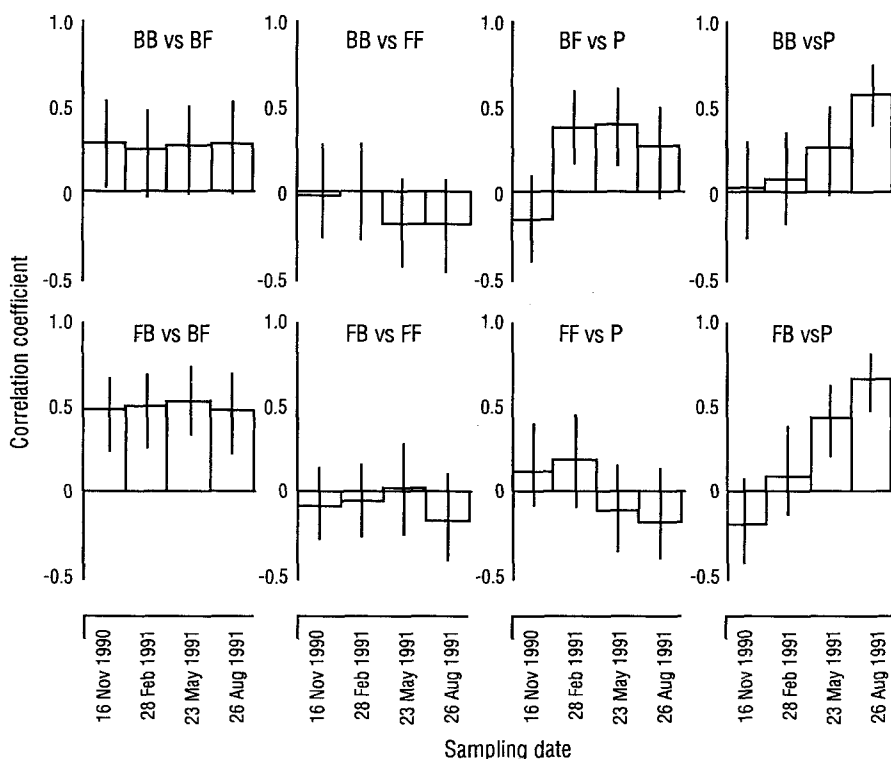


Fig. 1. Correlation coefficients ($n=50$) between microbial, microbial-feeding nematode and top predatory nematode groups in an asparagus agro-ecosystem, for four sampling dates. *BB*, *FB*=bacterial and fungal biomass; *BF*, *FF*, *P*=total number of bacterial-feeding, fungal-feeding and top predatory nematodes. Vertical bars represent 95% confidence intervals for r

The very low numbers of fungal-feeding nematodes relative to bacterial-feeding nematodes are probably due to differences in resource quality. Bacterial-feeders are capable of ingesting whole bacteria and their food-source has relatively few defences against grazing. However, fungi are morphologically relatively complex, contain a wide range of antigrazing (morphological and chemical) defences, and fungal-feeding nematodes are required to penetrate relatively resistant hyphal walls in order to obtain the nutritious cell contents (Swift et al. 1979). Thus the quality of the food resource would limit fungal-feeder numbers rather than bacterial-feeder numbers, in contrast to the predictions of the HSS hypothesis. These results have considerable implications for plant-dominated food-webs also, since they suggest that a food source which is more palatable is capable of sustaining a higher biomass of grazers.

Top predatory nematodes (highest trophic level) demonstrated a strong positive correlation with both bacterial and fungal biomass (lowest trophic level) but not with numbers of bacterial-feeding or fungal-feeding nematodes (intermediate trophic level), at the final sampling date in the asparagus site (Fig. 1). This trend also occurred at the maize site but not as strongly (data not presented). This suggests that numbers of top predators are directly related to the amount of food resource present at the bottom of the detritus food-web and competition is therefore likely to be the dominant interaction occurring at this level, at least at the final sampling date. It is also apparent from Fig. 1 that this trend strengthens over time, i.e. once the systems studied have had time to recover from the imposition of the various treatments. This relationship between the top and bottom trophic levels parallels that which may occur in some plant-based systems (Power 1992). The fact that the top and bottom trophic levels are more strongly correlated with each other than either is with the intermediate trophic level suggests that the intermediate level simply serves as a conduit by which resources pass from the bottom to top levels. Since in most systems carbon and nitrogen resource limitation is a factor restricting bacterial and fungal biomass production (Wardle 1992), it is also reasonable to include detritus as a fourth (basal) trophic level, and it could be hypothesized that top predator numbers are therefore a function of ecosystem primary productivity. This indicates that variation in primary production may influence trophic groups at higher levels than has previously been reported for either below-ground (Ingham et al. 1985; Yeates 1987) or above-ground (Kareiva and Sahakian 1990) terrestrial ecosystems.

One problem with correlation-based approaches for assessing food-web interactions [and which probably also applies to above-ground studies using a similar approach, e.g. McNaughton et al. (1989)] is that different trophic levels may be similarly affected by external factors, enhancing the apparent strength of relationships. In the present study, however, there was little evidence that the principal external factors affecting microbial biomass (e.g. soil moisture content and resource availability) directly affected nematode populations in a simi-

lar way. It should also be emphasised that nematodes are only part of the detritus food-web. Other groups of microbial-feeders (microarthropods and protozoa) were estimated in our study, but were highly variable in frequency and did not contribute significantly to the interpretation of data. These groups could also affect trophic interactions, but not in a consistent or predictable manner.

In conclusion, it appears that the dominant interactions influencing bacteria and fungi are predation and competition respectively, while microbial-feeding nematodes are limited by resource quality (and possibly predation), and top predatory nematodes are regulated by resource availability via the microbial biomass. An assessment of this type is possible only in a compartmentalised food-web where the basal organisms of each compartment are morphologically quite distinct and provide resources of vastly different quality. Although some studies have concluded that compartmentalisation does not occur within habitats (Pimm 1982; Pimm et al. 1991), these conclusions are based on consideration of only above-ground food-webs (Wardle 1991); it is apparent that the detritus food-web contains two distinct compartments (Moore and Hunt 1988), and the different regulatory forces operating on the organisms in these two compartments are induced by the differences between bacteria and fungi as food resources.

Acknowledgements. The authors thank M. Ahmed, F. Neville, K.S. Nicholson and R.N. Watson for help in gathering data, L.G. Greenfield, S.U. Sarathchandra and R.N. Watson for helpful comments on the manuscript, and K. Young for preparing Fig. 1.

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