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Does the positive feedback effect of nematodes on the biomass and activity of their bacteria prey vary with nematode species and population size?

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Abstract

Two nematode species (*Cruznema tripartitum* and *Acrobeloides bodenheimeri*) were selected to test the hypotheses that bacterial-feeding nematodes affect bacterial biomass and activity and that this feedback effect varies with nematode species and population size. For each species, nematodes of three initial population sizes were inoculated onto bacterial colonies in separate microcosms. Nematode population, bacterial biomass and CO_2 production were monitored in parallel microcosm settings. The responses of bacterial biomass to nematode species were different. Bacterial biomass increased significantly on d 8 in the presence of *Acrobeloides* when its initial numbers were 20 and 100 per microcosm; and bacterial biomass increased significantly on d 4 in the presence of *Cruznema* when its initial numbers were 5 and 20 per microcosm. Daily CO_2 production of the microcosms with initial population sizes of 5, 20 and 100 *Cruznema* or of 5 and 100 *Acrobeloides* was significantly greater than that in microcosms without nematodes. However, the CO_2 production of the microcosms with initial population of 20 *Acrobeloides* was not significantly different from that of the microcosms without nematodes. The increase in daily CO_2 production per microcosm by *Cruznema* was generally greater than that by *Acrobeloides* for the first few days of the experiment. Nevertheless, the increase in daily CO_2 production by an individual nematode was similar for both species and was a decreasing function of the initial nematode numbers. The feedback effect of each nematode species on its bacterial prey was estimated by fitting both bacterial biomass and CO_2 production data to a model. Model outputs demonstrated that the feedback effect of *Cruznema* on bacteria was greater than that of *Acrobeloides* during the course of the experiment and the feedback effect of each species was not linearly correlated to initial nematode population sizes. *Cruznema* increased bacterial biomass and activity by a factor of 3.75–4.55 over the first 4 d, while *Acrobeloides* increased it by a factor between 1.97 and 3.40.

Keywords: Bacterial-feeding nematodes; Dispersal; Food web model; Predator–prey interaction

1. Introduction

Positive feedback of a consumer on its food, or a predator on its prey, is one of the central themes in ecological food web studies (McNaughton, 1983; Langer and Gehring, 1993; Bronstein, 1994; Godinez-Alvarez et al., 2002). In the case of seed dispersal, seed-eating animals (frugivores) play a key role in the maintenance of plant populations because they act as the link between plant production and the subsequent recruitment of new individuals (GodinezAlvarez et al., 2002). Numerous studies have shown that herbivores increase plant productivity when they graze at an intermediate level (Owen, 1980; Dyer et al., 1982; McNaughton, 1983; Paige and Whitham, 1987). Some foraminiferal species grazing on seagrass secrete organic traces of glycosaminoglycans. The glycosaminoglycans stimulate bacterial and microalgal growth (Townsend, 1974; Cook, 1977) and observations of repeated grazing on secreted material suggested a particular type of feeding strategy (Hall, 1973; Bretz and Dimock, 1983).

When nematodes move out of bacterial colonies and they leave numerous tracks on agar plates. New colonies of bacteria grow rapidly along the nematode tracks but grow slowly, only by expansion of the original colony, when nematodes are absent. Abrams and Mitchell (1980) found significantly higher bacterial numbers in sewage sludge microcosms when bacterial-feeding nematodes were present. In a microcosm study, Ingham et al. (1985) found that all treatments containing

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nematodes and bacteria had higher bacterial numbers than similar treatments without nematodes. Ingham (1999) concluded that at low nematode numbers, feeding by nematodes stimulates bacterial growth. Nematodes help to distribute bacteria through the soil by carrying live and dormant microbes on their surfaces and in their digestive systems (Ingham, 1999). The theoretical work of Brown et al. (2004) indicates that direct positive feedback can have important effects on food web structure and dynamics. Feedback can stabilize predator–prey oscillations, and can induce a priming effect whereby resource enrichment leads to a net decrease in the resource pool. The magnitude of these effects depends critically on the strength of the feedback between the predator and prey. While the existence of positive feedback has been documented, quantitative estimates of the strength of the positive feedback have not been produced. We measured bacterial biomass and CO_2 production in the presence or absence of two nematode species in a microcosm experiments. We tested the hypothesis that positive feedback of nematodes on bacteria varies with nematode species and population size; and we obtained estimates of strength of positive feedback by fitting the bacterial biomass and cumulative CO_2 data to a model with the presence or absence of nematodes.

2. Materials and methods

2.1. Selection and culture of nematodes

Cruznema tripartitum and *Acrobeloides bodenheimeri* were selected as representative species of the families Rhabditidae and Cephalobidae. Nematodes in the family Rhabditidae are cp-1 'enrichment opportunists' and respond rapidly to resource enrichment. Nematodes in the family Cephalobidae are cp-2 'general opportunists' and respond more slowly to resource availability (Bongers, 1990; Bongers and Bongers, 1998; Ferris et al., 1995, 1997). Nematodes were collected from the field site of a long-term low-input sustainable agriculture experiment at the University of California Davis in the Sacramento Valley, California (Temple et al., 1994). Voucher specimens of the nematodes we used are deposited in the University of California Davis Nematode Collection with the following accession numbers: *A. bodenheimeri*—UCDNC 2908 and 2909; *C. tripartitum*—UCDNC 2910 and 2911. Nematodes were grown on nematode growth medium (NGM) (Sulston and Hodgkin, 1988): NaCl, 3 g; peptone, 2.5 g; agar, 17 g in 1 l of de-ionized water. The medium was autoclaved and cooled to 55 °C, then the following were added: cholesterol (5 mg ml^{-1} alcohol) 1 ml, 1 M $CaCl_2$ 1 ml, 1 M $MgSO_4$ 1 ml and 1 M KH_2PO_4 25 ml. The bacterium *Sinorhizobium meliloti 1020* (Meade et al., 1982) was used as food for both bacterial-feeding nematode species because we had observed in previous studies that both nematodes species grow healthily on this bacterium. Bacteria were cultured on TY medium: Tryptone 5 g, yeast extract 3 g, $CaCl_2 \cdot 2H_2O$ 0.9 g, Agar 15 g in 1 l of de-ionized water.

2.2. Microcosm preparation and CO_2 measurement

Sixty grams of Yolo loam soil (28.7% of sand, 46.4% of silt and 24.9% of clay) were weighed into a 60-ml centrifuge tube as a microcosm, soil moisture was adjusted to 90% of water holding capacity. Total soil C and N were 0.8 and 0.09%, respectively. The microcosms were then autoclaved for 2 h at 125 °C. Twenty microliters (around 347×10^6 cells) of bacterial suspension was spotted onto a sterilized cotton swab which was inserted into each soil column of the microcosm. Care was taken to make sure the head of the cotton swab was uniformly in good contact with the soil surface so that no obvious gaps were created. Either *C. tripartitum* or *A. bodenheimeri* of different initial population sizes (0, 5, 20 or 100 individuals) was inoculated onto the bacterial inoculum for each microcosm. There were five replicates for each nematode treatment. The purpose of the cotton swab was to minimize capillary dispersal of bacteria so that the spreading of bacteria could be attributed predominantly to nematode movement. The microcosms were tightly sealed with rubber septa and were kept at relatively constant 22 °C. The headspace of each microcosm was 10 ml. Each day 0.5 ml of headspace gas was extracted to measure its CO_2 concentration with an infrared CO_2 analyzer (Horiba, PIR-2000R, STERN Scientific Associates). The CO_2 concentration was calculated relative to peaks of CO_2 gas standards. Measurements were made on a daily basis for 8 d.

2.3. Nematode respiration

Since the total respiration of each microcosm was the sum of bacterial and nematode respiration, a parallel experiment was conducted to measure nematode respiration when no bacteria were inoculated. Each microcosm received 100 or 500 surface sterilized nematodes and cumulative CO_2 was measured for 4 consecutive days. Average daily CO_2 production per nematode for each species was obtained by normalizing with nematode numbers.

2.4. Nematode growth and simulation modeling

In order to subtract nematode respiration from the total respiration of the microcosm, not only must daily CO_2 production per nematode be estimated but also nematode population size. The nematode population was monitored in another parallel microcosm experiment with an initial population of 20 nematodes per microcosm. The microcosms were prepared the same way as described earlier, each with 60 g of soil. The nematodes were introduced into each microcosm after the inoculation of bacteria. Five microcosms for each nematode species were destructively sampled for extraction on a Baermann funnel every other day. Nematode growth curves for an initial population size of 20 for both species were made after eight extractions. Since the growth rate 'r' and carrying capacity 'K' for each species is fixed in a specific medium with no external inputs, the shape of the nematode growth curves was determined by the size of the

initial population. Growth curves for initial populations of 5 and 100 nematodes were modeled using a continuous-time logistic model based on r and K values estimated from an initial population of 20 nematodes per microcosm (Hastings, 1997). A least-square method (Hilborn and Mangel, 1997) was used for curve-fitting to the logistic model after log-transformation of the raw data:

$$N(t) = CKe^{rt}/(1 + Ce^{rt}), \quad (1)$$

where $C = N_0/(K - N_0)$, r is the growth rate of nematode population, K is the carrying capacity of nematodes, and N_0 is the initial size of the nematode population.

2.5. Bacterial biomass

Bacterial biomass was measured on days 0, 2, 4, 6, 8 and 30 after the inoculation of bacteria, with or without nematodes by using the chloroform fumigation–extraction method of Vance et al. (1987). Percentage change of bacterial biomass (P) by nematodes was expressed to demonstrate the effect of nematodes on bacterial growth. The percentage change of bacterial biomass (P) was obtained using the following equation:

$$P = 100\,\Delta B/B, \quad (2)$$

where $\Delta B = (B_n - B)$, B_n is the bacterial biomass in the microcosms with nematodes, and B is the bacterial biomass in the microcosms without nematodes. A separate set of microcosms was used for bacterial biomass measurement and the microcosms were prepared as described above. There were five replicates for each treatment at each sampling time.

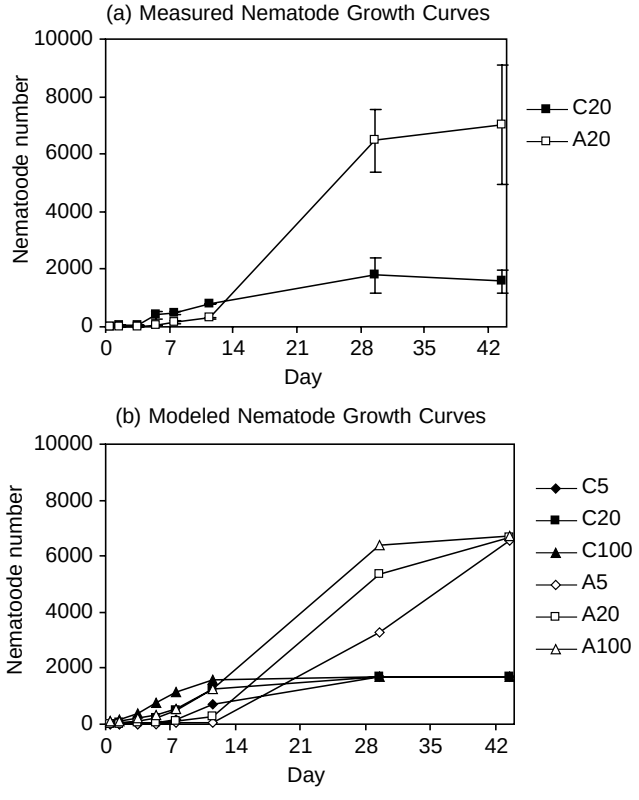

Fig. 1. (a) Measured nematode growth curves with initial population of 20; (b) modeled nematode growth curves with initial nematode numbers of 5, 20 and 100, respectively. Letters 'A and C' refer to *Acrobeloides bodenheimeri* and *Cruznema tripartitum*.

2.6. Modeling the feedback effect of nematodes on bacteria

We estimated the feedback strength of nematodes on bacteria by fitting both bacterial biomass and cumulative CO_2 data to a model in the presence and absence of nematodes. We assumed that bacterial biomass (B) and soil organic matter (R) satisfied the differential equations:

$$dB/dt = \alpha\beta BR(1 + g(N)) - (\rho_1 +)B - f(B, N) \quad (3)$$

$$dR/dt = -\alpha\beta R(1 + g(N)). \quad (4)$$

Here, α and β are the bacterial feeding rate and production efficiency; ρ_1 and μ are the bacterial maintenance respiration and mortality rates. Nematodes (N) affect bacterial dynamics via predation, $f(B,N)$, and positive feedback, $g(N)$. The cumulative CO_2 production predicted by the model is given by

$$C(t) = \int_0^t \alpha(1-\beta)B(s)R(s)(1 + g(N(s))) + \rho_1 B(s) + \rho_2 N(s)ds, \quad (5)$$

where ρ_2 is the respiration rate of the nematodes. While bacteria metabolize different types of organic matter at widely different rates, we assumed for simplicity that the resource pool was homogeneous and consisted of all the soil organic matter.

Parameter estimation was done by least-squares fitting of the bacterial biomass and the cumulative CO_2 production predicted by the model to actual measurements. We obtained approximate 95% confidence intervals for the parameter estimates via a likelihood ratio test (Hilborn and Mangel, 1997). We used the nematode-free treatment to obtain estimates for the bacterial parameters α_1 and ρ_1. We then obtained independent estimates of the strength of feedback ($g(N)$) for each of the nematode treatments.

The experiment was a completely randomized two-way factorial design and the factors were nematode species and initial nematode population size. Significance ($P \leq 0.05$) was determined by two-way ANOVA performed by species and population size, and Tukey's honestly significant difference was used to separate means. The error bars on the figures are standard errors of the means ($n = 5$).

3. Results

3.1. Nematode growth

At an initial population of 20 nematodes per microcosm, *C. tripartitum* grew at a much faster rate than *A. bodenheimeri* but the carrying capacity of the microcosms for *C. tripartitum* was much lower than for *A. bodenheimeri* (Fig. 1a). According to the models, the growth rates (r) of *C. tripartitum* and *A.*

bodenheimeri were 0.504 and 0.247, and the carrying capacities (*K*) were 1683 and 6748, respectively. For each nematode species, microcosms with higher initial numbers reached their carrying capacity earlier than those with lower initial numbers (Fig. 1b).

3.2. Nematode respiration

Daily CO_2 production per nematode for each species was obtained by normalizing in relation to nematode numbers. Mean nematode respiration rates were 38.8 ± 4.5 and 14.4 ± 2.8 ng CO_2-C nematode^{-1} d^{-1} for *C. tripartitum* and *A. bodenheimeri*, respectively.

3.3. CO_2 production in microcosms

Cumulative CO_2 production in each microcosm was measured and modeled through time (Fig. 2). In all microcosms, cumulative CO_2 was least for bacteria alone and CO_2 production increased significantly when nematodes were present. CO_2 production was greater in the presence of *C. tripartitum* than in the presence of *A. bodenheimeri*. However, increased CO_2 production was not linearly correlated with initial nematode numbers in the microcosms. For example, although CO_2 production in the microcosms with initial number of 100 *Acrobeloides* was greater than that of 20 or five *Acrobeloides*, CO_2 production in the microcosms with initial number of 20 *Acrobeloides* was less than that of five *Acrobeloides* (Fig. 2a).

Daily CO_2 production of all microcosms peaked on d 2 or d 3 and declined thereafter. Apparently, daily CO_2 production was higher during the first 4 d than during the second 4 d period for both nematode species (Fig. 3). The increase in daily CO_2 production per microcosm by *C. tripartitum* was generally greater than that by *A. bodenheimeri* for the first a few days of the experiment (Fig. 4). However, the increase in daily CO_2 production by an individual nematode was similar for both species and was a decreasing function of the initial nematode numbers. The increase in daily CO_2 production by an individual nematode was the most when its initial number was 5 per microcosm (Fig. 5).

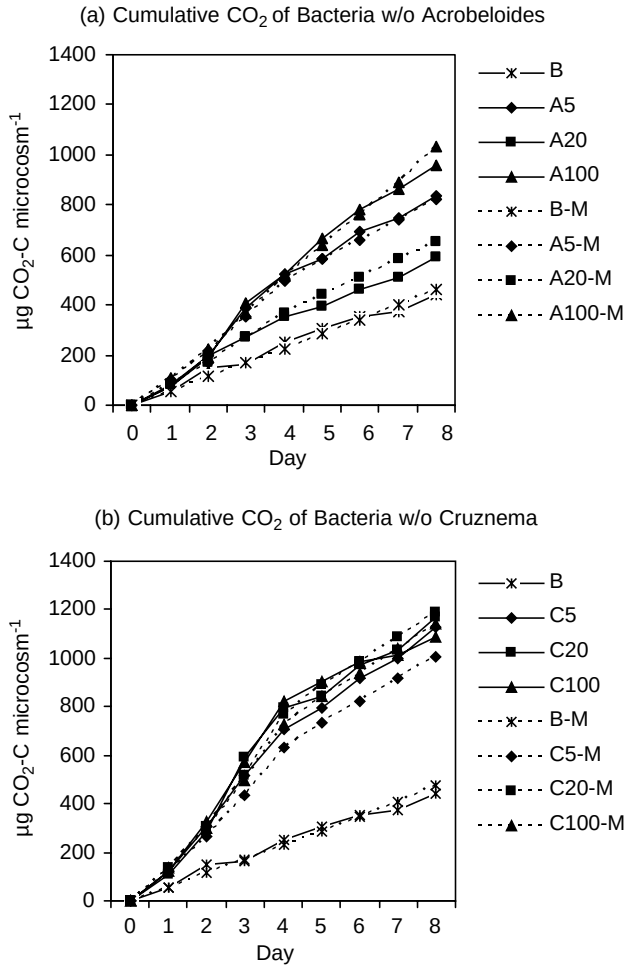

Fig. 2. (a) Measured and modeled cumulative CO_2 production of bacteria (B) with or without *Acrobeloides bodenheimeri* (A); (b) measured and modeled cumulative CO_2 production of bacteria (B) with or without *Cruznema tripartitum* (C). Numbers correspond to the initial nematode numbers. Modeled results are indicated by the attached letter 'M' or the dashed lines.

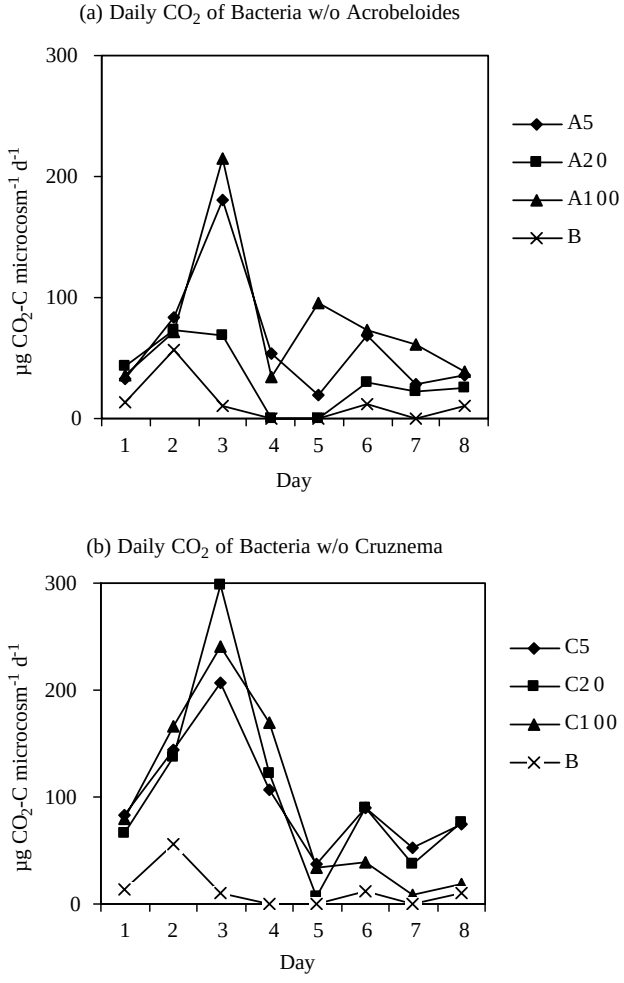

Fig. 3. (a) Daily CO_2 production per microcosm with or without *Acrobeloides bodenheimeri* (A); (b) daily CO_2 production per microcosm with or without *Cruznema tripartitum* (C). Numbers correspond to the initial nematode numbers.

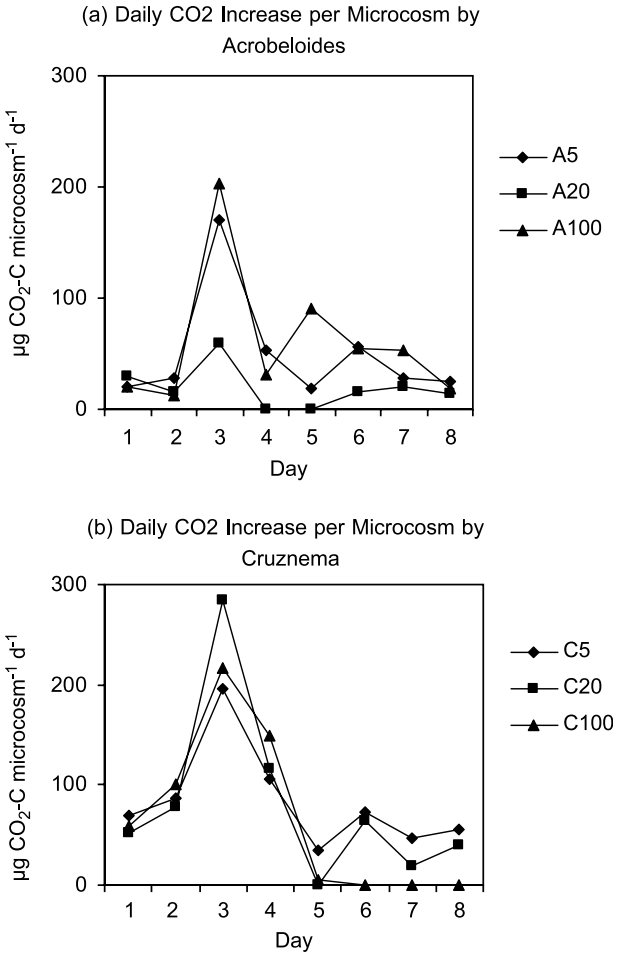

Fig. 4. (a) Increase in daily CO_2 production per microcosm by *Acrobeloides bodenheimeri* (A); (b) increase in daily CO_2 production per microcosm by *Cruznema tripartitum* (C). Numbers correspond to the initial population sizes.

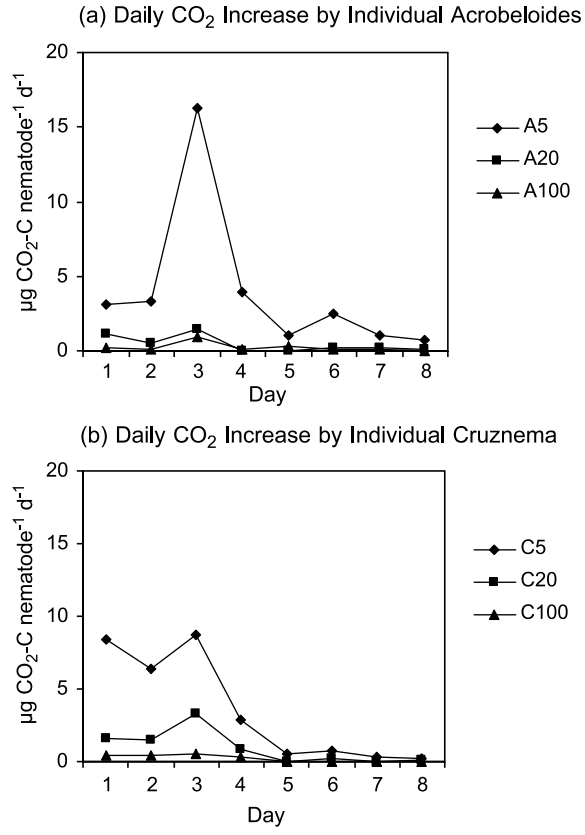

Fig. 5. (a) Increase in daily CO_2 production by an individual *Acrobeloides bodenheimeri* (*A*); (b) increase in daily CO_2 production by an individual *Cruznema tripartitum* (C). Numbers correspond to the initial population sizes.

3.4. Bacterial biomass

There was a significant increase in bacterial biomass on d 8 in the microcosms initially inoculated with 20 and 100 *Acrobeloides* per microcosm; the proportional increase of bacterial biomass was 3.31 ± 1.00 and 4.10 ± 1.14, respectively (Fig. 6a). Overall, there was no consistent trend for the change of bacterial biomass caused by *Acrobeloides*. The bacterial biomass increased significantly on d 4 in the microcosms with five or 20 *Cruznema* and the proportional increase of bacterial biomass was 2.72 ± 0.70 and 3.51 ± 0.44, respectively. There was a clear trend of bacterial biomass increase in the microcosms initially inoculated with 20 *Cruznema* in comparison with nematode-free control microcosms (Fig. 6b). In some cases, the change of bacterial biomass showed a decreasing trend in the presence of nematodes but those changes were not significant.

3.5. Feedback strength

To quantify the average strength of the positive feedback of nematodes on bacteria over the first 8 d of the experiment, we fitted the bacterial biomass and cumulative CO_2 data to a model (Eqs. (3)–(5)). First, we fitted the model to the nematode-free data to obtain estimates of bacterial feeding rate (α), assuming that bacterial production efficiency (β) was 0.6 (Darrah, 1991) and body weight was 2.2 pg cell^{-1} (Van Veen and Paul, 1979). We assumed that background mortality and maintenance respiration were insignificant over the short period of our experiment. The initial conditions for the model were obtained by using an initial bacterial population of 347×10^6 cells, and a resource pool of 10.4 mg g^{-1} (from the measured soil C content of 1.07%). By weighted least-squares fitting of the predicted bacterial biomass and cumulative CO_2 production, the maximum likelihood estimate and 95% confidence interval for the bacterial feeding rate were: $\alpha = 8.8$ (3.8, 10.6) pg C g^{-1} soil d^{-1} in the microcosms with *Cruznema*; and $\alpha = 7.6$ (1.6, 9.5) pg C g^{-1} soil d^{-1} in the microcosms with *Acrobeloides*. Next, we fitted the bacterial biomass and the cumulative CO_2 production predicted by the model to the data from each nematode treatment to obtain estimates of the feedback strength. Initially we were not able to fit a coupled predator–prey model to the data in order to reconcile the early behavior of the model with the long term dynamics of the nematode populations. This was likely due to changes in the strength of feedback over the course of the experiment. The positive effect of nematodes on bacteria peaked early, and then declined. To capture the apparent time dependence of the feedback, we

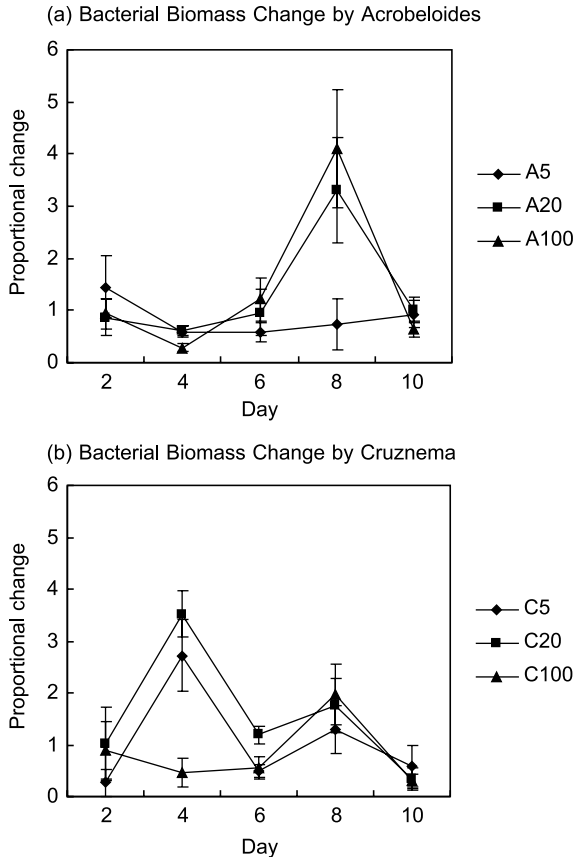

Fig. 6. (a) Proportional change of bacterial biomass caused by *Acrobeloides bodenheimeri* (A); (b) proportional change of bacterial biomass caused by *Cruznema tripartitum* (*C*). Numbers correspond to the initial nematode numbers.

assumed that the strength of feedback was different in the d1–d4 period ($g(N)=\Gamma_1$, a dimensionless parameter) from that in the d5 to d8 period ($g(N)=\Gamma_2$). By fitting the model to the bacterial biomass and the cumulative CO_2 production, we obtained estimates of the average strength of feedback over each of these 4 d periods (Table 1). In addition to the growth and respiration parameters that we determined experimentally, we assumed nematode feeding rates of $\phi=1.86$ and 1.75 μg μg^{-1} nematode d^{-1} (Ferris et al., 1997) and fresh weights of 749 and 115 ng nematode^{-1} (Ferris et al., 1995) for *C. tripartitum* and *A. bodenheimeri*, respectively. According to our model, *C. tripartitum* increased bacterial biomass and activity by a factor of 3.75–4.55 over the first 4 d, while *A. bodenheimeri* increased it by a factor between 1.97 and 3.40. For each species, the strength of the feedback dropped essentially to zero over the second 4 d period.

4. Discussion

4.1. Feedback of nematodes on bacterial growth and activity

In our study, bacterial biomass increased significantly on d 8 in the microcosms with 20 or 100 initial *Acrobeloides* and on d 4 in the microcosms initially inoculated with five or 20 *Cruznema* when compared with the bacterial biomass in the nematode-free control microcosms. *Cruznema* caused an earlier increase of bacterial biomass than *Acrobeloides*. This is consistent with the biology of these two nematode species. *C. tripartitum* is fast-growing with a short-life cycle whereas *A. bodenheimeri* grows more slowly and has a longer life cycle (Ferris et al., 1995). Both positive and negative effects of nematodes on bacteria were reported by Coleman et al. (1977), Cole et al. (1978), Anderson and Coleman (1979), Abrams and Mitchell (1980) and Ingham et al. (1985). We also found that the change of bacterial biomass showed a decreasing trend in some cases when nematodes were present but those changes were not significant. Ingham et al. (1985) stated that the response of microorganisms to faunal grazing may be dependent on resource availability and grazing intensity. We consider that grazing intensity and, more precisely, the ratio of bacteria-to-nematode numbers (B-to-N ratio) is critical in the predator–prey interaction. We postulated that there is an equilibrium threshold of the B-to-N ratio where bacteria numbers do not change when grazed by nematodes. Then, bacterial growth rate offsets the nematode predation rate at the equilibrium threshold. The bacterial population declines when the B-to-N ratio is smaller than the threshold and increases when the B-to-N ratio is greater than the threshold. In our study, equal amounts of bacteria cells (347×10^6) were inoculated into each microcosm. This would initially provide enough food for 343 *A. bodenheimeri* and 53 *C. tripartitum* adults based on the feeding rates of these nematodes estimated by Ferris et al. (1997). The population of mixed life stages used in this study probably would consume fewer bacteria (say 50%) than a uniform population of adults. Most likely, the number of bacteria cells would be adequate initially for the nematodes inoculated since the maximum initial population size was 100

Table 1
Estimates of feedback strength

Species and number	Γ_1 (d1–d4)	Γ_2 (d5–d8)
A5[a]	3.30	0.00
A20	1.97	0.00
A100	3.40	1.20
C5	3.75	0.00
C20	4.55	0.00
C100	4.50	0.00

Numbers correspond to the initial nematode numbers.
[a] A and C refer to *Acrobeloides bodenheimeri* and *Cruznema tripartitum*.

nematodes per microcosm. The positive feedbacks of bacterial-feeding nematodes on bacterial growth that we observed indicated that the B-to-N ratio was greater than the equilibrium threshold.

Microcosms with nematodes produced significantly more CO_2 than those without nematodes, indicating that bacterial activity increased in the presence of nematodes. Our results were consistent with those of Anderson and Coleman (1977), Coleman et al. (1977), Cole et al. (1978), Clarholm (1981) and Trofymow and Coleman (1982).

Although our bacterial biomass and CO_2 production data suggested an apparent positive feedback of nematodes on bacteria, this effect seemed transitory. We consider that bacteria responded to nematodes and reached their carrying capacity quickly but the bacteria declined thereafter under the grazing pressure of increased nematode population in a small and closed microcosm where resources were limited. This positive feedback of nematodes on bacteria should be more persistent in a larger scale system where there are many resource patches or in an open system where there is continuous resource input.

4.2. Nematode respiration

On an individual basis, mean values of nematode respiration were 39 and 14 ng CO_2-C nematode^{-1} d^{-1} for *C. tripartitum* and *A. bodenheimeri*. Since the nematodes we used were mostly at J2 and J3 stages, the fresh body weights of *C. tripartitum* and *A. bodenheimeri* were estimated to be 749 and 115 ng nematode^{-1}, respectively. (Ferris et al., 1995). Therefore, mean values of nematode respiration on a fresh weight basis were estimated to be 2.2 and 5.2 ng CO_2-C μg^{-1} nematode h^{-1} for *C. tripartitum* and *A. bodenheimeri*, respectively. Ferris et al. (1995) measured the respiratory and metabolic activities of eight species of bacterial-feeding nematodes at various developmental stages. The average metabolic rates of *C. tripartitum* and *A. bodenheimeri* were estimated as 3.4 and 6.9 ng CO_2-C μg^{-1} nematode h^{-1}, respectively. These values were little higher than, but comparable to, our results. The measurements were made with agar plates by Ferris et al. (1995) while in this study they were made with soil microcosms.

In field studies, nematode respiration is usually considered to be a relatively small proportion of total soil respiration; it has been reported as less than 1% of total heterotrophic respiration (Klekowski et al., 1972; Phillipson et al., 1977; Yeates, 1979; Seastedt, 1984; Hendrix et al., 1986, 1987). In the microcosm study, we found that nematode respiration was less than 1% of total respiration only when a nematode population was low (i.e. when initial nematode population size was 5 *A. bodenheimeri* per microcosm). However, the contribution of nematode respiration to total respiration increased with time and initial nematode population size. When the initial nematode numbers were 5, 20 and 100, the percentages of nematode respiration to total soil respiration ranged from 0.1 to 0.2, 0.4 to 1.4 and 2.0 to 4.0% for *A. bodenheimeri*; and they ranged from 0.3 to 2.2, 1.0 to 4.7 and 5.7 to 19.6% for *C. tripartitum,* respectively (Table 2). It is noteworthy to point out that the whole soil community was taken into account to partition soil respiration in the field studies while only one soil nematode species was present and considered in each microcosm used in our study.

4.3. Feedback strength

By fitting the bacterial biomass and the cumulative CO_2 data into a model, *C. tripartitum* increased bacterial growth and activity by a factor of 3.75–4.55 over the first 4 d, while *A. bodenheimeri* increased it by a factor between 1.97 and 3.40. For each species, the strength of the feedback dropped essentially to zero over the second 4 d period. The greater individual size, movement, and population growth of *C. tripartitum* allowed it to disperse bacteria more rapidly in the short term. This is consistent with the classification of Rhabditidae as enrichment opportunists, which maximize their population growth when conditions are favorable. Over the long term, however, Cephalobidae may have a greater positive effect on bacteria populations. The smaller body size of *A. bodenheimeri* enables access to smaller pore spaces, allowing it to transport bacteria to and from locations that are inaccessible to *C. tripartitum*.

Our parameter estimation procedure for feedback strength incorporates both bacterial biomass and the cumulative CO_2 data. For *Cruznema*, both data sets are consistent in indicating strong initial feedback that drops off over time. However, for *Acrobeloides*, the two types of data differ in the timing of the feedback. The exact reason for that was unclear. The parameter estimates are most consistent with the cumulative CO_2 data; they do not reflect the later peak in feedback apparent in the

Table 2
Importance of nematode respiration to total soil respiration (%)

Species and number per microcosm	Incubation time (h)							
	23	44	69	94	118	141	165	190
A5[a]	0.10	0.09	0.09	0.10	0.14	0.16	0.20	0.24
A20	0.43	0.43	0.53	0.63	0.81	0.97	1.20	1.38
A100	2.03	1.85	1.74	2.07	2.35	2.78	3.39	4.04
C5	0.25	0.26	0.33	0.44	0.69	1.00	1.53	2.18
C20	1.04	1.00	1.14	1.52	2.43	3.43	5.06	6.74
C100	5.67	5.12	5.32	6.25	8.87	11.93	15.96	19.56

Numbers correspond to the initial nematode numbers.
[a] A and C refer to *Acrobeloides bodenheimeri* and *Cruznema tripartitum*.

Acrobeloides bacterial biomass data. In this case, the parameter estimates are dominated by the CO_2 data because of the higher variability (i.e. high standard error bars) in the bacterial biomass measurements. In summary, the consistent response of both bacterial biomass and CO_2 to *Cruznema* gives us confidence in quantitative estimates of its feedback strength. The variability of bacterial biomass data in the *Acrobeloides* treatment suggests that here our estimates are less reliable.

To test the robustness of the results of feedback strength, we recomputed the feedback strengths by setting each of the growth, feeding and respiration variables in the model at 0.5 and 1.5 fold, respectively, of the values used. The only variables that significantly affected the feedback estimates were bacterial feeding rate (α) and maintenance respiration (ρ_1) . From the formula for cumulative CO_2 production (Eq. (5)), Γ should be approximately inversely proportional to α and linearly related to ρ_1. The effects of the nematodes on total CO_2 production in the microcosms was dominated by their positive effect on bacterial activity, rather than through predation or their own respiration; thus, the estimates of feedback strength were largely unaffected by changes in the nematode variables.

Our results are not very sensitive to the assumed lack of bacterial mortality ($\mu = 0$). Bacterial death represents an unknown flux of C through the system; the higher the mortality, the more C must be taken up by the bacteria to yield the observed CO_2 flux. This in turn increases the estimate of bacterial feeding rate (α), from the nematode-free data, and hence decreases the estimated feedback strengths. For example, if we assume that $\mu = 0.1$ (an average lifespan of 10 d), we find that $\alpha = 10.7$ pg C g^{-1} soil d^{-1} and then $\Gamma_1 = 2.7$ for the A5 treatment, a very slight change. The mortality and maintenance respiration rates of bacteria vary with species, temperature, and starvation status (Hunt, 1977); thus, it is difficult to determine what values are most appropriate in our system. However, our sensitivity analysis indicates that our estimates of feedback strength are robust over reasonable ranges of these parameters.

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