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Dynamics of bacterial populations in relation to carbon availability in a residue-amended soil

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Abstract

Bacterial response to alteration in C availability is important in understanding the microbial community structure and microbial interactions in soil ecosystems. Population dynamics of oligotrophic and copiotrophic bacteria in relation to soil C availability were examined and relationships between bacterial populations and water-extractable C, buffer-extractable C, mineralizable C or microbial biomass C were investigated. Both copiotrophs and oligotrophs were significantly stimulated by newly added C in the form of cover crop debris, but copiotrophs rapidly peaked at the very early stage of cover crop decomposition while peak populations of oligotrophs occurred at a later stage when available C decreased. Despite significant correlations between mineralizable C and water soluble C or buffer soluble C, dynamics of both copiotrophic and oligotrophic bacteria was best related to mineralizable C pool. Copiotrophs were logarithmically correlated to mineralizable C ($p < 0.0001$), while oligotrophs were quadratically related to mineralizable C ($p < 0.0001$), which is, to our knowledge, the first report showing that high C availability may have inhibited oligotrophs in natural soils. Oligotrophs were not significantly correlated to microbial biomass C, suggesting that oligotrophs only contributed a minor part to the soil microbial biomass pool.

1. Introduction

Knowledge of response of bacteria to C input is of significance in understanding population dynamics of natural or introduced microbes and their interactions, and to some extent, predicting effectiveness of microbial introduction into soil. However, the physiological response of bacterial populations to changes in substrate C availability in soil is poorly understood.

Most natural environments are characterized by oligotrophic conditions (Morita, 1988; Kjelleberg, 1993). Available C concentrations are low because organic matter content is low in many soils and much of the organic matter is not readily available for microorganisms due to its chemical recalcitrance (Army and Morita, 1983; Morita, 1988). Physical barriers also contribute by blocking access of microbes to the heterogeneously distributed nutrients (Smiles, 1988). Microorganisms adapt to low substrate environments (Semenov, 1991), and previous studies suggested that oligotrophic bacteria are predominant in soil, even on C-rich sites such as debris and root surface areas (Ohta and Hattori, 1983).

Copiotrophic bacteria have high V_{max} and K_m values and adapt to high nutrient environments, while oligo-

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trophic bacteria have high substrate affinity as evidenced by the low K_m values of their transport systems (Button, 1991). Oligotrophs, therefore, have competitive advantages over copiotrophs when substrate (C) concentration is low (Fry, 1990; Button, 1991) and could, in theory, outcompete copiotrophs if C concentration is the sole factor determining the outcome of the competition (Tilman, 1976, 1982). The competitive displacement has been well confirmed in simple systems where a few species or strains of bacteria were involved (Zambrano et al., 1993). A soil microbial community represents a continuum of microorganisms with various C requirements, with obligatory oligotrophs adapted to low C concentrations at one extreme and obligatory copiotrophs adapted to high C concentrations at the other extreme (Semenov, 1991). Multiple limiting nutrients (Tilman, 1982), habitat heterogeneity (Smiles, 1988), different colonization ability of microorganisms (Paul and Clark, 1996) and other factors (e.g., predation and microbial dormancy) are responsible for the coexistence of microorganisms of different C-acquiring ability. Richerson et al. (1970) suggested that coexistence is due to the continual development of patches that 'decay' before competitive displacement can fully occur. This can be very true in soil systems since the soil environment is in a continuous state of flux (Murray et al., 1992). Natural soils are featured with pulsed C input from root exudates and other organic materials following seasonal growing patterns of plants (Paul and Clark, 1996). The responses of bacteria to alteration in C availability directly affect the microbial community structure and functions, and plant-microbial interactions, which has important implications in agriculture. Evidence accumulated from the last two decades indicates that microbial competition for C and other nutrients may be mainly responsible for root disease suppression (Alabouvette, 1986; Mandelbaum and Hadar, 1990). C availability is also very relevant to the fate and functions of introduced microorganisms such as biocontrol agents since it affects not only their survival but also their antibiotic production (Benizri et al., 1995).

Studies on response of soil bacteria to changes in C availability have been hampered because of difficulties in characterizing and quantifying readily available C, and selecting optimal C-containing media for various physiological types of soil microorganisms. Soil bacteria are traditionally isolated on nutrient (C)-rich media which are unrealistic and not optimal or even detrimental to oligotrophic bacteria (Hattori and Hattori, 1980; Kaszubiak and Muszynska, 1992). Population dynamics recorded following traditional methods, therefore, poorly represent the behavior of oligotrophic bacteria.

In this paper, we report the results on dynamics of soil oligotrophic and copiotrophic bacteria as influenced by C availability manipulated through cover crop residue incorporation in an agricultural soil of low C availability. Bacteria were quantified on a resource (C)-rich medium and a resource (C)-poor medium, which were used in an effort to simulate C concentrations of the rhizosphere and bulk soil microhabitats, respectively. The major objectives of this study were to document the population response of oligotrophic and copiotrophic bacteria to changes in soil C availability, determine the relative contribution of oligotrophs and copiotrophs to soil microbial biomass as determined by fumigation extraction, and identify the C pools most correlated with oligotrophic and copiotrophic populations.

2. Materials and methods

2.1. Site description

The field plots were located at the Armstrong Experimental Station of the Department of Plant Pathology, at the University of California at Davis. The soil is a Yolo sandy loam (a coarse-loamy, mixed, thermic, Mollic Xerofluvent soil) with 45% sand, 40% silt, 15% clay and organic C content at 1.08%. The soil pH was 7.6 (determined in water in soil sampled 0–20 cm deep). The field plots had not been cultivated for 2 years and had low microbial activity (Grünwald et al., unpublished). An oat (*Avena sativa* L.)-vetch (Lana woollypod vetch: *Vicia dasycarpa* Ten.) cover crop mixture was planted in Fall, 1994 and bare fields without cover crops served as controls. Cover crops were harvested in late April, 1995, when oats were starting to head and vetch was flowering. Fresh cover crop biomass from all plots were cut, mixed and oven-dried (40°C) for 1 week. A subsample of oven dried residue (2300.0 g) was then manually mixed into each plot of 2.2 m^2 (1.1 m × 2.0 m) on 3 May 1995, amounting to about 2 g C Kg^{-1} soil. The oat-to-vetch

ratio of oven-dried biomass was 3.7 : 1. Beds (70 cm wide) were prepared in all plots after the residues were mixed into the top 20 cm of soil.

All plots were irrigated with micro-misters (two for each plot) following incorporation of the residue mixture and then at weekly intervals. The field design was a completely randomized design with six replicate plots for each treatment. Soil moisture and temperature were recorded by a CR10 datalogger (Campbell, Logan, UT) and their daily averages are summarized in Fig. 1. Two dataloggers were installed, each with four sensors for temperature and another four for moisture (i.e., eight sensors distributing into eight plots for both temperature and moisture).

2.2. Soil sampling

Soil cores to 20 cm depth were collected using a Dutch auger (6 cm in diameter) on Days 0, 12, 19, 26, 33 and 56 after incorporation of the vetch-oat cover crop and composited by plot on each sampling date. Soil samples were then sieved through a 4 mm mesh and organic debris bigger than 4 mm was cut and passed through the mesh. Sieved soils were immediately used for isolation of oligotrophic and copiotrophic bacteria and available C determination. A subsample of sieved soil was stored in 4°C cold room until used for microbial biomass C determination within 2–3 days after soil sampling.

2.3. Residue decomposition

A litterbag study was carried out to determine the decomposition rate of cover crop residues. Litterbags of 10 cm × 10 cm (made from WeedBlock, Waco, TX) containing ca. 2.50 g of oat-vetch mixture (same materials as those directly mixed into soils except all materials used bigger than 1 mm in diameter) were buried at a soil depth of ca. 15 cm at an angle of 45°, with six bags in each of six plots. On each sampling date, one bag from each plot (six bags for each treatment) was retrieved and residues were carefully recovered, dried at 60°C and weighed.

2.4. Quantification of soil C availability

Water soluble C and weak buffer extractable C were extracted by cold distilled deinonized water and phosphate buffer (3.33 mM KH_2PO_4 and 6.67 mM Na_2HPO_4, pH = 7.0), respectively. About 8.0 g soil (dry soil equivalent) was mixed with 25 ml of water or buffer, vortexed at high speed for 1 min, and shaken on an orbital shaker at middle speed for 1 h. The solution was then centrifuged at 14 500 × *g* for 15 min, and the supernatant further sterilized by filtration through a Magna nylon membrane filter (0.22 μm). Extracts were immediately frozen until analyzed for dissolved C using a Shimadzu total organic carbon analyzer (Shimadzu TOC-5050, Shimadzu Scientific Instruments, Columbia, MD). Mineralizable C was determined by CO_2 evolution through incubation in sealed mason jars at room temperature (22 ± 2°C). Field-moist sieved soil samples (20.00 g dry soil equivalent) were placed in one-litter mason jars and incubated in the dark. Evolving CO_2 was captured in 5.0 ml of

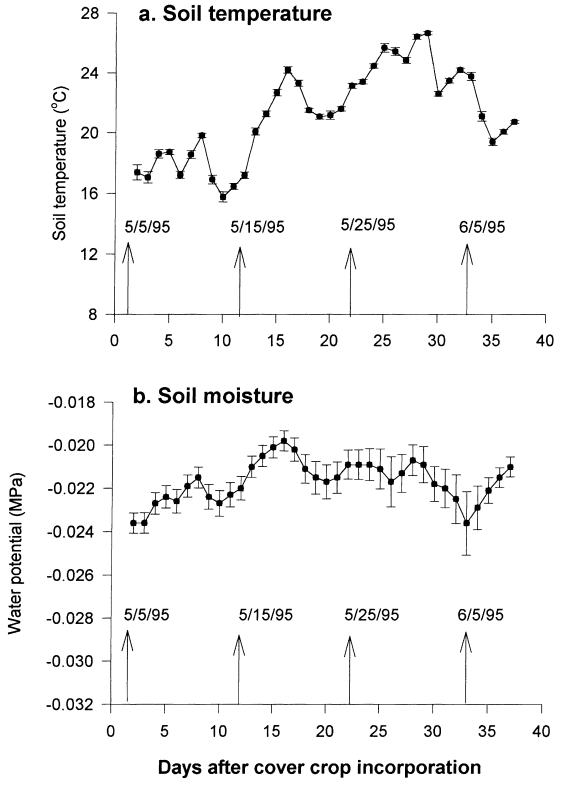

Fig. 1. Daily soil temperature (a) and soil moisture (b) over the experimental period for the study site at the experimental station of Plant Pathology Department, University of California, Davis, CA. When the error bars are absent, the SE is smaller than the symbol.

0.5 N NaOH contained in a beaker suspended in each mason jar. The NaOH solution was removed after 12 days of incubation and titrated for determining the amount of CO_2 evolved.

2.5. Quantification of oligotrophic and copiotrophic bacteria

To determine the number of oligotrophic and copiotrophic bacteria in soils at different decomposition stages of cover crops, soil extracts were plated on a high C content medium and a low C content medium. Both media contained 0.5 g $MgSO_4 \cdot 7H_2O$, 0.5 g KNO_3, 1.0 g K_2HPO_4, 0.060 g $Ca(NO_3)_2 \cdot 4H_2O$, and 11.0 g Agar Noble l^{-1} of solution. The medium for isolating copiotrophs contained 1.0 g C (glucose)/l of agar solution and the medium for isolating oligotrophs 5.0 mg C (glucose) plus 2.50 μg C ml^{-1} soluble C contained in the water used. Filter sterile cyclohexamide of (100 μg ml^{-1}) was added after the autoclaved agar medium was cooled down to about 40°C to inhibit fungal growth. The C content in the copiotrophic medium was chosen within the range of C content of root exudates (Darrah, 1991), while the C content in the oligotrophic medium was close to the lower limit of available C in bulk soils (Nelson et al., 1994). A subsample equivalent to 2.0 g dry soil from each composited sample was suspended in 18.0 ml of sterile distilled deionized water and vortexed at high speed for 1 min. Additional dilutions were made through serial dilution (down to 10^{-6}). Fifty μl of the 10^{-4} to 10^{-6} suspensions was plated on each of both media in duplicate. Bacterial colonies were counted 7 d and 14 d after the plating on nutrient-rich and nutrient-poor media, respectively. Strictly speaking, these two groups of bacteria do not exactly coincide with copiotrophs and oligotrophs since we did not test if our low nutrient isolates could grow on rich media (Suwa and Hattori, 1984). However, we will refer to the bacteria isolated on our rich media as copiotrophs and to those isolated on our low C media as oligotrophs.

2.6. Microbial biomass carbon

Microbial biomass C was determined by a chloroform fumigation- extraction method (Vance et al., 1987). Briefly, a 20.0 g (dry wt. equivalent) moist soil sample was extracted immediately with 60.0 ml 0.5 M K_2SO_4, shaken for 30 min and filtered (Whatman Paper No. 42) on a vacuum extraction set. A second 20.0 g sample was fumigated with chloroform for 48 h and then extracted with 60.0 ml 0.5 M K_2SO_4 as above. Extracts were immediately frozen until analyzed using a Shimadzu total organic carbon analyzer. Microbial biomass C was calculated from the total dissolved organic C by using a Kec-factor of 0.33 (Sparling and West, 1988).

2.7. Statistical analyses

Statistical analyses were completed using SAS (SAS Institute, Cary, NC). Analyses of variance (ANOVA) was carried out with a two-way factorial nested design (cover cropping as main plots and sampling stages as subplots). In order to analyze effects of sampling time, data were separately analyzed by dividing them into two subgroups (cover crop treatment and non-cover crop treatment). Pearson correlation coefficients were calculated between bacterial numbers and C variables, and among C variables. All the data on bacterial numbers were log transformed since the variance increased with means. The relationships between bacterial numbers (either oligotrophic or copiotrophic) and water- or buffer-soluble C or mineralizable C were fitted using SigmaPlot Jandel Corporation, 1992, which uses the Marquardt–Levenberg algorithm to find the coefficients (parameters) of the independent variable(s) that give the best fit between the equation and the data.

3. Results

3.1. Decomposition of cover crop residues and its effects on labile C pools

Soil temperature was lower at the beginning of the experiment than the average in previous years because of higher rainfall in Spring, 1995 (Fig. 1(a)). Soil moisture was fluctuating between −0.024 to −0.02 Mpa, which should not inhibit microbial activity (Fig. 1(b)). Cover crop residues decomposed rapidly following their incorporation, resulting in 45.3% mass loss of residues in litterbags in the first

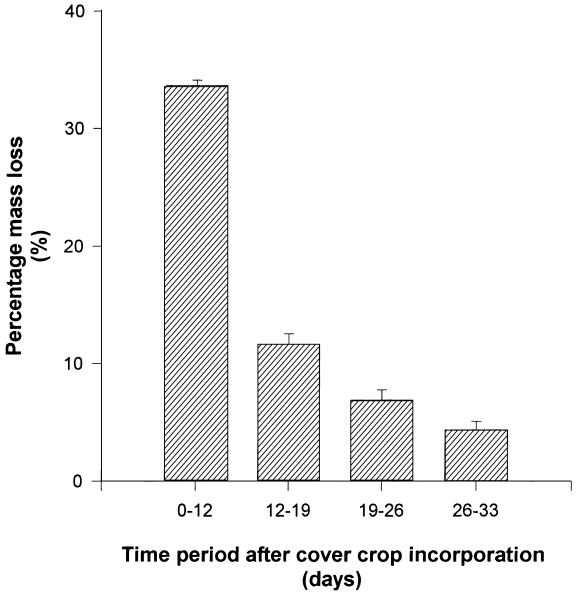

Fig. 2. Percentage mass loss of cover crop residues in the litterbags during the sampling periods. Values are means ± SE.

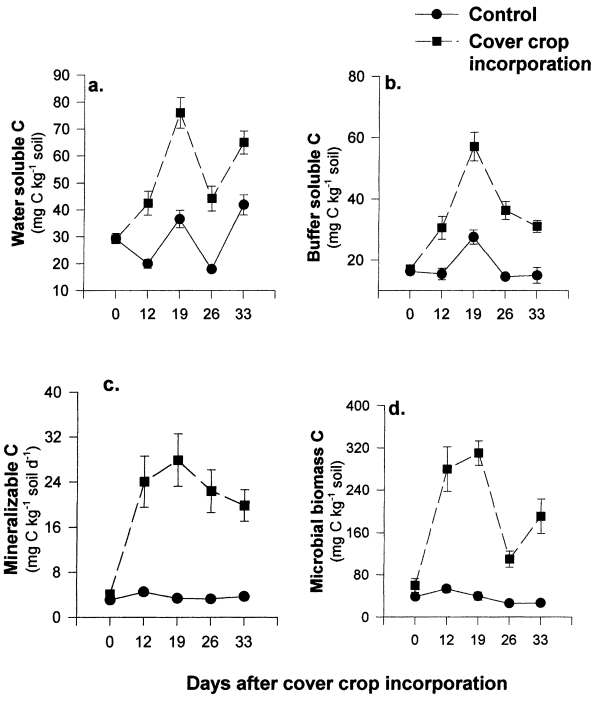

Fig. 3. Soil water soluble C (a), buffer-extractable C (b), mineralizable C (c) and microbial biomass C (d) before (Day 0) and after cover crop incorporation at the study site. Values are means ± SE.

19 days (Fig. 2). This result indicated that almost half of residue C had been respired by microbes or transformed into soil organic C and microbial biomass. This resulted in a significant increase in the size of all labile C pools, which peaked on Day 19 after residue incorporation (Fig. 3). Water-soluble C ranged from 29.8 mg C kg^{-1} soil before the incorporation to 76.0 mg C kg^{-1} soil on Day 19 (Fig. 3(a)). Strong fluctuation in water-soluble C was recorded. Relative increases in buffer-soluble C and mineralizable C due to cover crop addition were more significant than in water-soluble C. Buffer-extractable C increased more than three times to 57.1 mg C kg^{-1} soil from 17.1 mg C kg^{-1} soil (Fig. 3(b)), and mineralizable C increased almost seven times from 4.1 to 27.9 mg C kg^{-1} soil d^{-1} on Day 19 (Fig. 3(c)). Water soluble C (averaging at 40 mg C kg^{-1} soil) was significantly higher than buffer-extractable C (averaging at 26 mg C kg^{-1} soil) ($p < 0.001$). However, mineralizable C was based on CO_2 evolution per day (Fig. 3(c)) so that the total was significantly higher than water- and buffer- soluble C. Microbial biomass C was exceptionally low in the original soil at 59.6 mg C kg^{-1} soil, increased significantly following residue incorporation, and peaked at 310 mg C kg^{-1} soil by Day 19. A significant decrease in microbial biomass C by Day 26 may be due to exhaustion of available C source as well as high soil temperature prior to this sampling date (Fig. 1). The temperature effect on microbial biomass C was mainly on copiotrophs as oligotrophs were not affected (Fig. 4). Microbial biomass C recovered on Day 33 when soluble C increased possibly due to autolysis of the earlier biomass pool (Fig. 3(d)).

For non-cover crop soils, significant temporal variation in water soluble C was observed, buffer extractable C of Day 19 soil was higher than other samples (Fig. 3(b)). No significant changes in mineralizable C were observed after an initial increase (Fig. 3(c)). Microbial biomass C was extremely low being 38.4 mg C kg^{-1} soil, and increased to 53.4 mg C kg^{-1} soil at the early stage in non-cover crop soils, probably because of increased C availability for microorganisms due to soil disruption after preparation of the beds (Fig. 3(d)).

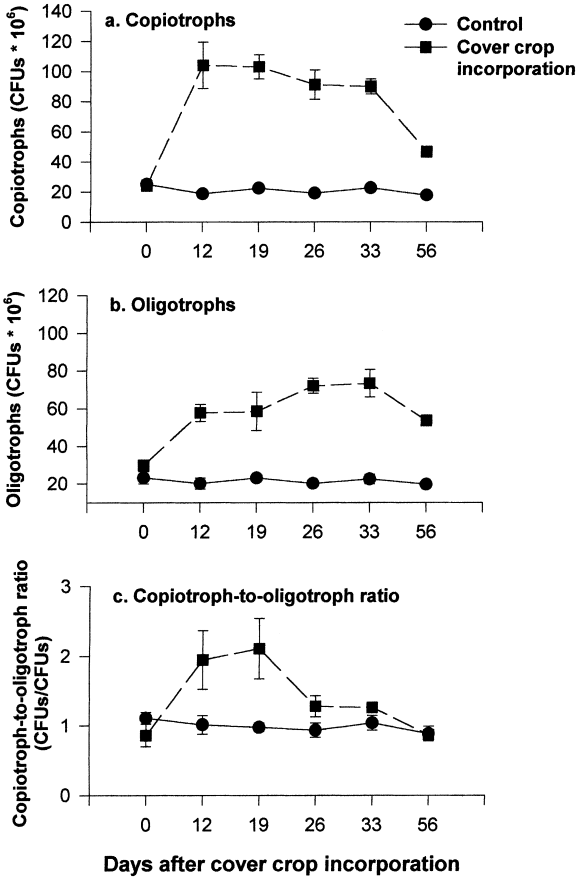

Fig. 4. Time course of (a) copiotrophic and (b) oligotrophic bacteria, and (c) the Copiotroph-to-Oligotroph ratio as influenced by cover crop incorporation. Values are means ± SE.

3.2. *Growth responses of copiotrophic and oligotrophic bacteria to changes in C availability*

Total microbial biomass C increased significantly following the cover crop incorporation (Fig. 3(d)) at least partially due to enhanced C availability for microbes (Table 1). Both copiotrophic and oligotrophic bacteria were significantly stimulated by C increase due to cover crop addition (Fig. 4), but population dynamics followed different patterns. In the cover crop amended soils, copiotrophs rapidly peaked at 1.04×10^8 cfu g^{-1} soil on Day 12 after residue incorporation (Fig. 4(a)), but increase in oligotrophs was much slower at the beginning, and peaked at 7.35×10^7 cfu g^{-1} soil on Day 33 (Fig. 4(b)). There were more copiotrophs than oligotrophs in residue-amended soils except those from the last sampling date, suggesting that copiotrophs were more stimulated by increased C. Copitroph-to-Oligotroph ratio increased rapidly following the residue incorporation and then decreased by Day 26 (Fig. 4(c)). The number of both copiotrophic and oligotrophic bacteria declined by the last sampling date and there was no trend implying that oligotrophs would overtake copiotrophs.

Copiotrophs were logarithmically related to water-soluble C (Fig. 5(a)), buffer-soluble C (Fig. 6(a)) and mineralizable C (Fig. 7(a)), while oligotrophs were quadratically related to those three labile C pools (Fig. 5(b), Fig. 6(b), and Fig. 7(b), respectively). Although there were similar trends in the relationships between bacteria (either oligotrophs or copiotrophs)

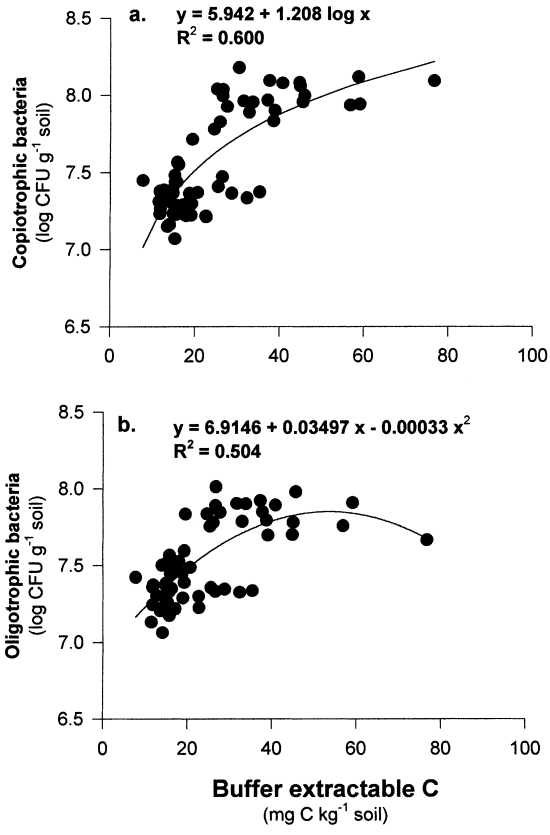

Fig. 5. Relationship between water-soluble C and populations of (a) copiotrophic and (b) oligotrophic bacteria.

Table 1
Linear correlation coefficients among bacterial numbers and available C pools in soils amended with cover crop residues

Parameters	Water-soluble C	Buffer soluble C	Mineralizable C	Microbial biomass C	Copiotrophs	Oligotrophs
Water-soluble C	1.00	0.79***	0.65***	0.65***	0.61***	0.41*
Buffer-soluble C		1.00	0.76***	0.66***	0.65***	0.21 NS
Mineralizable C			1.00	0.77***	0.78***	0.45*
Microbial biomass C				1.00	0.69***	0.22 NS
Copiotrophs					1.00	0.42*
Oligotrophs						1.00

*, ** and *** mean significant at $p = 0.05$, 0.01 and 0.001, respectively.
NS: not signifciant.

and three C pools, the relationships were closest with mineralizable C, and the difference in response of copiotrophs and oligotrophs to altered C supply was best revealed by the relations between bacterial numbers and mineralizable C. The relation between copiotrophs and mineralizable C was best described by a logarithmic function (Fig. 7(a)) as follows:

$$Y_c = 6.95 + 0.733 \times \log(X),$$
$$p < 0.0001, \quad R^2 = 0.827$$

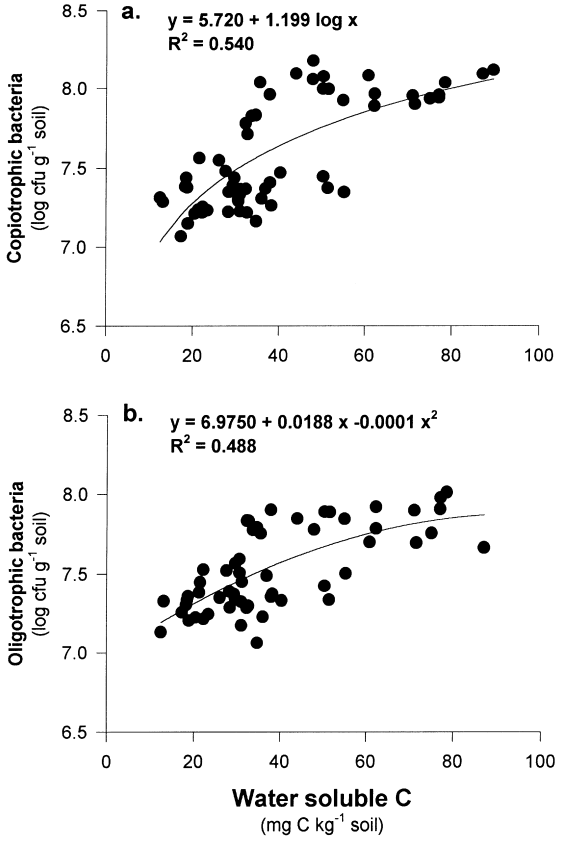

Fig. 6. Relationship between buffer-extractable C and populations of (a) copiotrophic and (b) oligotrophic bacteria.

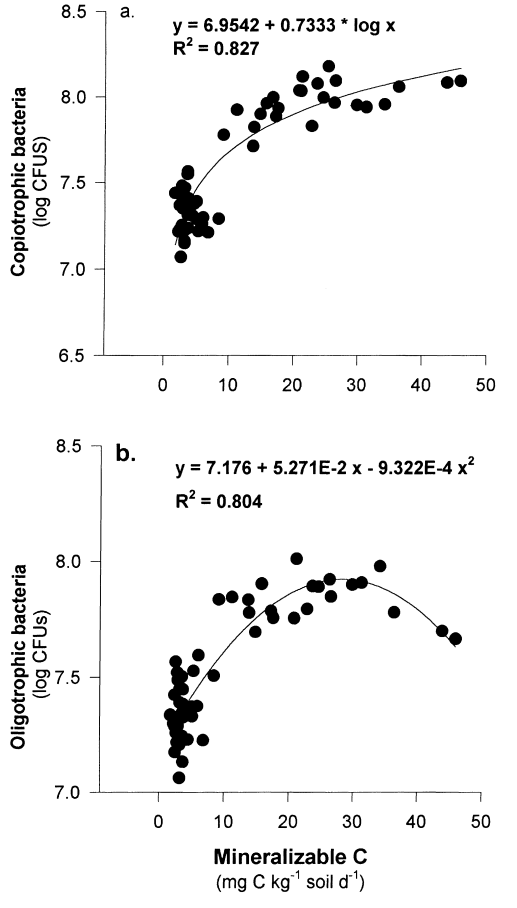

Fig. 7. Relationship between mineralizable C and populations of (a) copiotrophic and (b) oligotrophic bacteria.

where Y is log (CFUs) of copiotrophs and X is mineralizable C (mg C kg^{-1} soil day^{-1}). However, the log (CFUs) of oligotrophs (Y_o) was quadratically related to mineralizable C (Fig. 7(b)) as follows:

$$Y_o = 7.18 + 5.27 \times E - 2 \times X - 9.32 \times E - 4 \times X^2,$$
$$p < 0.0001, \quad R^2 = 0.801$$

3.3. Correlations among copiotrophs, oligotrophs and labile C pools and the relative contribution of copiotrophs and oligotrophs to soil microbial biomass C

The correlation between oligotrophs and copiotrophs ($r = 0.41$), although significant at $p = 0.05$, only accounted for 17% of the variance. The number of copiotrophs were significantly linearly correlated to water-extractable C, buffer-extractable C and microbial biomass C (Table 1). Oligotrophs were not significantly related to microbial biomass C as measured by fumigation extraction (Table 1), suggesting that they only contribute a minor part to total microbial biomass pool. Though copiotrophs are significantly correlated to microbial biomass C, the correlation only accounted for less than 50% of the variance (Table 1). This is reasonable since both bacteria and fungi significantly contribute to the total microbial biomass. Our results from direct counts of bacteria and fungi indicated that fungal biomass was about same as bacterial biomass (Grünwald et al., unpublished)

4. Discussion

Available C determined with different methods showed significant differences, as reported previously in both agricultural and forest soils (Davidson et al., 1987; Sikora and McCoy, 1990; Nelson et al., 1994). Nelson et al. (1994) recorded more C in weak buffer than in water extracts, which is not consistent with the results from the present experiment. In our soils, there was a substantial amount of refractory C in the water extractable C as evidenced by its yellow or brown color. Water extractable C concentrations were also variable in the non-cover crop treatments, possibly due to changes in temperature and then moisture (Biederbeck et al., 1994). The chemical compositions of soluble C may, therefore, be significantly different among different soils, which may determine the bioavailability of soluble C. Bioavailability of extractable C (either by H_2O or by other solutions) for microbes have long been debated. (Zsolnay and Steindl, 1991; Boissier and Fontvielle, 1993). Zsolnay and Steindl (1991) found that 85% of water-extractable organic C was biodegradable in an agricultural soil, but Boissier and Fontvielle (1993) reported that only 3.8–39.9% of dissolved organic C in leachates from two forest soils were biodegradable. These results suggest that at least part of soluble C may not be labile. In addition, significantly lower available C estimates from direct extraction methods compared to incubation methods indicated that direct extraction cannot detect a substantial part of C available for soil microorganisms. Over time, mineralizable C was best related to bacterial population dynamics and also provided the most stable estimates in non-cover crop treatments.

Results from the present experiments indicated that soil copiotrophs and oligotrophs responded to the increase in available C with significantly different patterns. Copiotrophs peaked when the highest C concentrations occurred but oligotrophs peaked at a later stage when the readily available C decreased (Fig. 6). The quadratic relationship between oligotrophs and mineralizable C indicated that oligotrophs may have been hindered or that oligotrophs could not compete with copiotrophs at high C concentrations. This is, to our knowledge, the first report showing that high C availability inhibited oligotrophs in natural soils, although previous reports indicated that high C concentrations were detrimental to pure culture of oligotrophs on agar or liquid media (Akagi et al., 1980; Fry, 1990). Akagi et al. (1980) reported that the colony number of a marine bacteria was maximal at 400 mg peptone-C l^{-1} of medium and then decreased significantly as C increased. The C concentrations in water and buffer solutions at which oligotrophs were inhibited in our experiments were lower than this number but they may be misleading since they were based on per gram of soil and localized C concentrations can be much higher on the surface of decomposing residues. In addition, some bacteria may adapt to wide range of C availability. Future work needs to directly test the oligotrophy of bacteria identified on the low C media.

Different correlation relationships between available C and oligotrophs and copiotrophs suggest that the relative dominance of each physiological group may be dependent on C availability. A change in relative dominance between oligotrophs and copiotrophs due to their differential response to an increase in available C has important implications. Firstly, changes in the C kinetics of bacterial populations could be of particular significance in understanding the microbial community structure and microbial interactions. Competition for available C and nutrients between root pathogens and other microbes has been proposed as the principal mechanism for suppression of some soilborne pathogenic fungi (Elad and Chet, 1987; Chung et al., 1988). Biocontrol agents should grow rapidly in C-rich environments such as the rhizosphere and the surface of newly-added debris so that it can overtake the pathogens. Secondly, the C requirement of the soil microbial community influences the effectiveness of microbial introductions. Therefore, knowledge of C utilization of the microbial community can theoretically provide information for improving the effectiveness of microbial introductions, as competitive exclusion can be one of several major barriers responsible for low efficiency of microbial introductions (Benizri et al., 1995).

Lack of significant correlation between oligotrophs and microbial biomass C may be due to the small size of oligotrophs since fumigation for 48 h has been shown to effectively kill oligotrophs (Hu and van Bruggen, 1997b). In seawater, many small and low-DNA-content bacteria, which have been referred as minibacteria, dwarfs and ultramicrobacteria, have high specific affinities typical of oligotrophs (Button, 1991). Button Button (1991), therefore, suggested that small bacteria might be more appropriately called oligobacteria. Bååth (1994) studied thymidine incorporation in soil bacteria of different cell size and suggested that small bacteria, although more numerous than larger ones, not only constitute a smaller proportion of bacterial biomass but also contribute to a lesser degree to direct C transformation in soil. However, the ecological functions of oligotrophs are not fully understood. A lower correlation between mineralizable C and oligotrophs than copiotrophs implies that oligotrophs contributed less to direct C mineralization than copiotrophs, but should not undermine the importance of oligotrophs in soil C metabolism and microbial interactions. Oligotrophs may contribute to C metabolism in a different way by which the metabolism of complex C sources could be stimulated due to their depletion of degradation products (Semenov, 1991; Hu and van Bruggen, 1997a).

In conclusion, both oligotrophic and copiotrophic bacteria were stimulated by increased C availability but with distinct patterns. Mineralizable C was best related to both copiotrophic and oligotrophic bacteria. Oligotrophic bacteria as detected in our experiments only contributed to an insignificant part of the soil microbial biomass pool as measured by fumigation extraction.

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