EFFECT OF LABILE INORGANIC PHOSPHATE STATUS AND ORGANIC CARBON ADDITIONS ON THE MICROBIAL UPTAKE OF PHOSPHORUS IN SOILS

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The effect of labile inorganic phosphate (P_i) status of the soil on the decomposition of added cellulose and on the immobilization, mineralization, and redistribution of native and added P in soils was studied in a greenhouse incubation experiment. Cellulose was added at 765 $\mu g\ C \cdot g^{-1}$ soil with and without P (9 $\mu g \cdot g^{-1}$ soil) every 30 days under adequate N, H_2O, and constant tempreature to two soils of different available P status. Lack of P eventually slowed down decomposition of added C, but this effect was partially compensated for by increased mineralization of organic P (P_o) forms. Added P was redistributed to both P_i (58-69%) and P_o (42-31%) forms; higher amounts of P_o were found in the soil with the highest P_i status. The correlation between microbial P uptake and solution P values was significant, and microbial C:P ratios ranged from 12:1 under high available P conditions to 45:1 where P was in low supply.

Les effets de la situation des phosphates inorganiques labiles (P_i) du sol sur la décomposition de la cellulose incorporée, et sur l'immobilisation, la minéralisation et la redistribution du P originel et ajouté ont été étudiés en serre nous incubation. Des apports de cellulose correspondant à 765 μg C/g de sol ont été effectués tous les trente jours avec ou sans fertilisation P (9 μg/g sol), en présence d'un régime d'alimentation hydrique et azotée adéquat et à température constante sur deux sols à bilan P différent. La pénurie de P a, à la longue, ralenti la décomposition du C d'appoint, mais l'effet a été partiellement compensé par la minéralisation accrue des formes organiques de P (P_o). Le P de fumure s'est réparti entre les formes inorganiques (58-69%) et organiques (42-31%) et, en outre, de plus fortes concentrations de P_o ont été retrouvées dans le sol à bilan P élevé. La corrélation obtenue entre le taux d'absorption de P par les mico-organismes et les valeurs de P en solution était significative et le rapport C/P fluctuait de 12:1 en régime de forte disponibilité de P à 45:1 en situation de faible diponibilité.

The development of techniques to measure the amount of phosphorus (P) and other nutrients released from soil biomass upon fumigating (lysing) microbial cells (Jenkinson and Powlson 1976) coupled with more accurate staining methods for measuring microbial biomass (Babiuk and Paul 1970; Paul and Johnson 1977) have provided the means of examining the dynamics of P cycling in soils (Cosgrove 1977; Cole et al. 1977). In an earlier investigation (Chauhan et al. 1979) of aspects of P cycling in a

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Chernozemic Black soil, the rate of P movement between soil inorganic (P_i), organic (P_o), and biomass (P_m) P compartments was measured following regular additions of grass and cellulose. The total content of P in microbial biomass was affected only slightly by addition of organic residue and/or fertilizer P to a soil with a high available P status (34 $\mu g \cdot g^{-1}$ resin-extractable P). The addition of fertilizer P did not change the percentage of added cellulose -C (47%) remaining in the soil after 9 mo incubation. The monthly addition of cellulose without fertilizer P depleted the labile P_i pool by more than 25% in 9 mo. This suggested that the continued addition of cellulose without P for a longer period of time would eventually have exhausted the reserve of labile P_i leaving the microbial population dependent on the rate of mineralization of P_o forms.

To examine the above hypothesis the dynamics of P within the soil system were examined in two soils representing high- and low-labile P_i status. This investigation had the objectives of (a) measuring the change in P forms (labile P_i and P_o) with time in two soils of different P_i status to which C sources were added every 30 days, and (b) relating these transfers to microbial activity.

MATERIALS AND METHODS

Two soils, the Bm horizon of a Chernozemic Black soil (29% clay, 2.0% organic C, and pH 7.8) of the Oxbow Association and the Ap horizon of a Chernozemic Dark Brown soil (17% clay, 2.3% organic C, and pH 6.8) of the Bradwell Association (Canada Soil Survey Committee 1978), were used in this experiment. These soils were air-dried at room temperature, ground to pass a 2-mm sieve, and thoroughly mixed prior to use. The available P status of the Bradwell soil (resin-extractable P-49.1 $\mu g \cdot g^{-1}$, $NaHCO_3$-extractable P-18.0 $\mu g \cdot g^{-1}$) was much higher than that of the Oxbow soil (resin extractable P-4.4 $\mu g \cdot g^{-1}$, $NaHCO_3$-extractable P-3.0 $\mu g \cdot g^{-1}$). In the first treatment, cellulose (43% C) was added at a rate equivalent to 765 $\mu g\ C \cdot g^{-1}$ every 30 days. In a second treatment cellulose was added at the same rate, and P as KH_2PO_4 was added at a rate equivalent to 9 $\mu g \cdot g^{-1}$ soil. In the third treatment the same quantity of P was added without the addition of C, and in the fourth treatment the original soil was incubated without addition of either C or P. Ammonium nitrate was used to adjust the C:N ratio of the cellulose treatment to 25:1. Required amounts of cellulose, N, and P were added and thoroughly mixed into soil every 30 days and incubated at field capacity at 24 ± 2°C. Algal growth on the surface of the soils was prevented by covering the surface of the pots with styrofoam beads. Moisture adjustments were made every second day.

Triplicate, 1-kg soil samples were used. At the end of each incubation period, 50-g subsamples were removed from each larger sample before further C or P additions. These subsamples were similarly treated with proportional additions of C and P, incubated in the same environmental conditions, but sampled at different times, depending on the stage of decomposition in the 30-day incubation period. An extra series of 50-g soil samples receiving the same treatment was incubated separately in airtight desiccators containing known volumes of standardized NaOH solution. This enabled daily measurements of CO_2 evolution to be taken. The latter series of incubations were started 5 days in advance of the main experiment; the rates of CO_2 production could thus be used to determine the times of sampling in the larger experiment. Measurements of microbial biomass, CO_2 evolution, $NaHCO_3$-extractable P_i and P_o-extractable P, P_m, solution P, and resin-extractable P were taken at the time of the maximum decomposition rate of the added organic materials, as determined by CO_2 production, and at a later stage when the CO_2 production had levelled off and approximately reached steady state conditions. At the end of the 9-mo incubation period, the total soil P was fractionated into various P_I and P_O forms. Experimental details have been described previously (Chauhan et al. 1979).

The methods of analyses used in this study are presented in Table 1. Further details are given below for some of the more recently developed techniques.

Microbial P (P_m)

Paired soil samples (air-dried <2 mm), one chloroform-treated and one untreated, were extracted at a 1:20 soil solution ratio with 0.5 M, pH 8.5 $NaHCO_3$ (Olsen et al. 1954). The difference in total P in the two extracts was found to approximate 25% of the total P_m in the two soils under study (Hedley and Stewart, Unpubl. data, Univ.

Sask). Liquid chloroform was applied directly to soils (1:1 wt/vol) for 30 min, then removed by aeration with a fan in a fumehood at 45°C. Chloroform-free dried samples were stored at room temperature for 6 days before extraction with $NaHCO_3$.

Moisture content and specific gravity of soil isolates were used to convert microscopic biovolume measurements to biomass (Van Veen and Paul 1979). This resulted in a multiplication of the bacterial biomass as calculated from literature values (Babiuk and Paul 1970) by a factor of 3.63. The fungal biomass was increased by a factor of 1.44. In the case of fungi the dry weight specific gravity value of 1.44 could represent an organism with a specific gravity of 1.3 and a moisture content of 76%.

Table 1. Analytical methods used in this study

Methods	Reference
$NaHCO_3$-extractable P	
(i) inorganic (P_i)	Olsen et al. (1954)
(ii) organic (P_o)	Halm et al. (1972); Bowman and Cole (1978a)
Microbial P ($CHCl_3$ treatment + $NaHCO_3$ extraction after 6 days)	Chauhan et al. (1979); Jenkinson et al. (1979)
Total (mineral and organic P)	Saunders and Williams (1955) (modified to use 2 N H_2SO_4), Halstead and McKercher (1975)
Inorganic P fractions	Peterson and Corey (1966) (modified for calcareous soils by Sadler and Stewart (1975))
Resin-extractable P	Sibbesen (1977)
Organic P fractions	Bowman and Cole (1978b)
Microbial biomas	
Bacteria	Babiuk and Paul (1970) (modified by Van Veen and Paul (1979))
Fungi	Paul and Johnson (1977) (modified by Van Veen and Paul (1979))
CO_2 evolution (NaOH absorbent in closed container)	
ATP	Paul and Johnson (1977)
Total C (dry combustion)	Allison (1965)
Solution P	Sadler and Stewart (1977)

RESULTS

Net changes in the organic C contents of the two soils following a 9-mo incubation with and without cellulose and/or P can be determined from the data for organic C content of the two soils (Table 2). Carbon determinations indicate that the Oxbow Bm treated with C + N + P still contained 4600 μg (67%) of the 6885 μg C added during the 9-mo incubation period. The Bradwell Ap retained less of the C with only an additional 4000 μg (58%) being found in the C + N + P treatment. The addition of C + N without P resulted in the retention of slightly greater amounts of C. Compared with the control soils, addition of P alone had no significant effect on soil C content.

Summation of the daily CO_2-C values and subtraction of data for the control indicate (Fig. 1) that 57% of the added C remained in the Oxbow Bm after 180 days in the cellulose + N treatment with 53% of the added C remaining in the cellulose + N + P treatment. The Bradwell Ap retained 43 and 39% of the added C in the cellulose treatments without and with added P, respectively. Further additions of C for another 3 mo resulted in a greater percentage of added C (47%) being retained in the treatment without P, whereas with P the same percentage (39%) was retained. In contrast, Chauhan et al. (1979) found in the Oxbow Ap soil that 47% of the added C remained after 180 days and

Table 2. Percent organic carbon content of the original soils after 9 mo of incubation (average of two replications ± SE)

Treatments	Oxbow (Bm) (% C)	Bradwell (Ap) (% C)
Original soil	1.97 ± 0.11	2.34 ± 0.11
Incubated soils		
Control	1.88 ± 0.05	2.21 ± 0.07
Cellulose + N	2.42 ± 0.09	2.64 ± 0.05
Cellulose + N + P	2.34 ± 0.11	2.61 ± 0.14
P treatment	1.88 ± 0.09	2.20 ± 0.09

the addition of P and C did not make any difference to CO_2 evolution.

The pattern of CO_2 evolution in the two soils indicates differences in the mode of attack on the added substrate. The Bradwell Ap horizon showed a rapid rise in CO_2 production upon the addition of cellulose at the beginning of each 30-day period. However, the height of the pulse attributed to added C decreased with each subsequent cellulose addition until, after 150 days, the increase in CO_2 evolution upon addition of extra substrate was only twofold. The Oxbow Bm showed significant pulses only after the first two additions.

Phosphorus additions increased the height of the CO_2 pulse. However, even with P additions, the CO_2 levels soon stabilized throughout the incubation period. The change from essentially first-order to zero-order kinetics, during which the rate of substrate transformation was unaffected by substrate concentration, showed that some factor besides P availability controlled substrate degradation, such that CO_2 evolution rates achieved a similar pattern of approximately

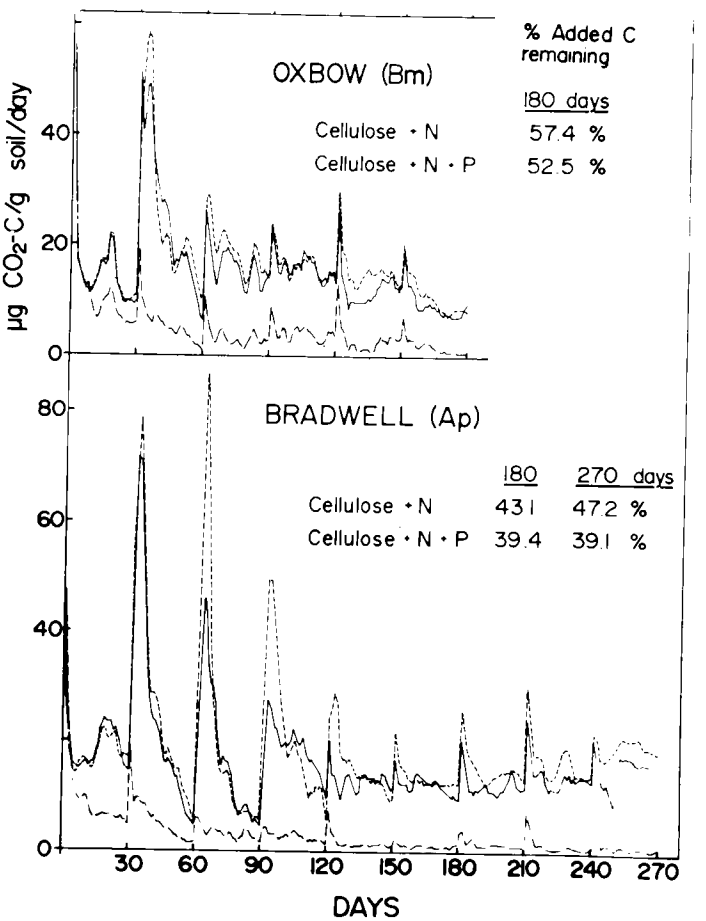

Fig. 1. Daily measurements of the CO_2-C produced per gram soil per day in the control and cellulose amended soils. Cellulose was added every 30 days at 765 μg C · g^{-1} soil.

20 μg CO_2-C · g^{-1} · day^{-1} in all soils studied. Only the Oxbow Bm, with original resin-extractable P and solution P values of 4.4 and 0.08 μg · g^{-1}, respectively, could be stated to be deficient in P. Equivalent values for the Bradwell soil were 49.1 and 0.8 μg · g^{-1}.

Estimates of combined bacterial and fungal C at different sampling times with treatment (Table 3) show that the addition of cellulose to both soils increased microbial C by a factor of 1.5 to 2.0. Values obtained at maximum CO_2-C productivity were higher than at the end of the incubation period (steady state) in the first two incubations. Average combined microbial C values obtained over the nine sampling dates in cellulose treatments were marginally higher in the Oxbow soil than in the Bradwell soil.

Net changes in P_i and P_o fractions in the Oxbow Bm and Bradwell Ap soil following a 9-mo incubation with and without cellulose and added fertilizer P can be determined from the data in Table 4. The recovery of added P (81 μg · g^{-1} soils) ranged from 98 to 111%. When the fertilizer P was added with cellulose, 58-69% of the added P was found in P_i forms. The addition of C without extra fertilizer P decreased the total P_i content by 15-25 μg P · g^{-1} soil and increased P_o by similar amounts. The addition of P fertilizer without a C substrate followed by incubation did not significantly alter the P_o content of either soil, and the added P was found in inorganic forms.

The two main indices of labile P_i in soils (resin-extractable P and $NaHCO_3$-extractable P_i) showed that the soils differed greatly in their ability to supply P (Table 4). The resin-extractable P was 4.4 μg · g^{-1} in the original Oxbow soil, whereas in the Bradwell Ap soil the resin-extractable P was 49.1 μg · g^{-1} soil. The differences in original solution P concentrations were also approximately tenfold, and both labile P_i indices correlated signficiantly with solution P values ($P < 0.001$) at each sampling date. Addition of C followed by incubation decreased the resin-extractable P in both soils. In the Oxbow soil, 3 μg P · g^{-1} soil were immobilized; whereas in the Bradwell soil, which had a greater supply of labile P, 11 μg P · g^{-1} soil were removed from the resin-extractable fraction by C addition and incubation. Similar trends could be seen with the $NaHCO_3$-extractable P_i value. Both these labile P indices were greatly increased by addition of fertilizer P, but when C was added with the fertilizer P, the increase in the labile P indices was not as great as when P fertilizer was added alone.

Cellulose additions without fertilizer P decreased NH_4Cl- and NH_4F-extractable P_i forms in both soils (Table 5) although the size of the decrease was much larger in the Bradwell soil than in the Oxbow soil. These

Table 3. Combined bacterial and fungal C (μg C · g^{-1} soil) at different sampling times in two soils incubated after different C + P treatment (values presented are the mean of duplicate analyses; SD < 15%)

Treatment	Sampling time (days)									X̄
	5	20†	30	34†	90	84†	120	124†	150	
					Oxbow (Bm)					
Control‡	185§	215	170	268	181	177	161	163	145	185
Cellulose + N	193	309§	277	356	441	466	448	447	395	370
Cellulose + N + P	342	279	292	382	286	392	454	387	356	352
					Bradwell (Ap)					
Control‡	261	229	180	329	157	218	160	186	159	208
Cellulose + N	275	393	224	533	244	357	313	404	300	338
Cellulose + N + P	282	287	282	513	210	393	319	390	280	328

† Maximum CO_2 evolution.
‡ Average of microbial C in control and soil + P treatments.
§ SD < 20%.

two fractions constitute the major source of labile P_i in calcareous soils (Sadler and Stewart 1975). Addition of P, either alone or with C, increased the first four P_i fractions in both soils and the NaOH-extractable P in the Oxbow soil. The effect of C additions on added P distribution was to decrease NH_4Cl- and NH_4F-extractable P_i significantly in both soils. In the Oxbow soil NaOH-NaCl-extractable P was also significantly decreased and the other two P_i fractions were lower. The increase in reductant-soluble P on P addition was greater in the Oxbow soil of lower pH value, suggesting that secondary inorganic P of lower availability was being formed. No change was noted in the Bradwell soil in NaOH- and H_2SO_4-extractable P_i fractions, which are thought to be more insoluble Fe-bound, and primary mineral (hydroxy apatite) P, respectively; but in the Oxbow soil some changes were noted in the NaOH-extractable P_i, suggesting that it may be utilized as a P source when labile P_I is very low.

Incubation of the soil without C amendments resulted in changes in the distribution of P_o in both soils (Table 5); the alkali-hydrolyzable and humic -P decreased while fulvic P increased. Incubation without added P but with C increased total P_o. Most of the increase occurred in the H_2SO_4-extractable and fulvic P fractions. Decreases in alkali-hydrolyzable P values were noted in both soils but the decrease was much larger in the Oxbow (Bm) soils. Humin -P values also increased in this treatment in both soils, but these results were obtained by difference between total P_o and the sum of the other P_o fractions and cannot be considered to be significantly different. Incubation with both added P and C showed significant increases in H_2SO_4-extractable P and fulvic -P with no significant change from the C-alone incubation in any other P_o fraction.

The $NaHCO_3$-extractable P_i, P_o and P_m values (data not shown), at various sampling dates corresponding to the maximum decom-

Table 4. Total organic and inorganic P and labile P indexes in the original soils and after 9 mo of incubation. All results are expressed as $\mu g\ P \cdot g^{-1}$ oven-dry soil and are the average of three determinations of each of three replicates (± SD)

	Original soil	Control soil	Cellulose + N-treated soil	Cellulose + N + P-† treated soil	P-treated† soil
	$\mu g \cdot g^{-1}$ soil				
	Oxbow (Bm)				
Total P					
Soil P	563 ± 10	565 ± 12	563 ± 13	645 ± 16	655 ± 21
Inorganic P	250 ± 4	254 ± 8	239 ± 7	310 ± 10	338 ± 14
Organic P‡	313	311	327	335	317
Labile P indices					
Resin-extractable P	4.4 ± 0.7	6.1 ± 1.0	3.3 ± 0.6	35.6 ± 6.2	49.6 ± 11.2
Solution P	0.08	0.08	0.03	0.52	1.04
$NaHCO_3$-extractable P	3.0 ± 0.4	3.9 ± 0.2	1.0 ± 0.1	20.9 ± 1.1	27.9 ± 0.3
	Bradwell (Ap)				
Total P					
Soil P	633 ± 10	635 ± 11	625 ± 11	717 ± 10	718 ± 14
Inorganic P	285 ± 7	290 ± 4	265 ± 7	337 ± 7	370 ± 7
Organic P†	348	345	360	380	348
Labile P indices					
Resin-extractable P	49.1 ± 3.7	51.3 ± 4.1	40.4 ± 3.0	95.6 ± 16.8	117.1 ± 18.6
Solution P	0.84	1.09	0.45	5.25	10.25
$NaHCO_3$-extractable P	18.0 ± 1.3	15.8 ± 0.9	4.5 ± 0.8	33.7 ± 2.1	48.8 ± 3.1

† P added = 81 $\mu g \cdot g^{-1}$ soil.
‡ By difference.

position rates of the added organic matter and steady state conditions, showed differences for each soil. The P_i concentration decreased with the addition of cellulose in the Oxbow Bm soil and reached very low levels (<1 $\mu g \cdot g^{-1}$ soil) by the end of 30 days and remained at these low levels throughout 150 days of incubation. P_m values consistently increased over the first 4 days of incubation following cellulose addition despite the fact that P_i values were extremely low. In contrast, P_o values tended to decrease at the time of maximum P_m uptake and to increase in P_o at the steady state stage.

The initial P_m values were over 50% higher in the Bradwell soil than in the Oxbow Bm soil and showed a similar if less distinct pattern during the first three incubation periods. Thereafter, P_m values did not show a distinctive pattern. P_i values in the treatment where C was added without P decreased from 18.0 to 13.2 $\mu g \cdot g^{-1}$ during the first 5 days of incubation and then decreased more slowly over the remaining 9-mo incubation to 4.5 $\mu g \cdot g^{-1}$. Where C was added with P, P_i values increased with each incubation to 32.7 $\mu g \cdot g^{-1}$.

Microbial C/P ratios calculated from these observations (Table 6) reflect the fact that biomass values were similar in both soils with C addition, but P_m production was greater in the Bradwell soil. Addition of P to both soils lowered C/P ratios; addition of C without P increased C/P ratios. Biomass C and P_m

Table 5. Organic and inorganic P fractionation data in the original soils and after 9 mo of incubation. All results are expressed as $\mu g\ P \cdot g^{-1}$ oven-dry soil and are the average of three determinations of each of three replicates (± SD)

	Original soil	Control soil	Cellulose + N-treated soil	Cellulose + N + P-† treated soil	P-treated† soil
			$\mu g \cdot g^{-1}$ soil		
			Oxbow (Bm)		
Inorganic P fractions‡					
NH_4Cl-extractable P	0.4±0.0	0.5±0.2	0.4±0.1	5.7±0.2	11.8±0.2
NH_4F-extractable P	5.8±0.2	9.8±0.6	5.8±0.6	38.7±0.4	55.6±4.6
NaOH-NaCl-extractable P	9.8±0.4	10.7±0.9	9.5±1.1	21.0±0.4	25.1±0.5
Reductant-soluble P	13.2±0.3	14.8±2.5	14.4±0.3	20.2±2.6	21.9±1.0
NaOH-extractable P	17.8±0.2	15.6±1.8	14.7±1.4	17.6±6.7	19.0±1.8
Organic P fractions					
H_2SO_4-extractable P	47.5±2.5	47.0±1.0	49.0±0.0	60.0±4.5	42.0±2.0
Alkali-hydrolyzable	30.5±0.5	24.3±3.0	16.8±2.2	12.8±1.8	20.0±2.0
Fulvic P	42.5±1.5	61.7±1.0	17.2±0.8	79.2±3.8	66.0±0.5
Humic P	105.0±3.0	99.5±3.2	95.6±0.6	96.0±4.2	101.7±3.7
Humin P§	87.5	78.5	91.4	87.0	87.3
			Bradwell (Ap)		
Inorganic P fractions‡					
NH_4Cl-extractable P	6.9±0.3	7.5±0.5	2.8±0.6	21.9±1.0	28.4±1.0
NH_4F-extractable P	36.5±0.2	37.1±1.2	25.1±2.0	61.6±1.4	71.7±1.5
NaOH-NaCl-extractable P	25.6±0.7	25.8±0.2	23.5±0.4	32.1±0.9	33.5±0.2
Reductant-soluble P	14.2±1.0	13.9±0.1	13.8±0.3	15.6±0.3	17.9±0.9
NaOH-extractable P	13.1±0.9	13.6±1.4	13.3±1.4	13.3±0.4	15.3±2.0
Organic P fractions					
H_2SO_4-extractable P	79.0±1.0	79.5±0.5	81.8±3.2	86.3±6.2	77.0±3.0
Alkali-hydrolyzable	30.0±2.5	25.5±1.5	22.3±0.8	23.5±2.0	25.3±2.2
Fulvic P	70.5±1.0	96.0±2.0	116.8±3.7	129.5±5.0	97.8±1.8
Humic P	107.0±4.0	85.0±3.0	83.5±4.5	79.5±3.5	83.5±2.0
Humin P§	61.4	57.0	63.6	61.2	64.4

† P added = 81 $\mu g \cdot g^{-1}$.
‡ Other inorganic P fraction; H_2SO_4-P not shown as relatively constant.
§ By difference.

values were not significantly correlated. Microbial P_m values were significantly correlated ($P > 0.001$) to solution P values over the complete sampling period.

ATP values taken at each sampling date (Fig. 2) show that the values obtained in the Oxbow soil were generally lower than those obtained in the Bradwell soil. In the Bradwell soil the ATP values obtained from the C additions were consistently higher than the control or P-alone treatments. Addition of P with C did not change the ATP levels from those obtained with C alone. In the Oxbow soil the ATP levels from all treatments were closer, but the C additions with P produced higher ATP values than C additions without P; these, in turn, were consistently higher than treatments that did not receive P. Calculated microbial C/ATP data (Table 7) reflect the fact that ATP levels in the Bradwell soil were higher than in the Oxbow soil and the fact that the microbial C values were comparable in both soils with similar C additions. Mean microbial C:ATP ratios obtained for control treatments were 281 and 203, respectively, in the Oxbow and Bradwell soils. Addition of C without P increased the average C:ATP ratio to 460 in the Oxbow soil and to 257 in the Bradwell soil. Addition of P with C consistently decreased the microbial C:ATP ratios. The magnitude of this decrease was greater in the Oxbow soil of low available P_i status.

DISCUSSION

The results obtained in this study are best discussed with reference to a flow diagram of the P cycle. This diagram (Fig. 3) conceptualizes solution P originating from the very slow weathering or primary P minerals (mainly hydroxyapatites in the soils under study) and being held in equilibrium with the labile P_i pool. In more weathered soils there will be a concurrent flow into secondary P minerals and some of these minerals may be occluded by Fe deposition on surfaces as weathering intensity increases (Smeck 1973). In neutral soils, flows into secondary P minerals are small and the main flow is into the labile P_i pool. The distribution of added P between solution and labile P_i depends on the capacity factor b (resin P/solution P = b) which Olsen and Watanabe (1963) showed to be relatively constant in many soils over the normal range of P fertilization (additions of P to 25 $\mu g \cdot g^{-1}$).

No significant change was noted in hydroxy apatite-P during the 9-mo incuba-

Table 6. Microbial C/P ratios† at sampling dates in each 30-day incubation corresponding to maximum CO_2 production. Values presented are the mean of duplicate samples

Treatment	Sampling time (days) 20	34	64	94	124	Mean‡	Mean§
			Oxbow (Bm)				
Control	39	8	29	10	20	21	26
Soil + P	12	8	28	6	14	14	17
Cellulose + N	37	19	27	22	54	32	45
Cellulose + N + P	22	12	34	22	22	22	29
			Bradwell (Ap)				
Control	40	12	10	6	5	15	16
Soil + P	28	10	7	6	5	11	12
Cellulose + N	56	14	12	17	22	24	21
Cellulose + N + P	41	17	10	11	12	18	16

† Microbial P extracted by $CHCl_3/NaHCO_3$ extraction was assumed to be 25% of the total microbial P (Hedley and Stewart unpubl. data).
‡ Mean C/P ratios at maximum CO_2 production sampling times.
§ Mean C/P ratios at all sampling dates.

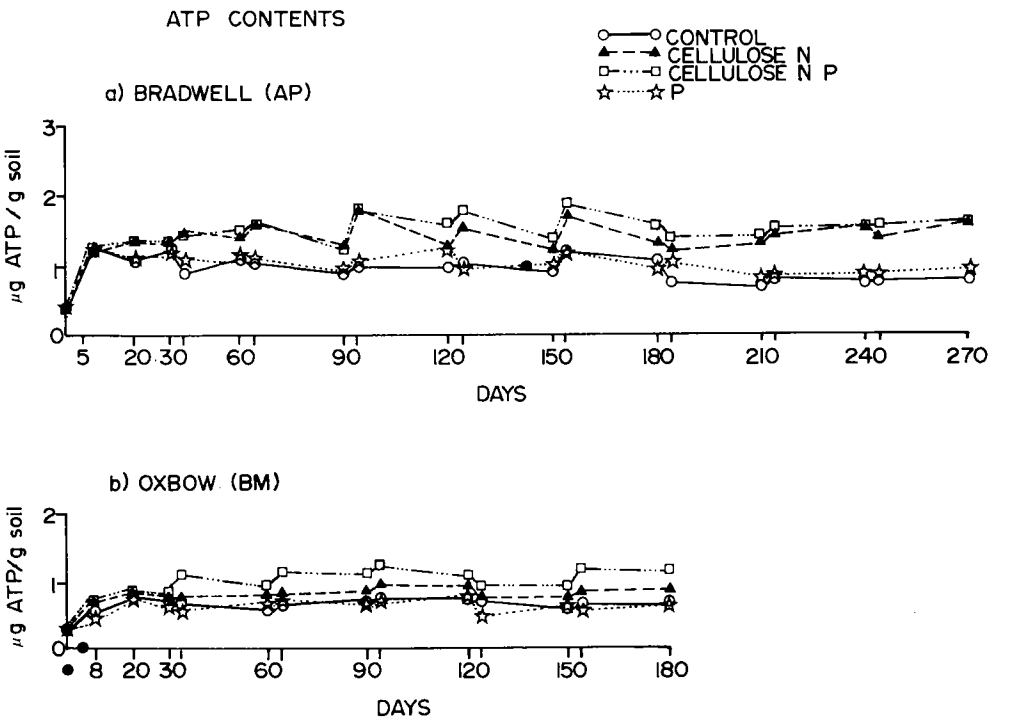

Fig. 2. ATP contents in both soils measured in four treatments with time.

tion. Small amounts of added P were found as secondary P_i minerals in the more acid soil (Oxbow Bm) and most of the added P was found in the labile P_i pool. The capacity factor of both control soils was not affected by incubation, but did change when cumulative amounts of added P became large (Fig. 4). The capacity factor of the Oxbow soil remained approximately constant at 95 until the cumulative addition of added P was approximately 27 $\mu g \cdot g^{-1}$. Thereafter, it decreased steadily to approximately 50 when 81

Table 7. Microbial C/ATP ratios at different sampling dates in two soils incubated with different C or P amendments. (Sampling dates chosen represented maximum CO_2 activity and steady state activity in each 30-day incubation period)

Treatment	Sampling time (days) 5	20†	30	34†	90	94†	120	124†	X̄
				Oxbow (Bm)					
Control	274	283	261	439	270	253	224	247	281
Cellulose + N	316	517	360	475	525	392	492	604	460
Cellulose + N + P	600	372	348	354	265	332	432	421	390
				Bradwell (Ap)					
Control	209	206	145	346	173	213	144	190	203
Cellulose + N	260	377	167	363	188	202	237	264	257
Cellulose + N + P	222	209	612	349	169	220	275	220	220

† Maximum CO_2 activity.

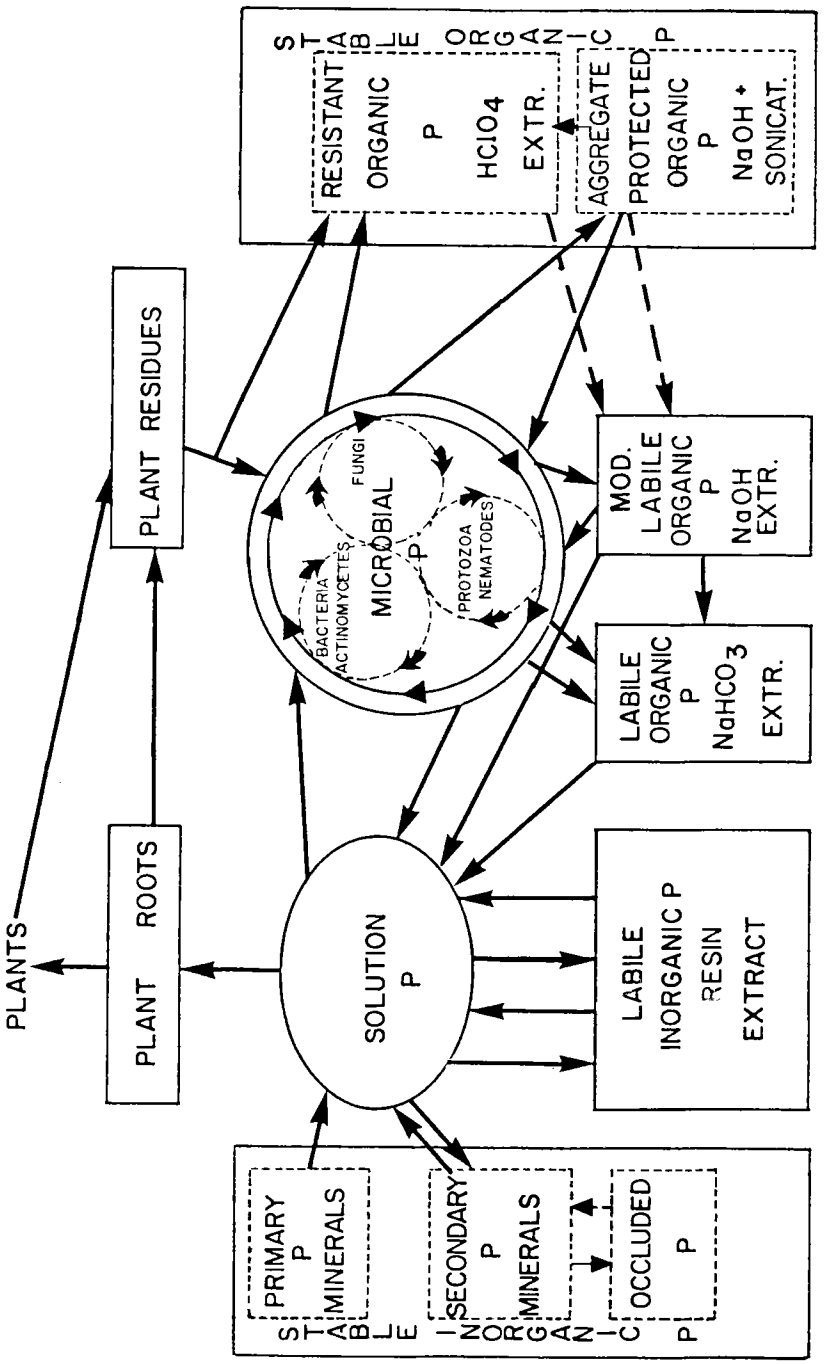

Fig. 3. Schematic illustration of the measurable components in the P cycle.

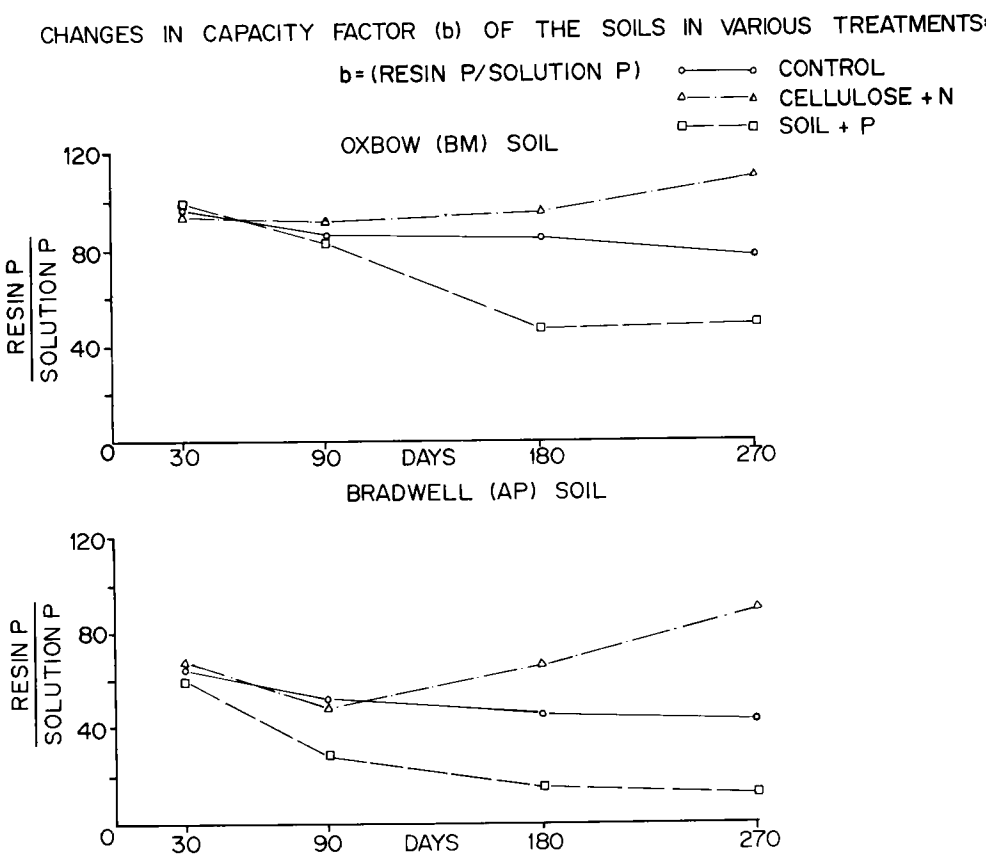

Fig. 4. Changes in the capacity factor of both soils with treatment and time.

$\mu g \cdot g^{-1}$ had been added without cellulose. With C and P additions the decrease in capacity factor reduction was slower and was approximately 70 after incubation and cumulative P additions of 81 $\mu g \cdot g^{-1}$. Additions of C without P did not cause much change in the capacity factor of well-buffered Oxbow soil. In the Bradwell soil, cumulative C addition increased the capacity factor, whereas cumulative P additions decreases it from its original value of 60. This means that the addition of extra fertilizer P would be divided initially among these two pools and that the increase in solution P resulting from addition of 9 $\mu g\ P \cdot g^{-1}$ would be greater in the Bradwell soil than in the Oxbow soil.

Higher solution P caused a greater uptake of P by the microbial populations. The P_m so accumulated would eventually be released (either through amoebal and nematode grazing as shown by Cole et al. (1978), or by death of microbial cells) releasing the contents of the microbial cell (RNA 30-50%, acid-soluble inorganic and organic P compounds 15-20%, consisting of ortho-meta, sugar, and adenosine phosphates, and various phosphorylated coenzymes, phospholipides $< 10\%$; and DNA 5-10%) to react with soil colloidal material. The rate of mineralization of the P_o released in this process will depend on phosphatase activity and on the type of P_o compound released (McKercher and Tol-

lefson 1978). Phosphatase production activity is inversely related to solution P concentrations (Speir and Ross, 1978).

Results obtained showed that microbial C:P ratios were closely correlated with solution P, with ratios as low as 12:1 and as high as 45:1 being recorded. Where solution P was low, the $NaHCO_3$-P_o values were found to fluctuate markedly and to decrease at times of maximum P_m production; when solution P was high, few changes in $NaHCO_3$-P_o were observed. Net changes in P_o composition upon treatment and incubation generally increased the fulvic acid P at the expense of alkali hydrolyzable and humic P. This would agree with the ideas presented by Anderson (1979) and McGill and Cole (in press). They postulated that the soil would contain a variable reserve of P_o that is associated with humic material. This reserve would differ as a function of both soil genesis and demand. Unfortunately, the changes in fulvic, humic and other P_o extracts were measured only at the end of 270 days of incubation and were not carried out after each 30-day incubation. Future work will attempt to measure these changes with time.

ATP values reflected both substrate and P availability with the result that average microbial C:ATP ratios ranged from 203:1 to 460:1. These values are considerably higher than the ratio proposed by Jenkinson et al. (1979) for soil organisms where no recent substrate has been added; however, the latter authors used a different ATP extraction technique. Low quantities of both solution P and labile P_i eventually slowed down the rate of decomposition of added cellulose in the Oxbow soil although an increased mineralization of P_o partially compensated for the low P_i values. Decomposition of added cellulose was also curtailed in the Bradwell soil after the $NaHCO_3$ P_i had been reduced.

Incubation of the soils without C or P additions did not cause significant changes in P_i or P_o forms but did increase the amount of P_o extracted as fulvic -P at the expense of humic P and alkali-hydrolyzable forms. Incubation with added C resulted in increases in total P_o at the expense of total P_i. Most of the P_i converted to P_o came from labile P_i forms in the Bradwel soil; but in the Oxbow soil, which did not have a large labile P_i pool, more unavailable forms of P_i appeared to have been utilized.

Added P was immobilized and redistributed in both inorganic and organic forms. The availability of solution had a marked effect on the forms of labile P_o measured in the soil with time. When an energy source was added without added P, P was immobilized from the various P_i forms and redistributed in the soil partially as P_o. When P was added without an energy source it accumulated in P_i forms with no change in net P_o. This study documents the type of P redistribution that can occur in soil and provides an explanation for seasonal variation in soil P_o observed by many authors in western Canadian soils.

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