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Changes in heated and autoclaved forest soils of S.E. Australia. II. Phosphorus and phosphatase activity

ISABEL SERRASOLSAS[1] and PARTAP K. KHANNA
CSIRO, Division of Forestry, P.O. Box 4008, A.C.T. 2600, Canberra, Australia; [1] *Present address: Department de Biologia Vegetal, Universitat de Barcelona, Avda Diagonal 645, 0828 Barcelona, Spain*

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Abstract. The effect of soil heat and autoclaving on labile inorganic P (Bray I), microbial P (P-flush) and on phosphatase activity was studied by heating five forest soils in the laboratory, which simulated the effects of heat during bushfires. Top soil was heated to 60 °C, 120 °C and 250 °C or autoclaved for 30 minutes. Soils were analysed immediately after heating and during seven months of incubation to assess immediate and longer-term effects of heating.

Labile inorganic P increased immediately after heating and autoclaving soils, with the highest amount recorded for the 250 °C treatment. Phosphorus associated with microbial biomass decreased with heat, and none or small amounts were detected in soils heated to 250 °C and autoclaved, because high temperatures killed the microbial population. Most of the P released from microbes acted as a source of labile inorganic P in soils low in inorganic P, and some of the released P was fixed by the soil. In one soil high in inorganic labile P and with undetectable amounts of microbial-P, the increase in Bray P on heating could only be assigned to solubilisation of other sources of total P. Because high temperatures denature enzymatic proteins, phosphatase activity diminished with the increase in temperature, and no activity was detected in 250 °C and autoclaved soils.

Phosphorus released by heating decreased during incubation in three of the five soils studied, approaching values observed in unheated soils. Simultaneously, an increase in microbial P was observed in these heated soils, indicating that the partial recovery of microbial biomass acted as a sink for the decrease in Bray-P measured. Phosphatase activity recovered only partially during incubation of heated soils.

Introduction

Fire is a major factor influencing the distribution and development of vegetation over much of Australia (Attiwill & Leeper 1987). Fire affects the fertility of forest ecosystems by altering the availability of some nutrients, by causing nutrient losses by volatilisation, and by affecting plant growth responses through changes in chemical, physical and microbial properties of soils.

Major effects of fires on mineral soils are related to heating, combustion, and ash addition. Some studies distinguish between the effects of ash addition (Marion et al. 1991; Fritz et al. 1994; Khanna et al. 1994) and soil heating (Khare et al. 1982; Kutiel & Shaviv 1989; Serrasolsas & Khanna 1995). Heating soils to temperatures above 100 °C produces both chemical and physical

changes. Soil is sterilised by heating to 125 °C, a temperature that may be reached at soil depths up to 2 cm under forest fires of moderate intensity (Humphreys & Craig 1981). At the temperature range of 200–800 °C, there is a marked increase in the readily-extractable iron and aluminium phosphates, and above 500 °C the phosphate-adsorption complex is irreversibly destroyed (Attiwill & Leeper 1987).

Many reports in the literature have indicated that in soils subjected to heat, levels of nutrients generally increase, particularly P (Sertsu & Sánchez 1978; Raison 1979; Kitur & Frye 1982; Trabaud 1983). Soil heating and the accompanying process of drying result in solubilisation of some organic matter due to chemical alteration and to the death of microorganisms (Jenkinson 1966) which release labile nutrients. A significant part of the P in microbial tissue may be present as inorganic P, and some inorganic P may be formed by the phosphatase-catalysed hydrolysis of cellular organic P (Brookes et al. 1982; Speir et al. 1986). Giovannini et al. (1990) and Saa et al. (1993) found that soil heating produced an intense mineralising effect on organic phosphorus resulting in an increase in inorganic P.

The improvement of soil fertility after fire diminishes with time, and forest growth may decline as a consequence of low P availability in the longer term (Binkley & Christensen 1992). Kutiel & Shaviv (1989), in laboratory incubations, found an increase in P availability after soil heating, but after a few weeks available P decreased to the original values. Different reasons have been assigned for the decrease in available P in the longer-term after fire, which include changes in the mechanisms of phosphorus adsorption and desorption (Silva et al. 1987; Kwari & Batey 1991; Romanyà et al. 1994), changes in the microbial population (Vázquez et al. 1993), and changes in the microbial immobilisation and mineralisation of P (Dunn et al. 1985; Polglase et al. 1992).

Fire affects soil enzymes, such as phosphatases, decreasing their amount and activity due heating and drying effects (Burns 1978; Tabatabai 1982; Adams 1992). In Australian forest soils, which are usually very poor in phosphorus, mineralisation of organic P, mediated primarily through phosphatase activity, appears to be an important process (Attiwill & Leeper 1987; Polglase et al. 1992, Thien & Myers 1992).

Some processes occurring in autoclaved (moist heat) soils may be similar to those occurring in soils heated in an oven (dry heat). Furthermore, autoclaving sterilises the soil (lysis of microbial cells), and in the process releases nutrients. Analyses following soil autoclaving may also give some indication of the labile-P (easily available or mineralisable).

The objective of the present study was to determine the immediate and longer-term changes in labile-P and phosphatase activity of some forest soils

Table 1. Some relevant soil characteristics (0–5 cm).

Code	Exchange. cations	Exchang. Al	Total P	Organic P	C/Porg.	P sorption maximum Xm
	mmol(+)/Kg		ug/g			ugPi/g
BFG	94	0	252	51	333	182.9
OUn	203	22	45	42	2124	94.6
ODu	49	8	68	31	1051	143.5
OGn	110	19	94	53	1166	1268.5
PC	139	90	458	316	335	1290.0

following heating to temperatures expected under bushfire conditions and during autoclaving. Changes in the labile phosphorus, phosphorus in microbial biomass, and phosphatase activity of the soils were measured following the treatments and after incubating soils under laboratory conditions of constant temperature for 210 days. A previous paper documented associated changes in C and N mineralisation in heated and autoclaved forest soils (Serrasolsas & Khanna 1995).

Materials and methods

Soils

The soils and the sampling procedure have been described in detail in part I of the paper (Serrasolsas & Khanna 1995). Briefly, five forest soils of different characteristics (Table 1; and Table 1 of Part I paper) were collected from experimental sites near Orbost in Victoria under mixed species (*Eucalyptus sieberi, E. baxteri* and *E. globoidea* in varying proportions) eucalypt forests (OGn, ODu, OUn), and near Canberra in the A.C.T. under *Eucalyptus pauciflora* (PC) and *Pinus radiata* (BFG) forests. Samples were taken from the surface (0–5 cm) of mineral soil at 10 randomly located points in winter 1992. These samples were well mixed to form a bulk sample and sieved (<5 mm). The samples were stored at field moisture content at 4 °C until use.

Treatments and incubation of soils

Treatments and incubation procedure have been described in detail in Part I of the paper by Serrasolsas & Khanna (1995). In short, four sub-samples, each of 400 g (forming a 2-cm thick layer), were separately heated for 30

minutes at 60 °C, 120 °C, 250 °C or autoclaved. Unheated soils (20 °C) were taken as a control. Part of the soil heated to 250 °C was inoculated prior to the incubation by mixing with 0.5% (by weight) of respective fresh soil to accelerate the recolonization of microbial populations.

Prior to incubation, soils were remoistened to 80% of field capacity. Heated, autoclaved and control soils were incubated for 210 days at 25 °C in the dark (4 replicates for each soil and treatment). Soils were placed in glass jars with a water container to avoid excessive moisture losses. Because of some drying, the soils were remoistened after 57 days of incubation. Jars were opened periodically for about 5 minutes to replace O_2. Labile inorganic P, microbial-P (P-flush), and soil phosphatase activity were measured in the treated soils before incubation and after 20, 60 and 160 days of incubation.

Soil analyses

Labile inorganic P was analysed in soils by the Bray-1 method using a shaking period for 5 minutes, and a 1:5 weight of soil:volume of extractant (Bray & Kurtz 1945). Inorganic P was determined following Murphy & Riley (1962).

As an estimate of microbial biomass, 'P-flush' was determined by the fumigation-extraction method using hexanol as a biocide (McLaughlin et al. 1986; Hossain et al. 1990; Thien & Myers 1992). Four ml of hexanol was added to a 10-g moist soil sample. After 24 hours of fumigation, soil was extracted using the Bray-1 method. P-flush was calculated as the difference in inorganic P between fumigated and unfumigated soil. P-flush was not corrected for either soil P fixation or any efficiency of recovery, the K_P factor, which might have accounted for insufficient fumigation and extraction of biomass P present in the soil.

Phosphatase activity was assayed following the methods of Tabatabai & Bremner (1969), which were slightly modified to suit our conditions. The analysis involved the measure of p-nitrophenol released during 30 minutes of incubation with Na p-nitrophenyl phosphate at 25 °C in water (instead of using a buffer) to maintain the original pH in the soil (Dalal 1982), because heating produced a slight change in soil pH. A blank, soil without Na p-nitrophenyl phosphate added, was analysed for each sample to subtract yellow colour not derived from p-nitrophenol released by phosphatase activity.

Total organic P was analysed by using the ignition method (Olsen & Sommers 1982). P extracted from unignited soil was used as a measure of total inorganic P, and the additional P, extracted from ignited soil, was taken as organic P. P sorption maximum was calculated following the classical Langmuir equation from the adsorption isotherms. Extractable cations and

aluminium were obtained by leaching moist soil with 0.1M $BaCl_2$ solution (Khanna et al. 1986).

Statistical analyses

Data from the four replicates for each treatment and soil were analysed using one-way analysis of variance to compare temperature differences and incubation time for each soil. The Duncan test was used to discern significant differences at a probability < 0.05. Regression analyses using all soils were also performed.

Results and discussion

Soils from the Orbost area (OUn, ODu and OGn) were low in total phosphorus (between 45 and 94 $\mu g.g^{-1}$) with very high C: organic P ratios (1051 – 2124), whereas BFG and PC soils had higher amounts of total P, 242 and 458 $\mu g.g^{-1}$ respectively, and lower C:organic P ratios (about 334) (Table 1). McGill & Cole (1981) reported that C:organic P ratios > 200 were associated with soils 'deficient' in P, whereas soils well supplied with available P had C:organic P ratios less than 100. Inorganic P extracted using Bray-I method was 10% of the total P in BFG, 2.2% in the OUn soil, and less than 0.7% for ODu, OGn and PC soils. Inorganic Bray P was positively correlated with C % (r^2 = 0.85, $p < 0.001$, $n = 16$), indicating organic sources contribute to Bray P through mineralisation in all soils, except the BFG soil, which contained very low organic matter but high Bray P. PC and OGn soils with high organic matter and clay contents had labile organic P in the Bray extracts (data not shown).

Immediate effects of heating on soil phosphorus and phosphatase activity

Labile inorganic P

Labile inorganic P (Bray I) increased in soils heated to 120 °C (ODu and PC soils only), and 250 °C (all soils) when compared with unheated control (Fig. 1). Compared with the control, increase in P at 250 °C was 1.5-fold (BFG), 3.5-fold (PC), 3.8-fold (OGn), 5.0-fold (OUn) and 10-fold (ODu soils). Organic Bray P (data not shown) increased with temperature in PC soil, whereas a decrease was found in OGn soil.

A number of studies have reported an increase in available soil P after heating (Kang & Sajjapongse 1980; Kitur & Frye 1983; Kwari & Batey 1991) or in soils collected after a forest fire (Dyrness et al. 1989; Marion et al. 1991; Romanyà et al. 1994). Different mechanisms have been suggested to explain

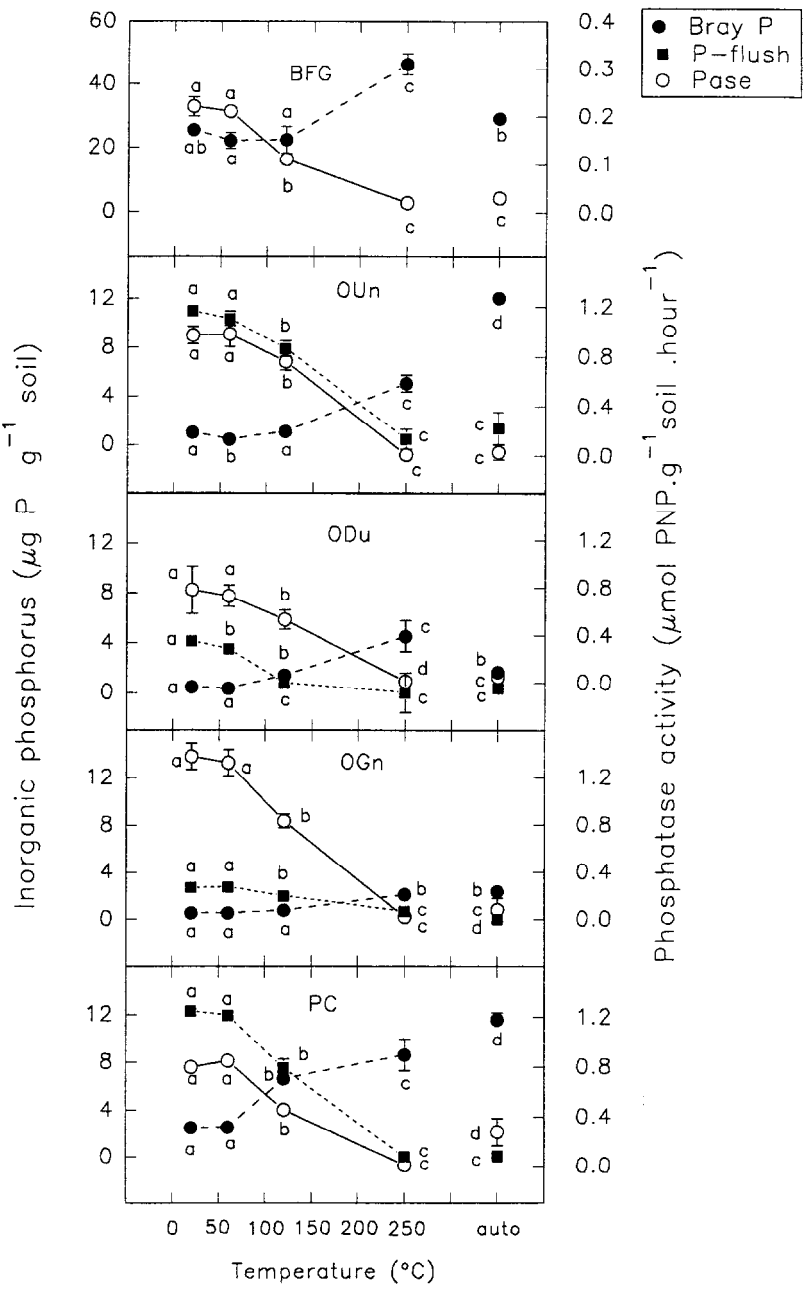

Fig. 1. Immediate effects of soil heating and autoclaving on the labile inorganic P (Bray 1), the P-flush (the difference in inorganic Bray P between fumigated and unfumigated soil) and the phosphatase activity. In BFG soil P-flush was undetectable. Different letters show significant differences ($p < 0.05$) among treatments. Note different scale of y axis for BFG soil.

this increase, such as organic matter solubilisation by chemical alteration (Jenkinson 1966; Walker et al. 1986), increase in organic P mineralisation (Sertsu & Sánchez 1978; Kutiel & Shaviv 1989; Saa et al. 1993), release of inorganic P from dead microorganisms (Marumoto et al. 1982; Seeling & Zasoski 1993) and solubilisation of readily-extractable iron and aluminium phosphates (Attiwill & Leeper, 1987).

Autoclaving increased labile inorganic P in the studied soils, with increases between 2.6- and 11-fold over control soils, except for the BFG soil which showed no change (Fig. 1). In most soils, the increase in labile-P produced after autoclaving was greater than the increase obtained when soils were heated to 120 °C. López & Barbaro (1988) and Xie & Mackenzie (1989) also reported an increase in P after autoclaving.

Microbial-P

Phosphorus associated with microbial biomass in the control soils was 5 to 15 times higher than labile-P in all soils, except in BFG, where undetectable amounts of microbial P were measured (Fig. 1). Microbial P was related to organic matter content, showing a positive relationship with %C ($r^2 = 0.69$, $p < 0.0001$, $n = 20$).

Microbial P significantly decreased when soils were heated to 120 °C and negligible amounts were obtained when heated to 250 °C, showing a negative relationship between temperature and P-flush for each soil ($r^2 = 0.81–0.98$, $n = 16$, $P < 0.0001$). DeBano & Klopatek (1988) and Polglase et al. (1992) reported that burning decreased the amount of biomass-P. Moreover, labile-P increased with the decrease in P-flush in heated soils ($r^2 = 0.65–0.92$, $P < 0.0005$, $n = 16$), except BFG. These results suggest that, for soils higher in microbial-P than in inorganic labile-P, microbial biomass may be an important source of labile-P upon heating. However, some of the P released from microbial sources was either not in an extractable form, or was fixed or immobilised again by the soil. Similar results were reported by Speir et al. (1986) who subjected souls to microwave radiation. Marumoto et al. (1982) suggested that in the incubated unfumigated and fumigated soils, microbial biomass P contributed considerably to the mobile P fraction in soil. Different sources of labile-P, other than microbial biomass or organic P solubilisation and mineralisation, must have caused the increase in inorganic labile P observed on heating BFG soil to high temperatures.

The microbial P-flush was very low (or undetectable) in autoclaved soils (Fig. 1). There was a close relationship between the increase in Bray P and the decrease in P-flush ($r^2 = 0.66$, $p < 0.0001$, $n = 20$), with the slope of the regression being close to unity. Hence, on autoclaving the decrease in P-flush was either of the same order (for ODu and OGn soils) or slightly

greater (OUn) than the increase in Bray P. This result suggests that the source of inorganic P in autoclaved soils was mostly microbial and only a small fraction of the microbial P released on autoclaving was either fixed by the soil or existed in organic form. Similarly, Seeling & Zasoski (1993) observed that increase of P in soils when sterilized by gamma says corresponded to P released from microbial biomass. In the BFG control soil, microbial P was undetectable and consequently Bray P increased little after autoclaving.

Phosphatase activity

Both negative and positive relationships of phosphatase activity with total organic phosphorus, labile organic P, and available P have been reported in the literature (Harrison 1987). These data suggest that the factors affecting phosphatase activity in soils, and its relationship with the mineralisation of organic matter, are very complex. In the present study, phosphatase activity in control soils was not related to total P, organic P, labile-P, or organic matter content, However, it was correlated with soil moisture content ($r^2 = 0.49$, $p < 0.0005$, $n = 20$), indicating that these enzymes may be very sensitive to drying. BFG soil, which was the driest of all soils, had the highest labile-P content but the lowest phosphatase activity.

Phosphatase activity decreased when soils were heated to temperatures higher than 60 °C, hence phosphatase activity and treatment temperature were correlated for each soil ($r^2 = 0.89$–0.97, $p < 0.0001$, $n = 16$). Soil moisture content decreased during heating, which as already described in control soils, showed a good relationship with phosphatase activity ($r^2 = 0.85$–0.97, $p < 0.0001$, $n = 16$). At 120 °C, the decrease in phosphatase activity was between 22 and 50% (Fig. 1) but at 250 °C it decreased by 90 to 100% of the values in the control. Heating (Burns 1978; Tabatabai 1982; Harrison 1983) and drying soils have been reported to reduce phosphatase activity and denature enzymatic proteins. Adams (1992) found that phosphatase activity decrease by 20 times in australian soils when dried, and no activity was found in soils affected by fire. Polglase et al. (1992) and Saa et al. (1993) also found a decrease in phosphatase activity after fire, but Debano & Klopatek (1988) observed no change when soils were heated under wet conditions.

Soil phosphatase activity decreased significantly (65–97% of the control) on autoclaving (moist heating) (Fig. 1). These decreases were greater than those observed when soils were heated to 120 °C (dry heat). Zou et al. (1992) used autoclaving to stop phosphatase activity in soils.

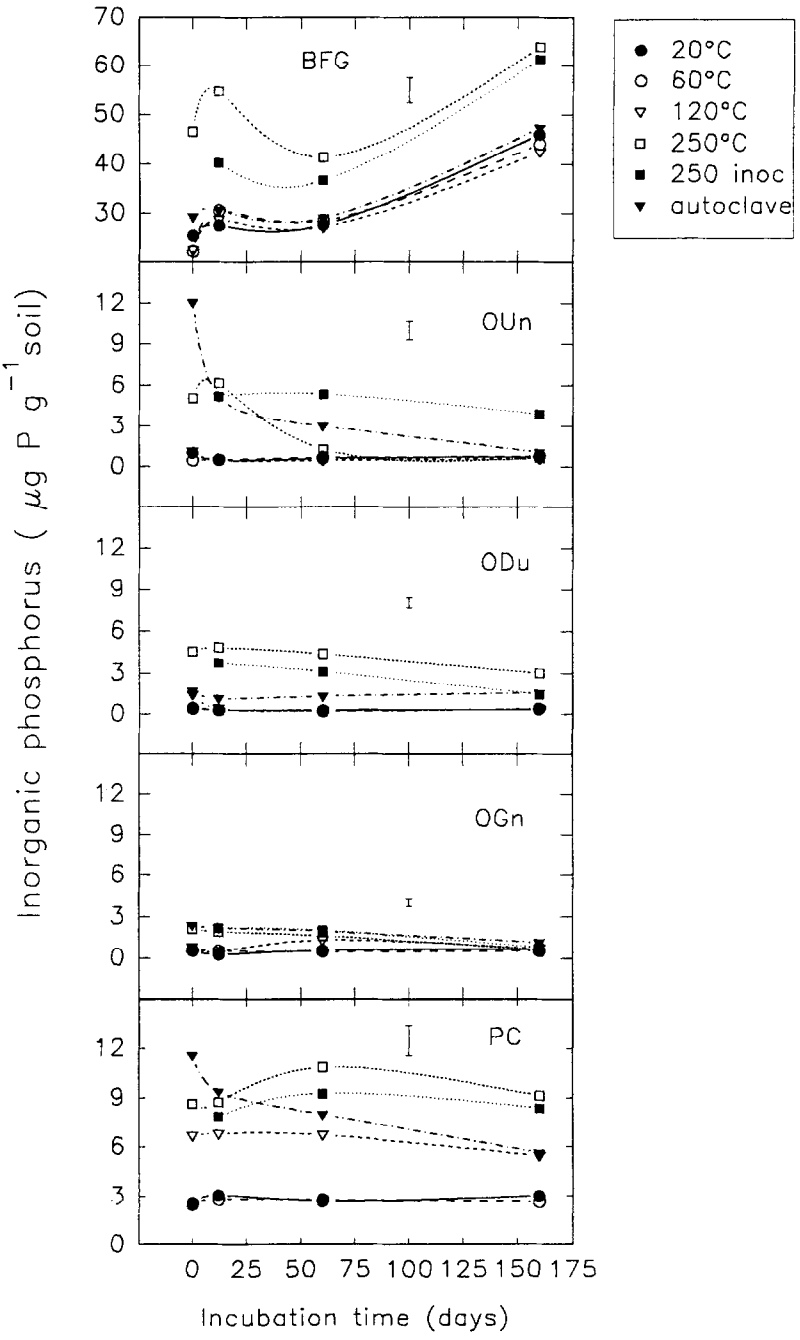

Fig. 2. Changes in the labile inorganic P (Bray P) of heated and autoclaved soils during incubation. Vertical bars are the standard error.

Soil phosphorus and phosphatase activity during the incubation of heated and autoclaved soils

Labile inorganic P

Labile P released after heating or autoclaving of OUn, ODu and OGn soils decreased during the incubation (Fig. 2), finally approaching values of the unheated control soils. In the heated PC soil, the amount of Bray P did not change during the incubation, despite its high P adsorption capacity (Table 1), but in the autoclaved soil, Bray P decreased, suggesting that mineralisation/ immobilisation processes were different in heated and autoclaved soils. BFG soil differed from the other soils by exhibiting an increase in the labile inorganic P in all treatments after 160 days of incubation (Fig. 2). These results suggest that P mineralisation or P desorption occurred (probably related to the soil dryness). In general, inoculation of 250 °C heated soil gave similar results to those for non-inoculated heated soil. DeBano & Klopatek (1988) and Kutiel & Shaviv (1989) also found increases in inorganic P after fire but a few weeks later the values were not different from the control. Both studies attributed the decrease to P adsorption or precipitation as insoluble compounds. Microbial processes strongly influence the supply of available P and microbial immobilisation may also act as a sink of phosphorus in such situations. Walbridge (1991) reported that soil microorganisms immobilised up to 90% of added $^{32}PO_4$ during laboratory incubations.

Microbial-P

During incubation, P associated with microbial biomass remained almost constant in 20 °C and 60 °C heated soil, except in BFG soil, where a large increase was observed (Fig. 3). BFG soil was very dry when sampled and a P-flush was undetectable but, when the soil was remoistened and maintained in favourable temperature conditions, microbial population recovered. In soils heated to more than 60 °C, a partial (BFG, OUn, ODu and PC) or a complete (OGn) recovery of the P-flush occurred during 160 days of incubation. Microbial P in inoculated soils was similar to that in non-inoculated soils, except for PC soil, where heated soils with inoculum had slightly lower P-flush than those without it. Autoclaved soils also showed an increase in P-flush with the incubation, with values similar or slightly higher (OGn) than those of the 120 °C treatment (Fig. 3).

In autoclaved soils and those heated to 120 °C and 250 °C, the decrease in inorganic labile-P during the incubation (Fig. 2) was accompanied by an increase in microbial P (Fig. 3) in Orbost soils (OUn, ODu and OGn), although the two did not match in amounts. This result suggests that microbial biomass acted as a partial sink for the decrease in Bray P measured during the recuperation process. In Orbost soils, a relationship between Bray P (log

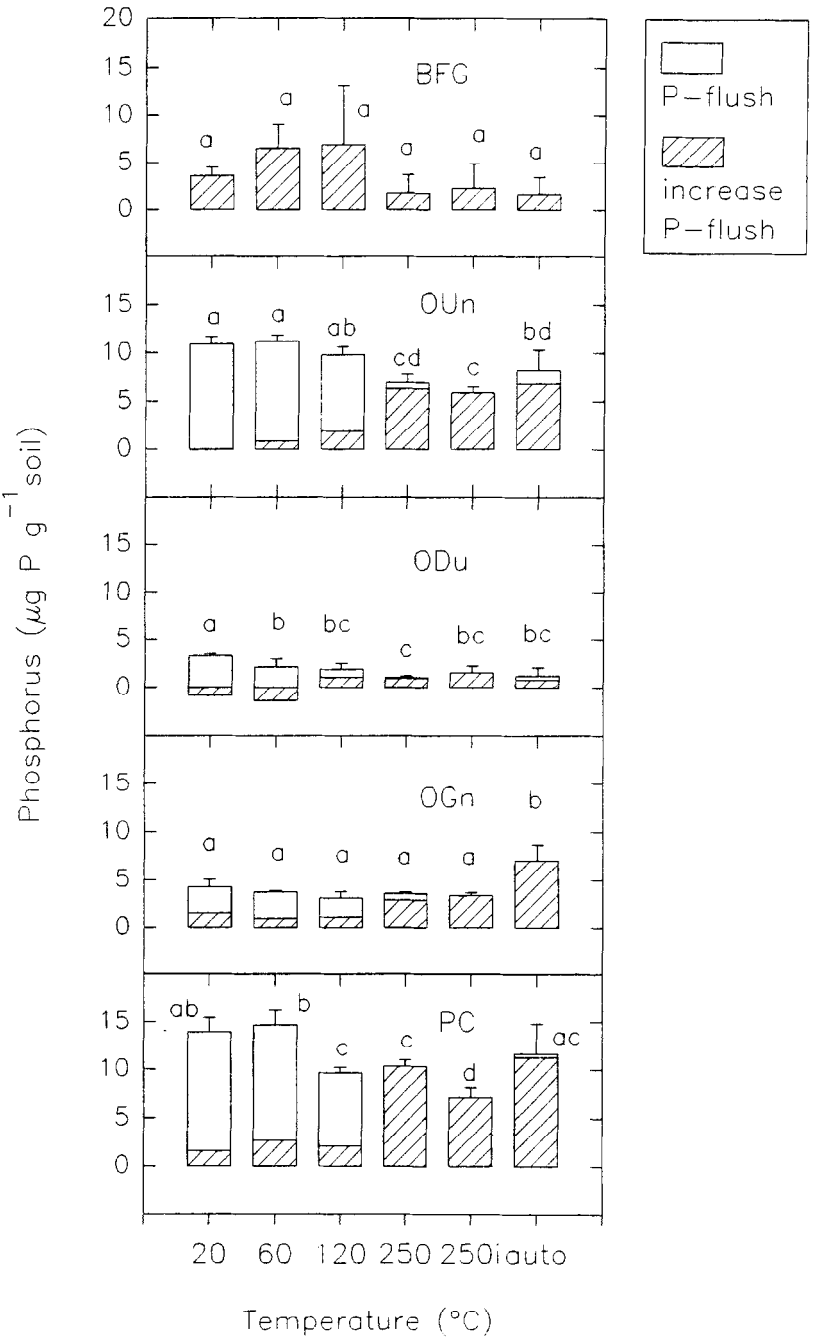

Fig. 3. P-flush after 160 days of incubation (white bars), and increase in P-flush during incubation (striped bars). Different letters show significant differences in P-flush ($p < 0.05$) among treatments.

values) and P-flush (log values) in autoclaved and 250 ° heated soils (with or without inoculum) was highly significant, giving r^2 values between 0.45 and 0.68 (n = 32, P<0.0001). Similarly, Polglase et al. (1992) observed a decrease in labile inorganic P released by fire and a progressive increase in labile organic P and P-biomass during the 5 years following the fire.

In soils with a small content of inorganic P (OUn, ODu and OGn) microbial biomass seemed to immobilise most of the inorganic labile-P released by heating or autoclaving, whereas P was both immobilised and mineralised in BFG and PC soils. Walbridge (1991) found that greater net P mineralisation occurred in fertilised compared to unfertilised soils under plantations and that soils of low P availability showed greater immobilisation of mineralised P than soils of high P availability which accumulated P in extractable forms.

Phosphatase activity

Phosphatase activity increased during the incubation of control and treated soils, probably due to the optimum moisture and temperature conditions of incubation (Nannipieri et al. 1979; Haynes & Swift 1988). Incubation conditions would affect phosphatase activity, which also depends on other soil characteristics such as available P and the size and activity of microbial population. However, the recovery of phosphatase activity was only partial during incubation of heated and autoclaved soils (Fig. 4), and inoculation of 250 °C heated soil did not improve the recovery. Although phosphatase activity was negligible after soil autoclaving, it reached values of those of the 120 °C treatment after 160 days of incubation.

Low recovery of phosphatase activity in heated and autoclaved soils may be due to retardation of microbial growth and inhibition of enzyme synthesis during incubation. Lack of improvement with inoculation indicated that the last hypothesis was more likely the case. Spiers & McGill (1979) and Pang & Kolenko (1986) found that microbial phosphatase activity was inhibited by an increase in the amount of inorganic P. In heated soils, synthesis of active phosphatases might not be required because of an increase in the labile-P or other forms of P released during heating, particularly in BFG and PC soils, which had P contents higher than in controls after 160 days of incubation. Adams (1992) proposed similar explanations for a lack of phosphomonoesterase and phosphodiesterase activity in burned soils six months after fire. Polglase et al. (1992) found an increase in phosphatase activity along an age sequence after fire and suggested that the forest became increasingly dependent on P released by mineralisation, finding a good relationship between labile organic P and phosphatase activity.

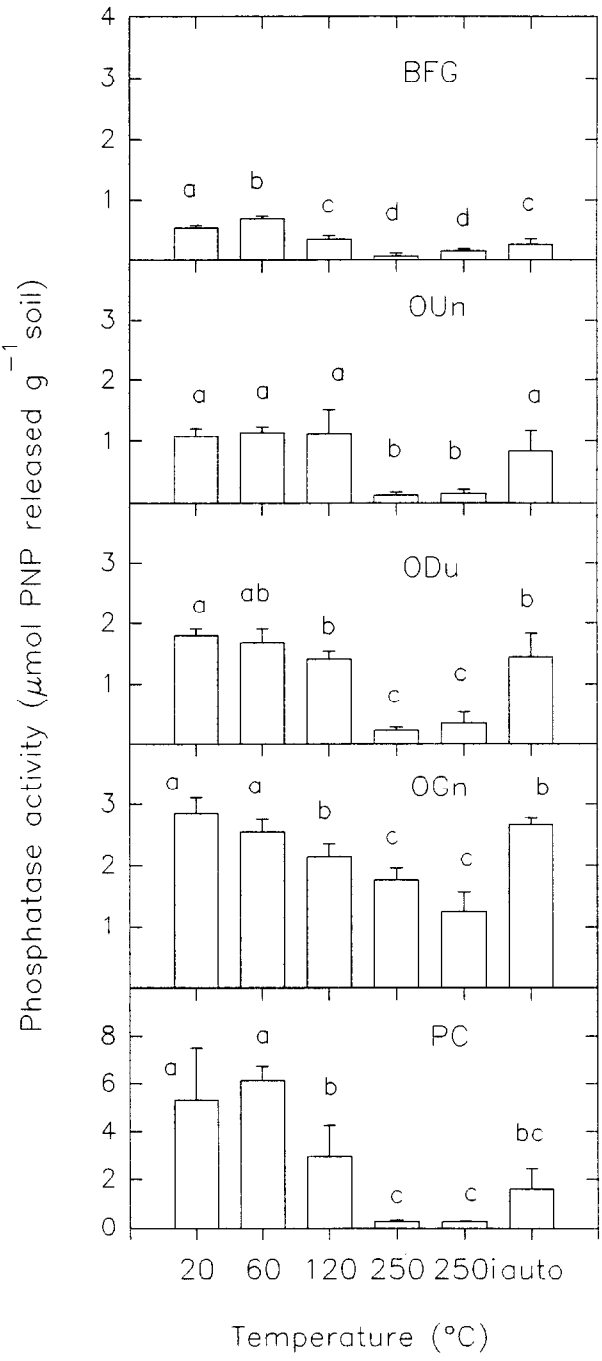

Fig. 4. Soil phosphatase activity (expressed as a PNP released) after 160 days of incubation. Different letters show significant differences ($p < 0.05$) among treatments. Note the different y axis scale in PC soil.

Conclusions

Heating and autoclaving soils have both immediate and long-term effects on phosphorus availability. As generally occurs after a bushfire, inorganic labile-P increased and microbial P (P-flush) and phosphatase activity decreased immediately after heating soils. These effects were greater when the heating temperature was higher following the order: 250 °C >= autoclaving >= 120 °C > 60 °C >= 20 °C. High temperature killed the microorganisms and denatured enzymatic proteins.

Inorganic P released after heating decreased (OUn, ODu and OGn), was similar (PC) or increased (BFG) during subsequent incubation. These different patterns were related to microbial P, total P and labile-P levels in soils. P-flush in heated soils recovered only partially and so also the phosphatase activity, suggesting long-term effects of heating on phosphatase synthesis, probably due to the high P released after fire.

In soils low in labile inorganic P (OUn, ODu, OGn and PC), the microbial biomass played an essential role as a turnover pool of P. Heating and autoclaving these soils released P from microbes. Part of this P released remained in available form for some time, but as the microbial population recovered during the incubation, a fraction of the P released by heating was immobilised again into the microbial biomass. On the contrary, in BFG soil, with high labile inorganic P and low microbial P, P released by heating was probably by solubilisation of a readily extractable fraction of the total P. The P so released was not immobilised in the course of incubation, but remained in extractable form.

Heating soils increased P availability of soils, which may improve P uptake by the growing vegetation after the fire. P released by heating may also be used by the growing microbial population or adsorbed by the mineral soil which would act as competitors for plants. Soil heating changes the form of labile pools of P in a simple way, but more complex changes occur in bushfires such as those related to the interaction between ash and soil.

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