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SOIL MOISTURE AFFECTS SURVIVAL OF MICROORGANISMS IN HEATED CHAPPARRAL SOIL

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INTRODUCTION: Fire is an integral part of the chaparral that occupies 8 million hectares in southern California. Because wildfire is incompatible with the growing use of chaparral areas for residences and recreation, the practice of selective prescribed burning is gaining wider use. The exact mechanism by which heat kills soil microorganisms is unknown; but we do know that steam heating is more effective at killing microbes than is dry heat killing. In this study, soil was heated to various temperatures in factorial combination with various soil moistures to determine the direct effects of fire and soil moisture on the survival of microorganisms in chaparral soil.

RESULTS/DISCUSSION: Heat and soil moisture function together in the inactivation of soil microbes. At moderate temperatures, net numbers of fungi increased as a result of heating. As temperature increased, diversity decreased, and both heat-shock (*heat stimulated*) fungi and bacteria, whose spores require heat to germinate were observable. Heat-shock fungi were not seen in plating of unheated soil. Temperatures beyond that which produced the heat shock community sterilized the soil. All three microbial groups were increasingly sensitive to heat with increasing soil moisture except at the highest soil moisture level. Sensitivity to heat for all three groups differed significantly: fungi>nitrite oxidizers> bacteria. The effect of soil moisture is not readily apparent. Water probably acts as a catalyst in the heat denaturing process. It lowers the amount of heat required to reach the activated state, denature biomolecules, and subsequently inactivate cells.

CONCLUSION: For fungi, mild heating increased germination of dormant forms yielding significantly higher counts than those in unheated soil. With increasing temperatures, microbe populations showed an exponential decrease. For heterotrophic soil bacteria, this decrease summarized as a function of soil moisture and temperature. Physiologically-active populations in moist soil were significantly more sensitive than were dormant populations in dry soil. A mathematical model shows qualitatively that more of the microbial biomass will be killed when the soil is moderately moist—as during prescribed burning—than when it is dry. Mineralization of killed microbial biomass in soil and release of plant nutrients may partially explain the increased plant growth and reduced response to fertilizer at burned sites.

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SOIL MOISTURE AFFECTS SURVIVAL OF MICROORGANISMS IN HEATED CHAPARRAL SOIL

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Summary—Prescribed burning, the planned application of fire to reduce the hazards of wildland fuels, is coming into wider use in southern California chaparral. Soil was heated to various temperatures in factorial combination with various soil moistures to determine the direct effects of fire and soil moisture on the survival of microorganisms in chaparral soil. For fungi, mild heating increased germination of dormant forms yielding significantly higher counts than those in unheated soil. With increasing temperatures, microbe populations showed an exponential decrease. For heterotrophic soil bacteria, this decrease was summarized as a function of soil moisture and temperature. Microbial groups differed significantly in sensitivity to temperature: fungi > nitrite oxidizers > heterotrophic bacteria. Physiologically-active populations in moist soil were significantly more sensitive than were dormant populations in dry soil. The mathematical model presented shows qualitatively that more of the microbial biomass will be killed when the soil is moderately moist—as during prescribed burning—than when it is dry. Mineralization of killed microbial biomass in soil and release of plant nutrients may partially explain the increased plant growth and reduced response to fertilizer at burned sites.

INTRODUCTION

Fire is an integral part of the chaparral that occupies 8 million hectares in southern California. Periodic wildfire is inevitable in the chaparral ecosystem because of long dry summers, accumulation of dead materials and litter, and many other factors in this Mediterranean-type climate (Hanes, 1971; Minnich, 1983). Because wildfire is incompatible with the growing use of chaparral areas for residences and recreation, the practice of selective prescribed burning is gaining wider use. It reduces the risk of intense, destructive wildfire by the planned burning of hazardous fuels under controlled conditions.

The effects of fire-induced soil heating on microbial population dynamics as well as on nutrient and succession dynamics have received little study. Fire releases nutrients held in slowly decomposing litter and in standing dead material (DeBano and Conrad, 1978) and reinitiates autosuccession (Hanes, 1971). Reports on the effect of fire on microorganisms in soil are many and varied: some report that populations decrease after burning, some that they increase, and others that they do not change (Frita, 1930; Corbet, 1934; Dungelli, 1938; Kivekas, 1939; Jaques, 1947; Cohen, 1950; Wright and Tarrant, 1957; Wright and Bollen, 1961; Ahlgren and Ahlgren, 1965; Niel *et al.*, 1965; Cooke, 1970; Jorgensen and Hodges, 1970; Widden and Parkinson, 1975). The varied reports probably reflect differences in timing of postfire sampling, fire intensity, soil and litter moisture content, soil type, litter depth and lack of accurate controls.

The exact mechanism by which heat kills soil microorganisms is unknown; but we do know that steam heating is more effective at killing microbes than is dry heating (Baker, 1970). Most prescribed burning has been conducted in the moist winter-spring season when the danger of a fire escaping is

low. Most wildfires occur during the dry summer-fall season. The question arises whether prescribed burns in the moist season—when soil microorganisms are most active—and wildfires in the dry season—when soil microorganisms are dormant—produce the same effects on the microorganisms.

MATERIALS AND METHODS

Soil was collected from Monroe Truck Trail and Bluebird Truck Trail, San Dimas Experimental Forest, Los Angeles County. The soil from Monroe Truck Trail is in the Cineba series (Typic Xerorthent) and that from the Bluebird Truck Trail in the Soper series (Typic Argixeroll). Samples were taken from the upper 5 cm of mineral soil under *Adenostoma fasciculatum* H. and A. and *Ceanothus crassifolius* Torr. in an area that had last burned in a wildfire 23 yr before. The soil, which was dry when collected, was sieved (<2 mm), and had a gravimetric water content of 3% on a dry weight basis.

Several kilograms of soil were moistened to 3, 9, 14 or 20% moisture and held for 14 days at 25°C. Subsamples of the soils were then placed in test tubes for heat treatment at five temperatures from 25 to 210°C for 30 min. Temperature and moisture levels were used in a 5 × 4 factorial combination with two replications.

Heat treatments were carried out in a water bath, or mineral oil bath for temperatures above 100°C, to allow rapid temperature adjustments of the soil in the tubes. Soil temperature adjusted to bath temperature in less than 3 min as measured by chromel-alumel thermocouples. After heating, the tubes with soil were cooled in a water bath at room temperature. The soil was held in capped test tubes at 4°C for no more than 2 days before processing for microbial numbers.

One to nine (W:W) dilutions of soil in 0.2% water-agar were made. The initial dilution was a

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1-min emulsification at high speed in a sterile Waring blender. Further dilutions were made in 0.2% water-agar. All plate counts used five plates per dilution for each replicate soil sample. Fungi were counted by dilution plates on Martin's IIA Agar (10 g dextrose, 2 g peptone, 0.25 g KH_2PO_4 , 0.25 g MgSO_4 , 15 g agar and 1000 ml distilled water) with 50 units ml^{-1} each of potassium Penicillin G and Streptomycin sulfate to inhibit bacterial growth. NPX (Tergitol, Baker Chem. Co.) was added at 0.1% of volume to the medium to prevent fungal overgrowth. Plates were held for 7-10 days at 25°C. Nitrite oxidizers were counted with the most-probable-number (MPN) methods of Alexander (1965). MPN tubes were incubated 5 weeks at 25°C. Heterotrophic bacteria were counted on plates of Tryptic Soy Agar after 3-4 days.

Statistical analysis

Microbial survival was expressed as the natural logarithm of 100 (N/N_0) where N_0 represents the number of microbes capable of producing colonies g^{-1} oven dry soil before heating, and N the number of microbes capable of producing colonies g^{-1} oven dry soil after heating. This transformation allows direct comparisons between microbial groups even though the number of colony-forming units g^{-1} of dry soil may differ by orders of magnitude. Differences in survival among microbial groups at various temperatures, soil moistures and times since moistening were determined by analysis of variance using the Statistical Analysis System (SAS) computer programs (Helwig and Council, 1979; Speed *et al.*, 1978).

Modeling

Survival was plotted against temperature for each microbial group. Least squares analysis (Bevington, 1969) was used to determine linear relationships between survival (S) and temperature (T) at each soil moisture, such that

$$\ln S = -kT + b \quad (1)$$

The calculated slopes ($-k$) and intercepts (b) for each microbial group were plotted against their corresponding gravimetric soil moistures and least squares analysis again used to solve for $-k$ and b as functions of soil moisture. This technique is similar to that used by Hurst *et al.* (1980) in studies of virus survival in soil. The significant relationships for $-k$ and b as functions of soil moisture, as determined by regression analysis, were then substituted into the overall model (equation 1) for thermal inactivation as a function of soil moisture and temperature.

The model of bacterial heat survival was tested by heating samples of the two soil types to 50, 60 or 70°C at 7, 12 or 16% soil moisture and bacterial survivors were counted. Predicted survival was plotted against measured survival for each soil and least squares analysis performed to check the model's validity in the two different soils.

RESULTS

Plots of survival against soil temperature for fungi, heterotrophic bacteria and nitrite oxidizers (Fig. 1) indicated a definite heating effect. This effect for fungi

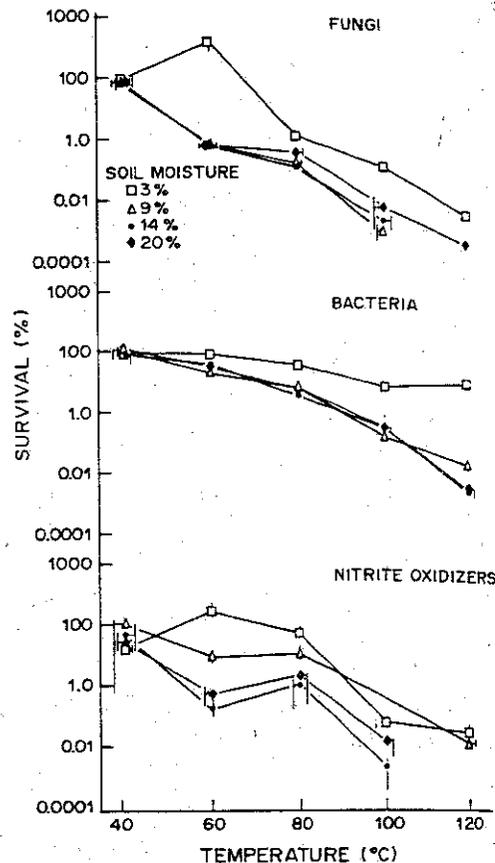


Fig. 1. Survival of physiologically active populations of fungi, heterotrophic bacteria, and nitrite oxidizers in heated soil at four soil moistures shows a heat shock effect for fungi. Values plotted are means ($n = 10$); bars represent $+1$ SE.

is seen as a net increase in numbers immediately after heating. At moderate temperatures net numbers of fungi increased as a result of heating. As temperature increased, diversity decreased, and both heat-shock (heat-stimulated) fungi and bacteria, whose spores require heat to germinate (Bollen, 1969; Maloway and Newton, 1974), were observable. Heat-shock fungi were not seen in platings of unheated soil. Temperatures beyond that which produced the heat-shock community sterilized the soil.

All three microbial groups were increasingly sensitive to heat with increasing soil moisture except at the highest soil moisture level (Table 1 and Fig. 1). Sensitivity to heat for all three groups differed significantly: fungi > nitrite oxidizers > bacteria (Duncan's multiple range test, $P = 0.05$).

The similarity of survival curves for all three microbial groups (Fig. 1) shows that the pattern of

Table 1. Coefficients of determination (r^2) for survival in heated soil as a function of temperature (Fig. 1) by soil moisture

Soil moisture (%)	r^2		
	Fungi	Heterotrophic bacteria	Nitrite oxidizers
3	0.825	0.796	0.652
9	0.942	0.957	0.718
14	0.977	0.916	0.808
20	0.944	0.916	0.857

heat inactivation is the Analysis of variance in temperature ($P < 0.0001$), temperature-moisture all significant factors organisms.

Heat and soil moisture inactivation of soil organisms to heat is a function of soil moisture (Powelson, 1975) show that capacity) fungi are more actinomycetes and the bacterial spores is a function of soil moisture. The heterotrophic bacteria in soil, are more soil than in dry soil. nitrifying bacteria a disturbance, including wet soil can reduce autotrophic nitrite. prolonged periods (The role of heat better understood directly affects survival such as proteins. microorganisms are unstable at elevated temperatures indirectly influence genetic regulation and

The effect of soil moisture. Water probably denaturing process required to reach molecules, and soil water also transfer process (Hillel, 1979) of heat by liquid movement of the water and releases approximately of heat energy.

would account for soil moistures. Temperature moisture (Fig. 1) water could serve. The vaporization to increase survival. O_2 which might (oxidation) reaction (Baker, 1970). On stream at 110°C of approximately vapor quite concentrated areas of the soil microorganism in

Thermal inactivation thought of as the

where N is the number of forming colonies the inactivated

heat inactivation is the same for all microorganisms. Analysis of variance results indicate that soil temperature ($P < 0.0001$), soil moisture ($P < 0.0001$) and temperature-moisture interaction ($P < 0.0001$), are all significant factors in heat inactivation of microorganisms.

DISCUSSION

Heat and soil moisture function together in the inactivation of soil microbes. Sensitivity of microorganisms to heat is affected by soil moisture. Studies on pasteurization of greenhouse soil (Martin, 1950; Powelson, 1975) showed that in moist soil (50% field capacity) fungi are most sensitive to heat, followed by actinomycetes and then bacteria. Water content of bacterial spores is an important factor; moderately dry spores show more heat resistance than do extremely wet or dry spores (Murrell and Scott, 1966). The heterotrophic bacteria, the most heat-resistant microbes in soil, are more sensitive to heating in wet soil than in dry soil (Dunn and DeBano, 1977). The nitrifying bacteria are known to be sensitive to any disturbance, including fire (Powelson, 1975). Fire over wet soil can reduce the populations of chemototrophic nitrite oxidizing bacteria in soils for prolonged periods (Dunn *et al.*, 1979).

The role of heat in microorganism inactivation is better understood than that of soil moisture. Heat directly affects survival since cellular components such as proteins, membrane lipids and nucleic acids are unstable at elevated temperatures. Heat may also indirectly influence survival by its powerful effects on genetic regulation and gene expression (Marx, 1983).

The effect of soil moisture is not as readily apparent. Water probably acts as a catalyst in the heat denaturing process. It lowers the amount of heat required to reach the activated state, denature biomolecules, and subsequently inactivate cells. Soil water also transfers heat by the latent heat transfer process (Hillel, 1981), which involves the absorption of heat by liquid water and convective or diffusive movement of the vapor to a point where it condenses and releases approximately 2.43 J kg^{-1} (580 cal g^{-1}) of heat energy. This latent heat transfer process would account for the greater inactivation at higher soil moistures. The greater survival at 20% soil moisture (Fig. 1) may indicate that large amounts of water could serve as a significantly large heat sink. The vaporization of water in the soil might also serve to increase survival by reducing the level of molecular O_2 which might be required for some denaturation (oxidation) reactions that cause cell inactivation (Baker, 1970). One gram of water when converted to steam at 110°C and 0.101 MPa (1 atm) has a volume of approximately 1.75 l. The production of this much vapor quite conceivably could flush O_2 from localized areas of the soil atmosphere and possibly reduce the microorganism inactivation rate.

Thermal inactivation of soil bacteria can be thought of as the reaction:



where N is the present bacterial population capable of forming colonies on laboratory medium and N_x is the inactivated bacterial community incapable of

forming colonies on laboratory medium. The magnitude of this reaction can be defined as the change in population (N) with change in temperature (T) and is proportional to a reaction constant (k):

$$dN/dT = -kN \quad (3)$$

The present population of bacteria (N) equals the initial population (N_0) less the inactivated cells (N_x).

$$N = N_0 - N_x \quad (4)$$

Rearrangement and integration of equation (3) gives

$$\ln(N_0 - N_x) = -kT + C \quad (5)$$

where C is an integration constant. Under initial conditions the heat killed population (N_x) is zero. Temperatures that would not cause a thermal inactivation are invalid in this equation, but for the purpose of evaluating C , temperature is set to zero and the integration constant (C) evaluated by solving equation (5).

$$C = -\ln(N_0) \quad (6)$$

This value of the integration constant can be substituted into equation (5) and the equation rearranged to

$$\ln((N_0 - N_x)/N_0) = -kT \quad (7)$$

Equation (7) predicts a logarithmic relationship between the fraction of the original population that survives and the temperature. This relationship is apparent in Fig. 1. Least squares analysis indicates that the linear nature of these relationships between survival and temperature was statistically significant ($P < 0.05$) (Table 1). The equations for the inactivation of microorganisms, whether by heat (Lea, 1947; Powelson, 1975), radiation (Johnson and Osborne, 1964; Jackson *et al.*, 1967; McLaren, 1969) or fumigation (Munnecke *et al.*, 1978), all show a linear response to increasing the dose of lethal agent as in Fig. 1. For each case, T would represent the dose of the lethal agent. A plot of the inactivation constant ($-k$) versus the gravimetric soil-water content for bacteria and fungi (Fig. 2) shows a very different response pattern for each. For bacteria, as soil-water

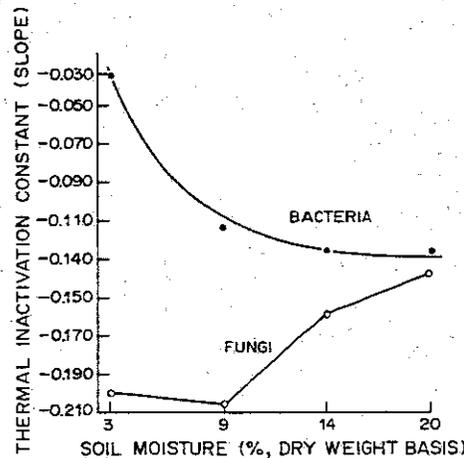


Fig. 2. The relationship of the thermal inactivation constant ($-k$) versus soil moisture for bacteria and fungi shows that fungi are more susceptible to heat, and that the pattern of response of the two communities is different.

content increases, $-k$ becomes more negative, approaching a maximum decrease of 0.14% per degree C. With increasing water content more water is available to catalyze inactivation reactions. The catalytic effect approaches maximum as the amount of water increases. This catalytic effect might also be due to an increase in thermal conductivity.

For fungi, $-k$ initially becomes more negative with increasing soil moisture and subsequently less negative but is always more negative than $-k$ for bacteria (Fig. 2). Hence, fungi are more susceptible to heat, which may be due to an inherently greater sensitivity of fungi as well as possible water-mediated heat transfer or catalytic effects. In contrast to $-k$ for bacteria, $-k$ for fungi becomes less negative with increases in soil moisture beyond 9% indicating that the inactivation reaction for fungi involves molecular O_2 . The greater lethal effect of aerated steam on fungi was demonstrated by Baker (1970). In the case of fungi then, increasing soil-water content would lead to increased steam formation, which could purge the soil of O_2 . The water could also serve as a heat sink reducing the rate of thermal inactivation. The convergence of $-k$ for bacteria and fungi at high soil moistures suggests that the inactivation mechanism for both may be similar at high soil moistures.

Quantitatively the survival of bacteria in heated soil can be defined as

$$S = 100(N/N_0)$$

where N_0 is the initial population and N the surviving population. The relationship between the logarithm of survival and soil temperature is linear (Fig. 1, Table 1):

$$\ln S = -kT + b \quad (8)$$

where $-k$ and b are functions of the gravimetric water content of the soil (θ). From regression analysis of the data shown in Fig. 2,

$$-k = (0.274/\theta) - 0.144, r^2 = 0.993, P < 0.005, \quad (9)$$

and from Fig. 3,

$$b = \ln(2905\theta - 5673), r^2 = 0.999, P < 0.001. \quad (10)$$

Equations (9) and (10) were substituted into equation (8) to produce an overall model of bacterial survival

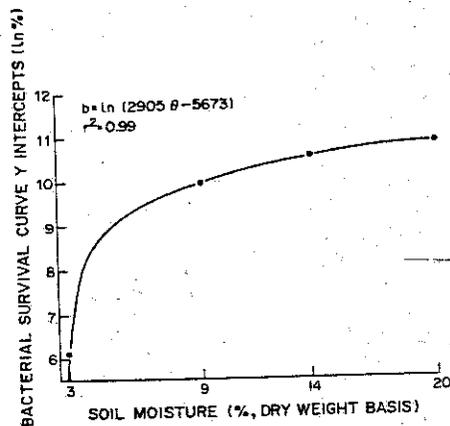


Fig. 3. Relationship of the intercepts (b) of the survival curves to soil moisture for bacteria shows that high soil moistures may provide limited protection for the soil bacterial population which is in contrast to the soil moisture effect on the inactivation constant ($-k$).

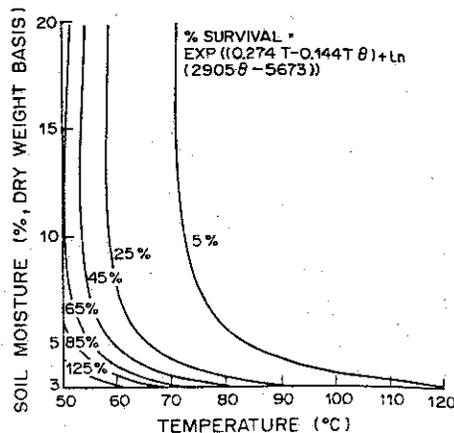


Fig. 4. Contour plot of bacterial survival in a heated Typic Xerorthent as a function of soil temperature and moisture (θ) illustrates the model. Values $>100\%$ represent heat stimulated germination of dormant forms.

in soil as a function of soil temperature and moisture (Fig. 4):

$$\ln S = [(0.274/\theta) - 0.144]T + \ln(2905\theta - 5673). \quad (11)$$

Equation (11) was tested for validity within the temperature and soil moisture ranges studied. A plot of measured bacterial survival versus calculated survival shows a good agreement ($RSS = 3294$, $r^2 = 0.94$) between the two (Fig. 5). When extended to a different, finer-textured soil (Typic Argixeroll), the model proves less accurate ($RSS = 8316$, $r^2 = 0.75$) (Fig. 5). Other factors, which the model

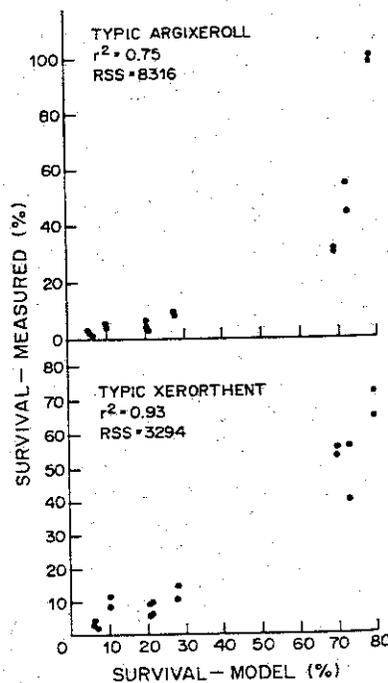


Fig. 5. Bacterial survival predicted with the model, which was developed for a Typic Xerorthent, shows a good correlation with measured survival in that soil. The model is less accurate in a Typic Argixeroll. Both the coefficient of determination for the regression (r^2) as well as the residual sums of squares (RSS) are shown as indicators of how well the model fits this empirical data.

does not take into account determining the thermal properties of this finer textured soil. Soil texture affects heat survival with finer textured soil than in sandy soil. This is most likely due to soil texture and greater volume of soil (Hillel, 1971).

The many factors that affect heated soil can be divided into physical, biological and chemical. Those affecting heat flux include soil density, soil heat capacity, soil heat conduction, biological activity, and direct biological effects. Factors which have a significant effect would include soil texture, soil microorganism activity, and soil moisture.

Survival differed significantly in a range test, $P < 0.0001$ (DeBano (1977) and DeBano (1977) and immediately heated soil. This difference in survival of dormant forms in dry soil. In our study, all respired soil moisture treatment (DeBano (1977)). The biological state (low) in the microflora in soil.

This information is important in soil. In a soil with 2% moisture and distributed uniformly in the top 10 cm, microbial C would produce a temperature increase of a typical prescribed biomass (nearly 9°C) and a greater proportion of subsequent mineralization may be one reason for the fertilizer by Chapman and Muller, 1975; Helander (1975) that achieves a soil temperature increase of 3%, i.e. typical of the effects of prescribed organisms are the

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does not take into account, are probably involved in determining the thermal inactivation of bacteria in this finer textured soil. Soil texture has been shown to affect heat survival with better survival in heavy-textured soil than in sandy soils (Bitton *et al.*, 1976). This is most likely due to the lower thermal conductivity and greater volumetric heat capacity of heavy-textured soils (Hillel, 1981).

The many factors that affect microbial survival in heated soil can be divided into three categories: physical, biological and both. Physical factors are those affecting heat flux through the soil, such as bulk density, soil heat capacity, particle size and heating duration. Biological factors are those that have a direct biological effect as do pH and water potential. Factors which have both a biological and physical effect would include soil moisture, which is an integral part of heat flux through soil and is required for microorganism activity.

Survival differed significantly (Duncan's multiple-range test, $P < 0.0001$), from that in a study by Dunn and DeBano (1977) in which the soil was moistened and immediately heated rather than waiting the 2 weeks after moistening as in this study. We attribute this difference in survival to the abundance of dormant forms in dry soil (Zechman and Casida, 1982). In our study, all responses are more like the 14% soil moisture treatment in the study by Dunn and DeBano (1977). The reason may be the active physiological state (lower proportion of dormant forms) in the microflora in soil with 14% moisture.

This information may be applied to a typical forest soil. In a soil with 200 mg microbial C 100 g^{-1} of dry soil (Anderson and Domsch, 1978), bulk density 1.2 g cm^{-3} and distribution of microbial biomass which is uniform in the top 5 cm of the mineral soil, the total microbial C would be $1200 \text{ kg-C ha}^{-1}$. A fire that produces a temperature of 70°C in moist soil (10%), i.e. a typical prescribed fire, would kill most of this biomass (nearly 95% of the heterotrophic bacteria and a greater proportion of the fungi) leading to subsequent mineralization and nutrient release. This may be one reason behind the lack of a response to fertilizer by chaparral after fire (Christensen and Muller, 1975; Helmers *et al.*, 1955). In contrast, a fire that achieves a soil temperature of 70°C in a dry soil (3%), i.e. typical wildfire conditions, would kill less than 25% of the soil heterotrophic bacteria. The effects of prescribed fires and wildfires on soil microorganisms are then apparently dramatically different.

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NITROGEN SOIL AS

Upland Farming D

Summary—The rates of r Brown, from the farm o nitrification, but did no bilization of NO_3^- -N wei mineralization accounte content of 60% were hi nitrification were estim:

INTRODU

The conversion of nitrogen organic and inorganic form immobilization, has been investigation in reference to availability. The mineraliz mated from the productio incubation (Stanford and Maynard *et al.*, 1983). Ho rates are measured as the mineralization and immo mineralized N contributes N pool, and the rest is ta and incorporated again i would be understood abo in soil if gross minerali were both evaluated sim

The rate of immobiliz measuring incorporation matter from applied ^{15}N bent and Tyler, 1962; Ste and Tucker, 1974). But the amendment of larg $^{15}\text{NO}_3^-$ -N are required b content of soils. Unde longed incubation resul immobilization rate be immobilized ^{15}N . The ecosystem caused by th tities of NH_4^+ -N and N should be considered estimate *in situ* imr method.

Determining the rat bilization using a ^{15}N following advantages: determine the rates ^{15}N -tracer during a the rates of mineraliz estimated simultaneo