Chapter 14
Microbial Communities in Fire-Affected Soils

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14.1 Introduction

Of all the ways in which human activities can affect soil environments, fires are perhaps the most dramatic. Whether set deliberately or accidentally, the worldwide impact that such fires have is extensive, including the loss of human and animal lives as well as economic and ecological damage (UNECE et al. 2000; UNECE and FAO 2001; Davidenko and Eritsov 2003; Kudoh 2005; FAO 2005). The United Nations Food and Agricultural Organization (2005) estimated that 350 million hectares burn annually, and that approximately 90% of those fires are of human origin. The frequency and severity of surface fires have also increased in many parts of the world due to changes in climate and land management practices (Houghton et al. 1992; Renkin and Despain 1992; Glantz 1996; Neary et al. 1999; Westerling et al. 2006). Large fires tend to draw media attention, particularly when they impinge on densely inhabited or well-known wildlife areas. Their rapid spread, extreme temperatures, and the barren landscapes they leave behind can alter the surrounding ecosystem for years, decades, or even permanently. It is no surprise, therefore, that a premium has historically been placed on extinguishing fires as they happen, rather than on studying their ecological significance. Only recently have scientists begun to understand the critical roles that some fires play in sustaining natural environments, and on the parts that soil micro-organisms play in that process.

Two basic types of fires are discussed in this chapter: surface fires and underground fires. Surface fires include both wildfires and prescribed fires and their effects are predominantly ‘top down’. That is, the fire source is aboveground, and the heat from the fire, although it can be intense enough to sterilize the surface soil, may not penetrate more than a few centimeters below the soil surface. Surface fire effects often consist of a patchwork of severely affected sites interspersed with less affected areas, the pattern of which is dictated by the availability of fuel, topography, and other factors.

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P. Dion and C.S. Nautiyal (eds.), *Microbiology of Extreme Soils. Soil Biology 13*

Underground fires, by way of contrast, have a ‘bottom-up’ impact. They are typified by the large coalmine fires found in the Jharia Coalfield of India (Agarwal et al. 2006), throughout much of northern China (Zhou et al. 2006), and throughout the coal-mining regions of the United States, most notably in Centralia, Pennsylvania (Trifonoff 2000). In these fires, steam and gases carrying vaporized combustion products from the burning coal below migrate, or ‘vent’, upward through soil fractures, cooling as they rise. As the gases from these ‘anthracite smokers’ cool, their dissolved chemicals either escape to the atmosphere or condense into the surrounding soils. Thus, underground fires are distinguished by subsurface soil temperatures that are generally much hotter than surface temperatures, and by soil chemical changes that tend to be clustered around actively venting soil fractures. In many ways, these fires resemble geothermal environments as closely as they do environments affected by surface fires. In this chapter, we use coalmine fires as the model system for underground fires in general.

Regardless of whether a fire has a top-down or a bottom-up impact, it alters many surface and subsurface soil properties as it migrates through an area. These properties include the availability of water, the structure and composition of soil particles, and the availability of nutrients. Sulfur, nitrogen, phosphorus, and carbon species, in particular, can experience dramatic shifts when pre- and post-fire environments are compared.

The extent and severity of these fire-induced changes is determined by many factors including the duration of the fire, the intensity of the fire, the rate of the fire’s spread, the topography of the burn area, the initial soil composition, the soil moisture content, fuel characteristics, weather conditions, the interval between fire events, and the frequency of fire events. However, the greatest of these is duration. A fast-moving aboveground fire of even moderate intensity does not persist long enough to transfer enough heat to the soils to cause substantial belowground chemical changes. Slow-moving fires cause severe and complex changes that can be long lasting or permanent. Fire temperatures can range from 50 to >1,500°C. Heat release can range from 2.11 kJ/kg of fuel to 2.1 MJ/kg. The effect of fire intensity is related to how well the energy produced by the fire is transferred to the soil. A slow-moving intense fire will have a greater impact than a fast-moving fire of the same intensity. Likewise, a slow-moving fire of low intensity may have as great an impact as a fast-moving fire due to the greater length of time the fire will be transferring the generated heat to the soil.

Ultimately, it is both the intensity and persistence of fires, as well as the resulting changes to the surface and subsurface soil properties that determine the fire’s impact on resident microbial communities. Although these communities are likely to play critical roles in both post-fire biogeochemical nutrient cycling and in the ultimate recovery of fire-affected environments, they have remained quite poorly studied. Most prokaryotic research, in particular, has focused on studies of post-fire microbial biomass, microbial metabolic assays, and culture-dependent assays (Ahlgren 1974; Dunn et al. 1979; Bissett and Parkinson 1980; Klopatek and Klopatek 1987; Klopatek et al. 1990; Fritze et al. 1993; Vazquez et al. 1993; Acea and Carballas 1996; Hernandez et al. 1997; Ross et al. 1997; Prieto-Fernández et al. 1998; Choromanska and DeLuca 2002; Andersson et al. 2004; Treseder et al. 2004; Naumova 2005; Giai and Boerner 2007). Only recently have culture-independent methods such as 16S rRNA gene sequencing, terminal restriction fragment length polymorphism (T-RFLP) analysis, phospholipids fatty acid analysis (PLFA), and denaturing gradient gel electrophoresis (DGGE) been combined with more traditional methods to give a more complete picture of the effects that fires have on specific prokaryotic communities, and on the roles that those communities play in the post-fire environment (Baath et al. 1995; Pietikainen et al. 2000; Jaatinen et al. 2004; Tobin-Janzen et al. 2005; Yeager et al. 2005; Izzo et al. 2006).

14.2 The Effects of Surface Fires on Microbial Environments

Because the fire-induced thermal, chemical, and physical changes to the soil environment directly drive microbial community responses, it is important to understand these factors before turning to a more complete discussion of microbial ecology. The soil changes that most clearly affect microbial community responses depend on the intensity of the fire, and correspond to changes in the availability of water, nitrogen, sulfur, phosphorus, and carbon.

14.2.1 Fire Intensity

The intensity of a surface fire, and its resulting impact on the microbial communities in underlying soils, varies according to the total amount of heat produced by the fire, the mode of transfer of that heat to the underlying soils, and the speed with which the fire progresses through an area. The total heat produced by the fire is governed by the nature of the fuel source and the fuel load. For example, grassland fires (Raison 1979; Ross et al. 1997; Neary et al. 1999) tend to have lower fuel loads and thus generate lower fire temperatures than fires in tropical woodlands or conifer forests. Because microbial mortality generally begins at around 50°C, but varies tremendously from species to species, the total heat produced by the fire is of paramount importance in determining the post-fire microbial community composition.

The modes of energy transfer from a surface fire to the soil are radiation, convection, conduction, vaporization/condensation, and mass transport (Neary et al. 1999). Electromagnetic radiation from the fire can play a significant role in energy transfer at the onset of a burn. Movement of air masses by convection can transfer heat from the active fire to nearby areas, heating nearby soils as well as spreading the fire. Conduction of heat by direct contact between hot or burning fuel and cooler soil can be important especially where fuel loads are heavy or where fuels themselves are massive such as with slash piles. The high specific heat capacity of water (4.184 J g^{-1}°C^{-1}) means that a substantial amount of energy is required to vaporize the water in soil. The enthalpies of heating and vaporization of soil moisture tend to mitigate any rise in soil temperature until all the water is vaporized. Indeed, the soil temperature cannot rise above 95°C until vaporization is complete (Campbell et al. 1994). The vaporized water carries latent heat through soils faster and deeper than other modes of energy transport such as radiation or conduction. Thus, whereas moist soils initially suffer lower temperatures, the overall impact of the fire may be more rapid and affect soil to a greater depth. The transfer of energy via mass transport generally has little to no effect on soil temperatures.

Once all of the moisture in soils under a fire has vaporized, soil temperatures typically rise to 200–300°C. However, under severe or slow-moving fires, surface soil temperatures can rise to as high as 700°C (DeBano et al. 1998). The depth-temperature profile for a soil under a fire is determined by intensity and duration of the fire as well as the moisture content of the soil. With fast-moving or low severity fires, belowground soil temperatures generally do not exceed 100–150°C at 5 cm depth and demonstrate no heating below 30 cm (Agee 1973; DeBano 2000). A slow-moving or intense fire will clearly have a more significant effect on both the maximum soil temperatures observed and the depth at which temperatures are raised.

14.2.2 Available Moisture

Available soil moisture levels are not only decreased initially as a direct result of vaporization, but may also suffer long-term reductions. At moderate temperatures, incomplete burning of organic matter can result in the formation of a hydrophobic coating in the mineral components of soil resulting in increased repellency and decreased soil permeability. This repellency can result in a persistent decrease in soil moisture in the post-burn soils or in greater run-off and erosion. Despite these tendencies, situations in which soil moisture has increased (Klock and Hevey 1976; Haase 1986) or remained the same (Campbell et al. 1977; Milne 1979) after fire have also been documented, and thus the overall impact that post-fire soil moisture has on microbial communities is varied (Letey 2001).

14.2.3 Available Nutrients

In an aboveground fire, the most dramatic and well-understood changes to available nutrients involve the volatilization, chemical transformation, and biogeochemical cycling of nitrogen, carbon, phosphorus, and sulfur. Although changes can and do occur to trace minerals such as As, Ca, K, Na, Fe, and Al (Grier 1975; Feller 1982; Macadam 1989; DeBano et al. 1998; Neary et al. 1999; Arocena and Opio 2003) the effects that these changes have on microbial communities remain mostly unstudied, and thus are not discussed in this chapter.

14.2.3.1 Nitrogen

At moderate temperatures, dead partially combusted plant and microbial biomass can be easily oxidized resulting in an increase in inorganic nitrogen immediately post burn (Diaz-Ravina et al. 1996). More extreme temperatures can result in volatilization of nitrogen (Giovannini et al. 1990). Total nitrogen decreases slightly as the temperature rises from 25 to 220°C but dramatically decreases between 220 and 460°C (Giovannini et al. 1990). Ammonium concentrations steadily increase up to 220°C but, like total nitrogen, drop quickly as the temperature rises above 220°C until very little remains at 460°C. It is presumed that this increase in NH_4^+-N is due to mineralization of organic nitrogen. Nitrate concentrations are initially unaffected by fire, even moderate to intense fires. However, NO_3^--N is produced by biochemical nitrification of ammonium in the time following the fire resulting in NO_3^--N concentrations that can be significantly higher in the weeks or years post-fire (Covington et al. 1991).

Therefore, although total nitrogen may decrease, the bioavailable forms of nitrogen, nitrate and ammonium, may be at elevated levels for several years following a burn. Ammonium tends to adsorb onto the mineral soil and become immobilized. Unless regrowth of vegetation occurs soon after the fire, the nitrate can be easily lost to leaching, thus depleting the total nitrogen for long periods. Conversely, if regrowth is rapid, soil organic nitrogen concentrations can rapidly recover to pre-fire levels (Adams and Attiwill 1984; Weston and Attiwill 1996).

14.2.3.2 Carbon

Fire severity as described by the maximum sustained surface temperature under a fire affects the degree of consumption of litter and soil organic matter. A low severity burn where the soil temperatures do not exceed 250°C can cause partial scorching of litter. As depth in the soil increases, the insulating ability of the soil mitigates the heating of soils. Thus, with surface temperatures at or below 250°C, soil temperatures down to 2.5 cm rarely exceed 100°C and at 5 cm the temperature is typically below 50°C. The lower temperatures at depth result in only partial distillation of organic matter above 2.5 cm and little to no effect below 5 cm. A moderate burn characterized by surface temperatures up to 400°C results in temperatures at 2.5 and 5 cm of up to 175 and 50°C, respectively. These temperatures result in very significant charring of litter, some charring of organic matter to 2.5 cm and the start of distillation of organic matter above 5 cm. In a severe burn, surface temperatures exceed 675°C, resulting in complete combustion of the litter. The soil down to 2.5 cm can experience heating to 190°C with concomitant charring or consumption of large portions of the organic matter. Even at depths of 5 cm, soils are being heated to 75°C resulting in significant distillation of volatile organic matter and some charring (DeBano et al. 1977).

14.2.3.3 Phosphorus

Organic phosphorus is readily converted to inorganic forms of phosphate. Even in low severity fires where temperatures do not exceed 200°C, the concentration of organic phosphorus decreases markedly. In an artificial heating experiment, organic phosphorus was completely depleted from soils above 220°C (Giovannini et al. 1990). Organic carbon is easily lost, however, total phosphorus remains fairly constant due to its low volatility. The organic phosphate is instead converted to orthophosphate, the predominant form of bioavailable phosphorus (Cade-Menun et al. 2000). The concentrations of inorganic and available phosphorus peak at soil temperatures of approximately 450°C (Giovannini et al. 1990).

Other factors play a role in determining how much of the inorganic phosphorus produced by a burn is available. Bioavailability peaks at a pH of around 6.5 (Sharpley 2000). The ash produced in a fire tends to move the soil pH higher toward this value. However, in calcarerous soils phosphate can complex very strongly to calcium, resulting in removal of phosphorus from the available pool. In acidic soils, phosphate can bind with other soil metals such as iron, manganese, and aluminum. In summation, aboveground fires easily convert most or all of the organic phosphorus to inorganic phosphorus, thus initially increasing the bioavailability. How long the increase in bioavailable phosphorus persists depends on soil pH, the composition of the mineral soil, and the rate of uptake of available phosphorus by recolonizing vegetation.

14.2.3.4 Sulfur

In an artificial heating study, Badia and Marti (2003) found that a slight steady increase in total sulfur occurred upon heating gypsiferous soils up to 500°C and upon incorporation of ash into the soil, but that no change in total sulfur occurred in calcarerous soils. In another study, Castelli and Lazzari (2002) found that total sulfur peaked a year after a controlled burn in both grass-covered and shrub-covered soils. After a second controlled burn three years after the first burn, the total sulfur in the soils under grass cover dropped back to the original (before the first burn) levels below 1 cm depths. In the same study, available sulfur under shrub cover immediately jumped significantly, but then dropped back to pre-burn levels within two years. The available sulfur under grass cover was not affected. In both cases, the available sulfur did not change with the second controlled burn. These two studies indicate that the sulfur chemistry of soils is affected by aboveground fires in manners similar to other nutrients.

14.3 The Effects of Underground Fires on Microbial Environments

Underground coalmine fires have very different effects on soil chemistry than those caused by aboveground fires. The reasons stem from three major factors. The heat source is below the surface, the duration of the belowground fires can be considerably longer than surface fires, and the composition of the coal fuel is quite different from that found in typical prescribed or wild aboveground fires. These factors lead to unique physical and chemical properties and processes.

14.3.1 Fire Intensity

In an aboveground fire, the highest temperatures the soils experience are at the air–surface interface. Conversely, the lowest temperature of an affected soil is at the air–surface interface with a belowground fire. In other words, the soil temperature gradient in a belowground fire is inverted from that observed in aboveground fires.

In addition, the impact of the fire is not evenly distributed spatially. The primary modes of energy transfer from the fire to the surface and near-surface soils are convection and conduction. Convection of hot combustion gases takes the paths of least resistance, following the small fractures and faults in the subsurface. The gases tend to escape to the atmosphere in vents. The temperature of the surrounding soils is highest near the vent as a result of the transfer of thermal energy from the hot gases to the surrounding soils. These hot soils are then able to transfer heat away from the vent via conduction. Eventually, this heat is slowly lost to the atmosphere. Thus, the surface temperature decreases with increasing distance from the vent. In addition to heat brought to the surface by convection, the hot subsurface rock and mineral matter can transfer heat to the surface directly by conduction. This conduction results in surface regions that are quite hot while displaying no outward signs of venting of hot gases. Indeed, the authors have measured surface temperatures above the Centralia Pennsylvania mine fire exceeding 400°C in nonventing areas (Tobin-Janzen, unpublished results). The underground environment (including both structure and composition) is not uniform. Therefore, the heat transferred by conduction is spatially uneven. The end result of the modes of heat transfer is that the surface temperatures above an underground fire are distributed in an irregular pattern.

Another significant difference between aboveground and belowground fires is the duration. Aboveground fires persist at a certain location for hours to weeks. The available fuel is consumed quickly and when gone, no further burning is possible. Stated another way, aboveground fires are fuel limited. The rate of progression of belowground fires is much slower, and can range from ten meters per year to several hundred meters per year. Even at the fastest rates, underground fires progress more slowly than aboveground fires. This slow movement means that an area on the surface that becomes affected by the underground fire may experience these effects for years. Indeed, certain areas in Centralia have been affected continuously for decades (Trifonoff 2000).

The principal reason for the slow movement is a shortage of oxygen. That is, belowground fires are oxidant limited. Oxygen is replenished through the fractures in the subsurface structures. Indeed, weather systems affect the progress of the fire. Low-pressure weather systems result in more venting of gases whereas little venting takes place during high-pressure systems. Another consequence of this shortage of oxygen is that the underground fire is a reducing fire. Thus, the reduced and volatile forms of nitrogen (ammonium) and sulfur (S° and H_2S) are formed and transported to the surface.

14.3.2 Available Moisture

In general, as the hot combustion products of the fire rise through the mineral and soil column, those components with low volatilities begin to condense. One simple manifestation of this phenomenon is the formation of a very moist semi-liquid layer beneath active vents. When the hot gas encounters cooler soil, water condenses creating a very hot mud between 0.5 and 1 m beneath the surface. (Tobin-Janzen, unpublished results). Above this level, the soil moisture varies tremendously, and the soil can even be quite dry, more closely resembling soils affected by aboveground heat sources (Tobin-Janzen et al. 2005).

14.3.3 Available Nutrients

The chemical composition of coal is markedly different from the organic fuel burned in aboveground fires. Coal is a highly variable fossilized form of ancient plant matter that has been significantly altered by exposure to elevated temperature and pressure. In addition to the organic components, coal contains significant inorganic materials. When burned, the inorganic components can melt and volatilize. Indeed, these inorganic phases pose technological problems for the use of coal as a clean energy source. The combustion products, including the inorganic phases, can percolate to the surface and near-surface environments, where they have been shown to condense into a variety of minerals, including elemental sulfur, downeyite (SeO_2), orpiment (As_2S_3), laphamite ($As_2(Se,S)_3$), ammonium chloride, gypsum ($CaSO_4 \cdot H_2O$), and mullite ($Al_6Si_2O_{13}$; Finkelman and Mrose 1977; Lapham et al. 1980; Dunn et al. 1986). Indeed, the authors have employed X-ray powder diffraction to identify pure ammonium chloride and needlelike elemental sulfur crystallizing on the surface of the ground above the Centralia Pennsylvania mine fire (Janzen, unpublished results). Although the rate of deposition of these compounds is not high, the impact caused by a long and slow-burning underground coalmine fire has the potential to be significant. Also, as described above, the distribution of combustion gases and volatile chemical species at the surface is not even. Rather, it is a function of the subsurface structure. Thus localized areas of high chemical concentrations, temperature, and soil moisture are interspersed with areas of lower concentrations and more moderate temperatures.

14.3.3.1 Nitrogen

Tobin-Janzen et al. (2005) studied the inorganic nitrogen (NH_4^+-N and NO_3^--N) levels in surface soils overlying the Centralia, Pennsylvania coalmine fire over a two-year period. During that time, the mine fire front progressed through the sample site, and surface soil temperatures increased an average of 16.1°C. Many of the hottest areas showed elevated ammonium (as high as 13.79 mg/kg) and nitrate (as high as 103.1 mg/kg) levels, however, these concentrations were not correlated with absolute temperature values, nor to proximity to an active vent, as some areas with elevated temperature, close proximity to an active vent, or both, also had inorganic nitrogen concentrations that were comparable to those in nearby unaffected soils. Rather, inorganic nitrogen levels were related to more complex environmental trends, such as the length of time an area had been affected by the mine fire and whether the overall soil temperatures were rising or falling in the area due to the movement of the mine fire front.

14.3.3.2 Sulfur

The sulfur-containing gases percolating up from the burning coal have a profound effect on the soil chemistry of the overlying soils, and thus represent one of the most striking differences between underground mine fire-affected soils and those affected by surface fires. For example, in unpublished work, the total sulfur concentrations are clearly affected by the underground fire (Fig. 14.1). The concentrations are significantly higher near the vent. Interestingly, the sulfur concentrations are not highest directly at the vent. Rather, they increase to a maximum approximately 0.5 m

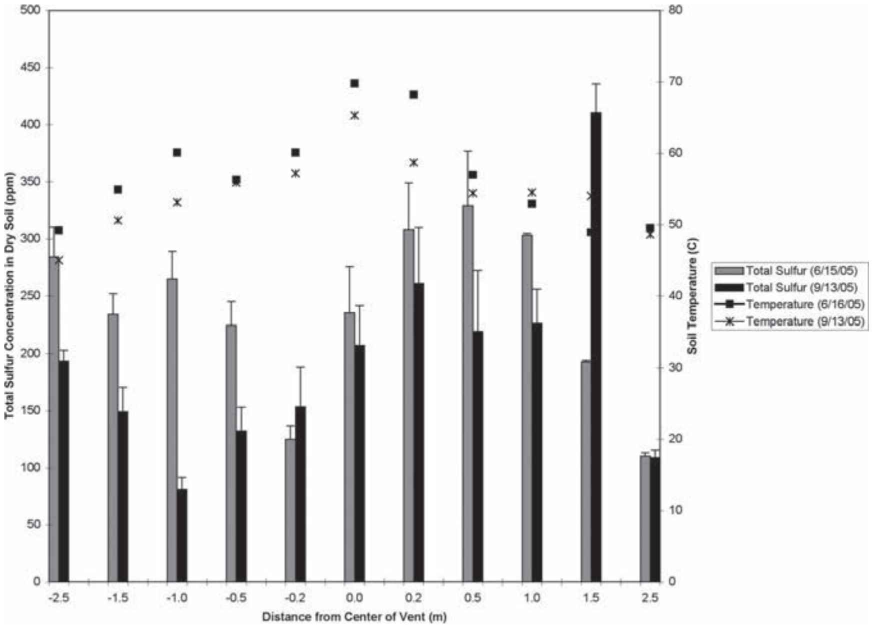

Fig. 14.1 Spatial distribution of total sulfur around an active vent above the Centralia, Pennsylvania mine fire. The concentrations of total sulfur were measured in dry soil on two days during the summer of 2005. The results are correlated with soil temperature at a depth of 5 cm and distance from the vent. Triplicate analyses were performed on each sample and the error bars represent the 95% confidence intervals

from the vent, then decrease with decreasing distance from the vent. At greater distances from the vent the concentrations of total sulfur again begin to drop due to the depletion of volatile sulfur components of the gases at greater distances from the source. Similar results have been observed for elemental sulfur (S^0).

Using thermodynamic principles, Stracher has proposed a stability relationship between the partial pressure of S_2 gas and temperature (Stracher 1995). He developed a model predicting which phase, orthorhombic or S_2 gas, would be stable under a given set of conditions. Depending on the partial pressure of S_2, the temperature at which the solid form of elemental sulfur becomes the favored species varies. At very low partial pressures of S_2, sulfur prefers to be solid at low temperatures. As the pressure rises, the solid form becomes favored at higher temperatures. Thus, at the vent where temperatures are highest, the gaseous form is predominant. Moving a short distance from the vent, the temperature is lower, allowing sulfur to solidify. Farther from the vent, the sulfur has already been depleted in the effluent gas, thus no further deposition is possible.

14.4 Microbial Communities in Fire-Affected Soils

The response of microbial communities to fire varies primarily with the nature of the fire. The fire may have a top-down or a bottom-up profile, its intensity and duration may vary, as also vary the chemical, physical, and biological changes it generates in the surrounding environment. Not surprisingly, the fire's intensity and persistence tend to be the most important factors in governing post-fire microbial community numbers and diversity. Nevertheless, other factors, such as the release of organic toxins, including polychlorinated dibenzo-p-dioxins (PCDDs), dibenzofurans (PCDFs), and polycyclic (or polynuclear) aromatic hydrocarbons (PAHs), into the surrounding soils can dramatically and negatively affect microbial biomass and diversity (Kim et al. 2003). Conversely, the increase of inorganic nitrogen and sulfur levels in fire-affected soils can allow microbes capable of exploiting these molecules to thrive in many post-fire environments, particularly if they are able to withstand the fire's high temperatures or to recolonize fire-affected areas quickly as they cool.

14.4.1 Fire Intensity and Frequency

The fire's intensity, as determined by its total heat, the transfer of that heat to the under- or overlying soils, and the migration rate of the fire, is generally the most important single factor driving microbial community responses in most environments (Neary et al. 1999; Hart et al. 2005; Tobin-Janzen et al. 2005). Heat from the fire is by itself often high enough to sterilize soils, with surface temperatures above mine fires exceeding 730°C (Lapham et al. 1980), and those in surface fires capable of exceeding 675°C. Even nonsterilizing heat levels can directly lyse bacterial cells, and reduce their reproductive capabilities (Covington and DeBano 1990). As a result, total microbial numbers as well as microbial community diversity tend to decrease dramatically immediately post-fire (Dunn et al. 1979; Fritze et al. 1993; Prieto-Fernández et al. 1998; Tobin-Janzen et al. 2005), although some exceptions to this rule have been observed (Newman et al. 2003).

Soil moisture, which varies with both above- and belowground fire conditions as previously described, can intensify the fire's impact on microbial cells. Moist heat is much more efficient at killing soil micro-organisms than dry heat, with threshold values for fungal and bacterial survival estimated at 80°C and 60°C for fungi, and 120°C and 100°C for bacteria in dry and moist soils, respectively (Dunn and DeBano 1977; Dunn et al. 1985). Thus, increased soil moisture can be responsible for augmenting a fire's short-term impacts on microbial communities. Conversely, decreased soil moisture can exacerbate a fire's long-term impacts. Summer droughts, for example, have been proposed to be responsible for the slow recovery of bacterial and fungal community biomass following both surface and underground fires (Cilliers et al. 2005; Tobin-Janzen et al. 2005; Yeager et al. 2005). Finally, the condensing steam from underground mine fires moistens the overlying soils, and may actually help to increase microbial survival in fire-affected soils, even during summer droughts (Tobin-Janzen et al. 2005).

The migration rate of a fire likewise determines its impact on soil microbial communities. Low intensity, rapidly moving surface fires do not generally exceed surface temperatures of 250°C, and microbes at depths as shallow as 25 mm generally survive. By contrast, in high-intensity surface fires with surface temperatures exceeding 675°C, microbes as deep as 50 mm underground experience selective die-off (Neary et al. 1999). By comparison to surface fires, underground fires tend to move very slowly, and their effects can last for decades or longer. The Centralia mine fire, which started in 1962, is expected to burn for at least another 100 years, and the Jharia coalmine fire has been burning in India since 1916.

Thus, the long-term effects on soil microbial communities in these areas, although yet unstudied, are expected to be extensive. Over a one-year period, our laboratory (Tobin-Janzen et al. 2005) used T-RFLP analysis of domain Bacteria 16S rRNA to ascertain that the complexity of microbial communities decreased uniformly as temperatures in the site increased. Furthermore, these changes were not correlated with other environmental factors such as soil pH, soil moisture, inorganic nitrogen, or total sulfur, but rather with general trends in the mine fire progression itself. It will be of interest to determine what happens to these microbial communities as the impact time stretches from months to decades.

Another important manner in which the intensity of surface fires and underground fires differ from each other is in the bottom-up nature of underground fires. Because the fire source is belowground, subsurface temperatures become progressively more elevated as soil depth increases. Although the subsurface microbial communities below 50 cm have not yet been extensively assayed in our laboratory, our unpublished observations suggest that as temperatures increase with depth, the total microbial biomass, as determined by the amount of bacterial DNA that can be extracted from the soil samples, decreases as well. Despite this decrease, we have successfully amplified domain Bacteria 16S rRNA genes from soil samples at depths of up to 50 cm, and at temperatures of up to 87°C.

The overall impact of a fire's intensity on microbial communities varies tremendously with the species composition of that community. Pietikainen et al. (2000) demonstrated that bacteria tend to be more resistant to fire-induced heat than fungi. However, not all bacteria are similarly resistant, nor are all fungi similarly susceptible. In fact, Izzo et al. (2006) used greenhouse experiments to demonstrate that certain species of ectomycorrhizal fungi may actually compete more successfully for roots in the presence of fire, and *Neurospora* ascospores germinate in response to heat or fire (Emerson 1948; Jesenska et al. 1993; Pandit and Maheshwari 1996).

Heterotrophic bacteria often show the sharpest declines in numbers following fires, presumably as a result of the combustion of readily available food sources. By contrast, autotrophic bacterial numbers can actually increase as nutrients are released from their organic forms. In our work above the Centralia coalmine fire, for example, autotrophs are frequently dominant members of the bacterial communities present in fire-affected soils. However, *Nitrobacter* are generally more heat-sensitive than heterotrophic bacteria, (Dunn and DeBano 1977; Dunn et al. 1985), and actinomycetes are generally more heat-resilient than other culturable heterotrophs (Cilliers et al. 2005). Recent experiments have shown that many of the most common bacteria in fire-affected soils include endospore formers (Ahlgren 1974; Moseby et al. 2000; Yeager et al. 2005). This finding is not surprising, as these endospore formers probably survive short-term intense heat as endospores, and then rapidly germinate once soil moisture, temperature, and nutrient levels have returned to sustaining levels. Ultimately, thermophilic bacteria are the most resilient of all microbial species, and are often preferentially selected by fire conditions. Our team and others have demonstrated that they often make up the dominant populations in fire-affected soils (Norris et al. 2002; Tobin-Janzen et al. 2005; Yeager et al. 2005).

14.4.2 Nitrogen-Cycling Bacteria

Available nitrogen is often a limiting nutrient in pre-fire environments (Allen et al. 2002; Yeager et al. 2005). However, both surface and underground fires can release inorganic nitrogen as a result of the combustion of organic molecules. This nitrogen initially exists as NH_4^+-N, but is quickly oxidized to NO_3^--N (DeLuca and Zouhar 2000; Tobin-Janzen et al. 2005; Yeager et al. 2005). Soil bacteria are probably critical components in this oxidation, and yet they have remained poorly studied in post-fire environments until recently. Yaeger et al. (2005) used molecular analysis of *nif*H and *amo*A genes to study nitrogen-fixing and nitrifying bacteria following a forest fire. They demonstrated that although there was a decrease in overall microbial biomass, including that of nitrogen-cycling bacteria, the nitrogen-fixing community actually became more diverse within a month after the fire. By contrast, a single ammonia-oxidizing type, belonging to *Nitrosospira* spp. cluster 3A, dominated in the post-fire soils.

Our laboratory has similarly demonstrated the presence of ammonia-oxidizing bacteria, as determined by the presence of *amo*A genes, in hot mine-fire affected soils with elevated NH_4^+-N and NO_3^--N, and at temperatures of up to 60°C (Tobin-Janzen et al. 2005). Furthermore, we have isolated spore-forming *Geobacillus* that can reduce nitrate to N_2O at 60°C (Kauffman and Tobin-Janzen 2005). Thus, nitrogen-cycling bacteria appear to be important components of both surface and underground mine fire environments, where they are most likely exploiting the elevated nitrogen levels, and where they could be contributing to greenhouse emissions in the fire areas.

14.4.3 Sulfur-Cycling Bacteria

Perhaps the most interesting difference between environments affected by belowground versus surface fires is the high levels of sulfur that can condense into the soils above the former. In this regard, subsurface fires tend to more closely resemble fumaroles and other similar geothermal environments, in which surface soils are affected by hot gases containing varying levels of H_2O, CO_2, SO_2, H_2S, H_2, N_2, CO, and CH_4 (for further details, see Delmelle et al. 2000; Giggenbach and Sheppard 1989).

Janzen et al. (unpublished results) have recently studied the sulfur levels surrounding an active vent above the Centralia coalmine fire, where they demonstrated that the highest levels of sulfur did not necessarily correlate with the highest soil temperatures, but rather with temperatures that favored condensation of the sulfur into the soils, rather than its loss to vaporization (Fig. 14.1). In order to determine if sulfur-metabolizing bacteria were capitalizing on the high levels of sulfur in these soils, our laboratory collected soil samples from the same boreholes, and identified total bacterial community members using 16S rRNA gene sequencing.

In Fig. 14.2, it can be seen that the bacterial community members of this fire-affected soil are in fact enriched for thermophilic bacteria, including thermophilic sulfur metabolizers, nitrogen-cycling bacteria, and endospore-forming bacteria. The community itself was only modestly diverse, with the dominant bacterial groups including Actinobacteria, Alphaproteobacteria, Deltaproteobacteria, Betaproteobacteria, along with *Acidothermus, Clostridium*, and *Geobacillus* species. These results are in good agreement with the trends seen in other hot, fire and geothermally affected soil environments (Norris et al. 2002; Yeager et al. 2005).

14.5 Conclusions

Although the micro-organisms capable of surviving and thriving in fire-affected areas are poorly studied at this time, studying their life cycles and environmental effects is likely to produce important discoveries. Microbes found in fire-affected

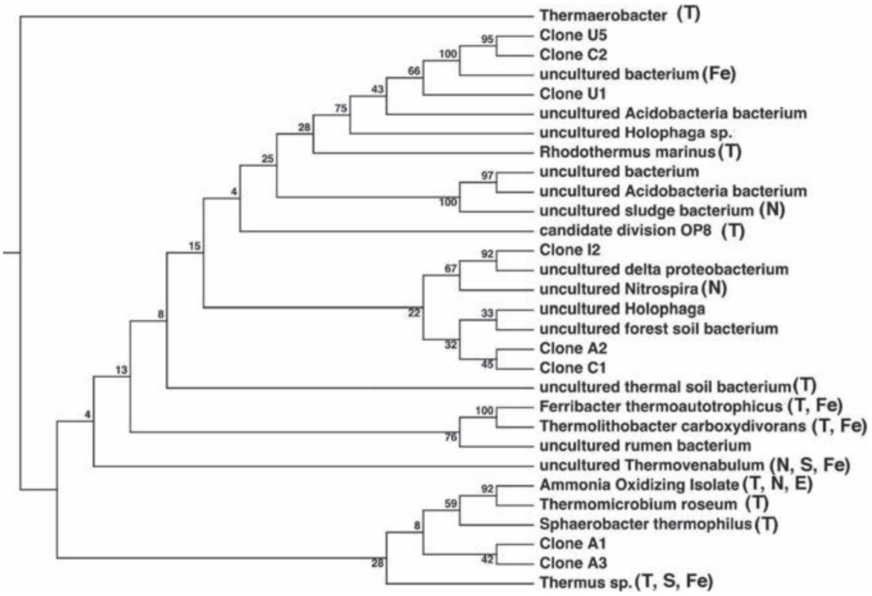

Fig. 14.2 Dendrogram of 16S rRNA gene sequences obtained from the field samples surrounding the active vent depicted in Fig. 14.1. Samples designated 'Clone C' and 'Clone I' originated from the boreholes one meter to the left and right of the active vent, respectively. Samples designated Clone A and Clone U came from an affected surface site (50°C) located outside of the study area depicted in Fig. 14.1. Taxa containing known thermophiles (T), endospore-formers (E), and nitrogen (N), sulfur (S), and iron (Fe) cycling bacteria are indicated. The dendrogram was generated using nearest neighbor analysis and the CLC Combined Workbench Program (CLC Bio). Bootstrap values from 100 resamplings are shown above each internal node. *Thermaerobacter* 16S rRNA was used as the outgroup

areas most likely play critical roles in the biogeochemical cycling of nitrogen and in rhizosphere ecology, and thus can be expected to play important roles in the recovery of fire-affected ecosystems. Thermophilic bacteria, in general, have already provided biotechnology with some of its most powerful tools, and thermophilic sulfur-metabolizing bacteria are currently at the heart of several studies geared toward producing more efficient methods of bioleaching metals and desulfurizing flue gases (Huber and Stetter 1998; Kaksonen et al. 2006). Inasmuch as these bacteria appear to be enriched in hot mine-fire affected soils, continued research into their biology, environmental roles, and metabolism will be particularly interesting. Finally, not all fire-associated bacteria are benign. Iron and sulfur-metabolizing bacteria catalyze the rate-limiting step responsible for acidification of drainage effluents in coal mining environments, and the nitrogen-cycling bacteria identified in this study and others may also be responsible for releasing the greenhouse gases NO and N_2O into the environment. Thus, further study of these interesting extremophiles holds the promise of beneficial technological advances in a variety of compelling areas.

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