July 26. 1994

Reviewer:

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Comments:

This paper presents a general overview of bacteria in the environment. After a general introduction to the bacteria; their habitats, movement, and environmental limitations, the bacteria are divided into 15 functional groups. The more detailed descriptions of the functional groups gives excellent insight to the diversity of bacteria.

The author does an excellent job of concisely describing the importance and complexity of bacteria in the environment. The number and choice of functional groups should allow for maximum flexibility in determining the effect of management options on bacteria. For example, many bacteria will fit into more than one functional group. This will allow one to look at the effects of management options from many directions, i.e. energy source, competition, climatic changes, etc.

It would have been most useful to have specific management options to address in the management considerations section.

Preface

The following report was prepared by University scientists through cooperative agreement, project science staff, or contractors as part of the ongoing efforts of the Interior Columbia Basin Ecosystem Management Project, co-managed by the U.S. Forest Service and the Bureau of Land Management. It was prepared for the express purpose of compiling information, reviewing available literature, researching topics related to ecosystems within the Interior Columbia Basin, or exploring relationships among biophysical and economic/social resources.

This report has been reviewed by agency scientists as part of the ongoing ecosystem project. The report may be cited within the primary products produced by the project or it may have served its purposes by furthering our understanding of complex resource issues within the Basin. This report may become the basis for scientific journal articles or technical reports by the USDA Forest Service or USDI Bureau of Land Management. The attached report has not been through all the steps appropriate to final publishing as either a scientific journal article or a technical report.

September 30, 1994

Kurt Nelson
Terrestrial Group Co-leader
Eastside Ecosystem Management Project
112 East Poplar St.
Walla Walla WA 99362-1693

Dear Mr. Nelson:

I have revised my report on functional groups of bacteria based on the comments I received. As we discussed on the telephone, I feel that the functional groups in general fall along genus rather than species lines, and where I have a genus listed in two groups, the same species would usually fall in both groups. I could find no empirical evidence as to which species within a genus would be found in the area covered by the project, and therefore was reluctant to give species names. I have divided the management considerations section into land use considerations and bacterial monitoring. I have emphasized forestry, grazing, and mining in the land use section.

This should complete the requirements of my contract, and I would appreciate payment of $7500 as listed on purchase order number 43-0E00-4-9169. I hope the report is useful to you. Please do not hesitate to contact me if you require further information. Good luck with the project!

Sincerely,

A. Muehlchen

Andrea M. Muehlchen
Plant Pathologist
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EASTSIDE ECOSYSTEM MANAGEMENT PROJECT: FUNCTIONAL GROUPS OF BACTERIA

prepared by: Andrea M. Muehlchen

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EASTSIDE ECOSYSTEM MANAGEMENT PROJECT: FUNCTIONAL GROUPS OF BACTERIA

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GENERAL CHARACTERISTICS

Bacteria occupy a wide variety of habitats and perform many ecological functions. They produce a vast array of chemical metabolites, many of which affect other organisms (Lynch 1976). Some fix carbon dioxide into organic compounds and are part of the primary level of the food chain. Many are extremely important in cycling nutrients in the soil and in water, making the nutrients more or less available to plants and other organisms. Air, water, and soil quality can be altered by the activities of bacteria. Species associated with plants and animals can be beneficial or pathogenic to their hosts.

Bacteria exhibit many ways of exploiting their environments. Species differ greatly in their biochemical capabilities and utilize many different substrates. Some form mutualistic associations with other bacterial species or other organisms. Most bacteria are exposed to gradients either of substances such as nutrients or of physical factors such as temperature and radiation, and they often have adaptations which allow them to find or remain in the location in these gradients which best meets their needs (Schlegel and Jannasch 1981). Some are able to move by gliding or the use of swimming appendages called flagellae. Bacteria are often associated with liquid-solid orair-liquid interfaces (Schlegel and Jannasch 1981). In many habitats the ability to attach to solid surfaces provides advantages. Attachment can allow bacteria to remain near a nutrient source or to exploit the accumulation of nutrients atparticle surfaces. They can attach by sheath, gumlike polymers, or filamentous appendages. Some bacteria are found at air-liquid interfaces such as pond surfaces. They can benefit from direct exposure to oxygen in the air, accumulation of hydrophobic substrates either from the water or air, and high light intensities. Many species adapted to this interface contain gas vacuoles which allow them to float.

Most bacteria in soil are adsorbed or attached to particles, although this varies with soil type, pH, and other factors (Gammack et al. 1992). Movement through soil, however, can occur by mass flow, passive diffusion, or active motility in saturated soil, or by growth. Dispersal can either be of the free bacteria, or of the bacteria on soil particles. Soil animals affect movement of bacteria by affecting the flow of water through soil, by ingesting soil and bacteria (e.g. earthworms),

or by transporting them on external surfaces. The growth of roots and fungal hyphae can also act as vectors. Bacteria can be dispersed above ground in aerosols. Aerosols are usually formed when rain hits a solid surface, but wind can also be responsible. Bacteria can also be moved in windblown dust (Gammack et al. 1992).

The distribution of bacteria is governed by limiting factors, and each species will exist where levels of factors such as temperature, moisture, nutrient availability, and pH fall within its specific range of tolerance (Dommergues et al. 1978). Because soil is a complex system, the determination of where a soil microorganism would be found based on limiting factors must take into account interactions between environmental factors, alterations of the organism's range of tolerance by other factors, and variations of environmental factors in both time and space. Variation in space is particularly important in soil because soil is a heterogeneous matrix composed of many different microhabitats. Soil is usually aggregated, and the center and exterior of the aggregates differ greatly in availability of oxygen, moisture, and other factors.

Many environmental factors can be limiting to bacteria (Dommergues et al. 1978). One of these that dramatically affects the growth of bacteria is the availability of energy, either-as light or in the form of chemical energy. Because light is usually not available in soil, most soil bacteria use chemical energy. Light can, however, be an important factor for those bacteria associated with plants. Another important factor which limits bacterial growth is temperature. Each species or strain will have its own minimum, optimum, and maximum growth temperatures, and these can be modified by other factors. Water tension or water availability is also likely to be limiting to bacteria. While most bacteria require moist environments, tolerance of high water tension varies widely with species. Oxygen requirements also vary widely with species. In soil, oxygen levels are governed largely by soil structure and water content. Oxygen levels often determine soil redox potential, which in turn determines whether compounds are found in their oxidized or reduced states. Another factor which affects bacteria is pH. Biological factors such as competition or production of antibiotics and other inhibitory compounds can limit bacterial growth. Soil microfauna such as protozoa and nematodes act as predators. Bacteriophages may also limit the activity of bacteria. While identification of factors which limit bacterial growth and activity is usually possible, accurate prediction of changes in bacterial-populations and processes due to changes in these factors is extremely difficult (Dommergues et al. 1978).

Broad groupings of bacteria can be made based on sources of energy and cellular carbon. Phototrophs use light as an energy source, while chemotrophs use chemical energy. Chemoorganotrophs oxidize organic compounds, while chemolithotrophs oxidize inorganic compounds. Autotrophs fix carbon dioxide while heterotrophs utilize organic compounds as their source of cellular carbon. (Heterotrophs are also chemoorganotrophs.) Various combinations of the above groupings (e.g. photoautotrophs) are possible. Some species are able to switch between these groups depending on their situation.

The functional groups dealt with in this report are (1) photoautotrophs, (2) methanogens, (3) heterotrophs, (4) nitrogen fixers, (5) nitrifyers, (6) denitrifyers, (7) sulfur oxidizers, (8) sulfur reducers, (9) iron and manganese oxidizers, (10) iron and manganese reducers, (11) phosphorus, calcium, and potassium solubilizers, (12) plant growth-promoting rhizobacteria, (13) ice nucleating bacteria, (14) plant pathogens, and (15) animal pathogens. Bacteria are ubiquitous, and members of each group could be expected wherever their specific requirements are met. Information regarding populations of bacteria in the Columbia Basin is lacking, however, and surveys would be required to accurately determine which functional groups are represented at a given location.

NUTRIENT CYCLES

Carbon

In many environments bacteria play a key role in the cycling of carbon (C). One part of that cycle is primary production or the fixing of carbon dioxide (CO_2) into organic compounds. Some bacteria can fix C chemoautotrophically, using the oxidation of inorganic compounds to provide energy for $C0_2$ fixation. A more important group are photoautotrophic, using the energy in sunlight to fix $C0_2$. Photoautotrophic bacteria include cyanobacteria and green and purple photosynthetic bacteria (Atlas and Bartha 1987) . Methanogenic bacteria reduce $C0_2$ to methane (CH_4) under anaerobic conditions. The released CH_4 can then be used by a relatively small group of bacteria called methylotrophs.

<u>1) Photoautotrophs</u>

Photosynthetic bacteria include the cyanobacteria, which, like plants, use water as an electron donor and liberate oxygen, and the green and purple sulfur bacteria, which carry out photosynthesis anaerobically and do not evolve oxygen (Atlas and Bartha 1987, Gottschalk 1979). The cyanobacteria are the most

diverse and widely distributed group of photosynthetic bacteria, including more than 1000 species (Atlas and Bartha 1987). They fix $C0_2$ via the Calvin cycle. Some are capable of limited heterotrophic growth, but $C0_2$ is the preferred source of C for all species (Tabita 1987). Some cyanobacteria can fix nitrogen in addition to carbon. Cyanobacteria are important in the upper levels of water bodies and on soil surfaces. Many planktonicforms contain gas vacuoles which allow them to float in a zone of higher light intensity and shade out competitors below (Walsby 1987). The role of cyanobacteria in desert soil crusts will be discussed in a later section.

The green and purple sulfur bacteria use reduced sulfur compounds such as hydrogen sulfide (H_2S) as electron donors. They are typically aquatic and are often found at-the interface of water and sediment, where they can form pink to purple red or green mass accumulations (Pfennig 1989). Some also contain gas vacuoles that permit them to float in the water column at the level where light, oxygen, and H_2S are optimal for anaerobic photosynthesis (Atlas and Bartha 1987). The source of the H_2S used can be geochemical as in sulfur springs, or biological as in the sulfide released by sulfate-reducing bacteria (Pfennig 1989).

2) Methanocrens

Methanogenic bacteria are strictly anaerobic archaebacteria that can use $C0_2$ as an electron acceptor (Atlas and Bartha 1987). They reduce $C0_2$ using hydrogen gas produced in fermentation. Although morphologically diverse, methanogens reduce $C0_2$ by the same enzymatic pathway (Jones et al. 1985). The conversion to cellular C in methanogens is by the reductive acetyl CoA pathway, which they share with most autotrophic sulfate reducers (Fuchs 1989). Some methanogenic bacteria can utilize formate, methanol, methylamine, and acetate as the electron donor for growth and CH_4 production, but all can use hydrogen gas (Balch et al. 1979, Gottschalk 1979). Methanogens are unable to use complex carbohydrates and proteins, and depend upon the fermentation products of other microbes to use as their substrates. They form associations with other microorganisms which maintain the low level of oxygen required, and providesubstrates. They are found in anaerobic soils and sediments where organic matter is being decomposed, and are very important in the rumen, where they allow fermentation by other microorganisms to continue by removing hydrogen gas from the system (Gottschalk 1979).

3) Heterotrophs

The other components of the microbial carbon cycle are the conversion of organic compounds into other organic compounds, and

the breakdown of organic compounds with the accompanying release of energy and $C0_2$. Those bacteria that fix $C0_2$ will also break down organic matter in respiration (Atlas and Bartha 1987). Many bacteria are able to grow heterotrophically, obtaining all their energy and cellular carbon from pre-existing organic material. They are extremely important in the formation of humus in soil, the cycling of other minerals tied up in organic matter, and the prevention of buildup of dead organic materials. Heterotrophic bacteria are found in many diverse groups, can be aerobic or anaerobic, and are capable of utilizing a broad array of organic compounds. Microorganisms are unique in their ability to carry out anaerobic or fermentative degradation of organic matter (Atlas and Bartha 1987), although C turnover is greater under aerobic conditions (Boyd 1984). They are also responsible for the digestion of polymers such as cellulose and lignin, which multicellular organisms are unable to utilize. Some are able to break down man-made synthetic materials (Atlas and Bartha 1987). Microbial decomposition is favored by an adequate supply of nitrogen and phosphorus, neutral to alkaline conditions, good aeration, and adequate moisture (Boyd 1984). Physical breakdown of materials by insects, earthworms, and other animals also favors decomposition by exposing more surface area to microbial attack.

Good soil structure is extremely important for plant growth, water penetration, gas exchange, and resistance to erosion (Gray and Williams 1971). Heterotrophic bacteria play an important role in maintaining soil structure by their involvement in the formation and stabilization of water-stable soil aggregates. Polysaccharides are one of the major agents of soil aggregation, and it is thought that the soil polysaccharides are likely to be of microbial origin and are more resistant to breakdown than animal and plant polysaccharides (Gray and Williams 1971, Lynch 1976, Tisdall and Oades 1982). Bacteria also release other organic compounds which affect aggregate structure and other soil properties such as water holding capacity. Bacterial cells themselves can hold soil particles together by adhesion or mechanical binding, and even after the bacteria die, their remains continue to bind the particles (Lynch 1976, Tisdall and Oades 1982).

Many heterotrophic bacteria are specialized to the environmental conditions under which they are found. Some can form digestive associations with large herbivores and are vital to the nutrition of these animals. Ruminant animals such as deer, elk, and cattle consume food that is high in cellulose, yet do not produce cellulase enzymes themselves. Bacteria in thedigestive tract perform this function. The rumen is an anaerobic chamber that is maintained at 30-40C and pH 5.5-7.0 (Atlas and Bartha 1987). In addition to cellulose digesters, the rumen also

contains starch digesters, hemicellulose digesters, sugar fermenters, fatty acid utilizers, methanogenic bacteria, proteolytic bacteria, and lipolytic bacteria (Atlas and Bartha 1987, Keeton 1980).

Nitrogen

Nitrogen (N) is an extremely important element to all forms of life. It is found in amino acids and many other organic compounds. It exists in stable valence states from -3 to +5 (Atlas and Bartha 1987, Blackburn 1983, Sock, Koops and Harms 1989). Large amounts of N are in N_2 gas in the atmosphere, but utilizable combined forms are limiting in many ecosystems. Ammonium (NH_4+) and nitrate (NO_3-) , inorganic salts of nitrogen, are water-soluble, and are the main forms used by organisms. A few select groups of bacteria are the only organisms known to be able to fix N_2 into combined forms. The critical steps in the N cycle, N_2 fixation (N_2 to NH_4+) , nitrification (NH_4+to NO_3-) , and denitrification (NO_3- to N.) , are all mediated by bacteria. Bacteria are also important in ammonification, the release of ammonia (NH_3) through breakdown of organic matter (Blackburn 1983) . Some of the NH_3 is lost as gas to the atmosphere, but- in neutral to acidic environments, most is in the form of ammonium ions (NH_4+) which are available for uptake by many plants and microorganisms (Atlas and Bartha 1987).

<u>4) Nitrogen Fixers</u>

Nitrogen fixation is the most important input of combined N into non-cultivated land (Burns and Hardy 1975) N_2 fixation is carried out by the enzyme nitrogenase (Atlas and Bartha 1987). It is very sensitive to oxygen, and organisms have to either exist in an anaerobic environment or keep the enzyme protected from oxygen. N_2 fixation is recorded in at least 26 genera of bacteria (Burns and Hardy 1975). It is carried out by free-living bacteria such as *Azotobacter* and *Clostridium*, and by bacteria which form mutualistic associations with plants. A high energy input is required for N_2 fixation, and plants help supply this energy in the form of organic compounds. Many free-living bacteria fix N_2 preferentially in the rhizosphere, where root exudates help support the reaction. The presence of mycorrhizae also appears to enhance N_2 fixation (Burns and Hardy 1975). Excess fixed N is in turn taken up by the plant. In water, N_2 fixation is carried out by cyanobacteria, which supply the energy required for the process through photosynthesis (Atlas and Bartha 1987).

On land, most N_2 fixation is carried out by bacteria which form nodules on plants, particularly by species of

Rhizobium. As a free-living heterotroph in the soil, Rhizobium does not fix N_2, but when it enters the roots of leguminous plants, it undergoes changes which allow the process to occur. The association is very specific, and only a particular species of Rhizobium can enter into a symbiotic relationship and nodulate a particular species of legume. The survival of Rhizobium in soil and its ability to infect roots are sensitive to soil conditions such as temperature, pH, and nitrogen availability The N. fixation process requires adequate molybdenum, sulfur, and iron (Atlas and Bartha 1987). N_2 fixing nodules can also be formed on some nonleguminous plants by some species of Rhizobium, cyanobacteria, and actinomycetes (Sprent 1987). The actinomycete Frankia is the best known of these and forms nitrogen fixing nodules on alder and other species of woody shrubs and trees (Akkermans 1978) . Frankia can also grow and fix N_2 on root surfaces (Ronkko et al. 1994). Some liverworts, mosses, gymnosperms, and angiosperms form associations with the cyanobacteria Nostoc and Anabaena (Akkermans 1978, Atlas and Bartha 1987). The cyanobacteria fix N_2 and are supplied with photosynthate by the plant rather than fixing C02 themselves as when they are free-living. There are also N_2 fixing lichens which are symbioses of cyanobacteria and fungi (Sprent 1987).

In arid and semiarid areas throughout the world, N_2 fixing cyanobacteria, either free-living or in lichens, form an important part of features known as crytobiotic crusts (Belnap 1993, Sprent 1987). The bacteria can withstand long periods ofdrought yet resume metabolic activity, including N_2 fixation, within minutes of rehydration. Light is usually abundant and organic matter scarce, thus the ability of cyanobacteria to fix both N and C allows them to survive and to support other members of the crusts including fungal symbionts, desiccation-tolerant mosses, and heterotrophic, nitrifying, and denitrifying bacteria (Sprent 1987). The bacteria also appear to increase the availability of other nutrients in the crusts (Belnap and Gardner 1993). These crusts can have a significant role in preventing soil erosion, as the bacteria produce polysaccharide sheath material which binds soil particles together and retains moisture (Belnap and Gardner 1993). When the crusts are physically damaged, however, they are very slow to recover (Belnap 1993, Belnap et al. 1994).

5) Nitrifyers

In nitrification, NH_3 or NH_4^+ are oxidized to nitrite (NO_2-) and then to nitrate (NO_3-). NO_3-, is readily taken up by plants and because of its negative charge, moves freely through soil. Both NO_3- and NO_2-are also more susceptible to leaching than is NH_4^+. They can become a health hazard when they reach groundwater. Nitrification can also prevent nitrogen losses in soils where NH_3

volatilization is a major factor (Bock, Koops and Harms 1989). Nitrification is limited to species of a few genera of aerobic autotrophic bacteria (Focht and Verstraete 1977). Nitrifiers are found in most aerobic environments where organic matter is mineralized, and on rocks where NH_4^+ is liberated through weathering (Bock, Koops and Harms 1989). Many are restricted to specific environments. The oxidation of NH_3 and $NH_4^+$to NO_2^- is carried out in most soils by species of *Nitrosomonas,* while the oxidation of NO_2^- to NO_3^- is carried out by *Nitrobacter* (Bock, Koops and Harms 1989). Species of *Nitrosospira, Nitrosococcus,* and *Nitrosolobus* can also be involved in the former oxidation, while species of *Nitrospira.* and *Nitrococcus* can be involved in the latter. The two processes are usually closely coupled. Both oxidations are energy yielding, and the bacteria involved are chemolithotrophic, utilizing the energy to fix CO_2. Because the energy yields of the oxidations are small, large amounts of N are turned over for relatively small cell yields (Blackburn 1983, Focht and Verstraete 1977). Nitrification is inhibited by anaerobic conditions or high acidity.

6) Denitrifvers

Under anaerobic conditions, NO_3^- ions can act as electron acceptors, resulting in dissimilatory NO_3^- reduction. Some bacteria reduce NO_3^- through NO_2^- to NH_4^+. This can occur in stagnant water and sediments. In denitrification, NO_2^- is reduced through NO_2^- and nitric oxide to nitrous oxide (NO_2) and finally N_2 gas. Denitrifying organisms in soil include species of Pseudomonas and *Alcaligenes,* while others such as *Paracoccus denitrificans* are found in aquatic environments (Focht and Verstraete 1977). The products of denitrification are usually a mixture of N_2O and N_2, the ratio depending on the organisms involved and the environmental conditions (Atlas and Bartha 1987). Under reduced oxygen tensions, less N_2O is evolved (Focht and Verstraete 1977). At lower pH, more N_2O is released. In soils high in organic substrates, denitrification tends to progress to completion and less N_2O is released. N_2O in the stratosphere undergoes oxidation to nitric oxide which is involved in the destruction of ozone (Focht and Verstraete 1977, Hooper 1989). Oxygen will always be used preferentially as an electron acceptor by the bacteria responsible for denitrification (Focht and Verstraete 1977). Denitrification is therefore strongly supressed by oxygen, and although some denitrification can occur in anaerobic microsites in well aerated soil, denitrification increases when oxygen is displaced by water as after rain or irrigation (Hutchinson and Mosier 1979). Different genera of bacteria may be responsible for denitrification under different levels of NO_3^- NO_2^-, organic matter, oxygen, pH and temperature (Focht and Verstraete 1977).

Sulfur and Selenium

Sulfur (S), one of the ten most abundant elements on earth, is an important component of proteins and other cellular compounds. It is very reactive, with oxidation states ranging from -2 to +6 (Atlas and Bartha 1987). Plants take up S in the form of sulfate, while animals require S in organic forms via their food (Jorgensen 1983). Selenium (Se) is an element closely related to S that is required by bacteria and animals but is toxic at higher levels. Livestock in many areas, including the Columbia Basin, have suffered from white muscle disease, which results from Se deficiency (Rosenfeld and Beath 1964). High levels of Se on the western plains of the U.S. cause alkali disease of cattle (Doran 1982, Mayland et al. 1989). Selenium is cycled by similar or the same pathways as is S (Doran 1982). Both S and Se are mobilized in the environment by weathering, ore processing, gaseous emissions from volcanic activity and the burning of fossil fuels, and the disposal of wastes (Doran 1982). The Se contained in sewage sludge is in a form available for biological uptake and may be a significant source in areas where sludge is applied (Doran 1982, Mayland et al. 1989).

Bacteria regulate S and Se availability in the soil through mineralization and immobilization and through oxidation and reduction. Many bacteria mineralize these elements through decomposition of organic residues which contain them, releasing inorganic S or Se compounds into the soil (Doran 1982, Germida et al. 1992). They immobilize them by incorporating them into cell components, thus making them unavailable for uptake by plants and other organisms. Many microorganisms are also capable of releasing volatile gases of S and Se from both inorganic and organic sources of the elements, thus contributing to their global cycling (Bremner and Steele 1978, Doran 1982, Germida et al. 1992, Kelly and Smith 1990). More specialized groups of bacteria are responsible for the oxidation and reduction of S and Se. The two elements differ in that selenite is less available than sulfite and selenate is only formed under strongly oxidizing alkaline conditions, while sulfate is common in soils and water (Doran 1982, Postgate 1979). However, the conversions of the two elements are so similar that only S will be dealt with here.

<u>7) Sulfur Oxidizers</u>

The oxidation of H_2S and other reduced S compounds to elemental S and sulfite and further to sulfate (SO_4^{2-}), is carried out by several specific groups of bacteria. H_2S is toxic to many heterotrophic microorganisms, and SO_4^{2-} is the form of S required by plants and many other organisms, so these transformations are very important to the soil community. When oxygen is present,

some chemolithotrophic bacteria can oxidize reduced S compounds such as H_2S to support their growth (Atlas and Bartha 1987, Ehrlich 1981). These organisms are often found at the interface of anaerobic sediments, where H_2S is formed, and oxygenated water (Jorgensen and Revsbeck 1983). Sulfur globules are formed during the oxidation, and by some bacteria can be further oxidized to SO_4^{2-} in the absence of H_2S. Sulfur oxidations are carried out by species of *Thiobacillus* and by filamentous sulfur bacteria such as *Beggiatoa, Thiothrix,* and *Thiovulum* (Atlas and Bartha 1987, Germida et al. 1992). Some are obligate chemolithotrophs,obtaining their energy from the oxidation of S compounds and their carbon from the reduction of CO_2. Others are facultative chemolithotrophs, and can utilize other compounds. *Thiobacillus* species range in optimum temperature for growth from 30-50C and pH from 2-8 (Kelly 1989) . H_2S can also be oxidized phototrophically under anaerobic conditions (Atlas and Bartha 1987, Ehrlich 1981, Germida et al. 1992). Photosynthetic sulfur bacteria oxidize H_2S to elemental S and photoreduce C02. These reactions are carried out mostly by members of the Chromatiaceae and Chlorobiaceae.

8) Sulfur Reducers

The reduction of S compounds by soil microorganisms is also important to cycling of the nutrient. Elemental S has recently been shown to act as an electron acceptor in the anaerobic metabolism of *Desulfuromonas acetoxidans* (Pfennig and Biebl 1981). SO_4^{2-} can be reduced in two distinct ways. Many organisms are capable of assimilatory SO_4^{2-} reduction. Plants and many microorganisms use SO_4^{2-} as their source of S and reduce these ions to H_2S which is immediately incorporated into proteins and other organic compounds (Ehrlich 1981). In dissimilatory SO_4^{2-} reduction, specialized anaerobic bacteria utilize SO_4^{2-} as a terminal electron acceptor in anaerobic respiration (Ehrlich 1981). These bacteria include species of *Desulfovibrio, Desulfotomaculum,* and several other genera. Sulfate reduction, can occur over a wide range of pH and salinity, but only a limited number of compounds can be oxidized, which often acts as the limiting factor in the process. The most common electron donors used are pyruvate, lactate, and molecular hydrogen. SO_4^{2-} reduction is inhibited by oxygen, nitrate, or ferric ions. Sulfate reducing bacteria are often found in bogs, swamps, and poorly drained soils where anaerobic conditions exist (Bremner and Steele 1978). Even in well-aerated soils, however, SO_4^{2-} reduction can occur in anaerobic microsites (Germida et al. 1992). The sulfide formed from SO_4^{2-} oxidation is a chemical reducing agent, which helps preserve the anoxic environment necessary for continued activity of the bacteria (Postgate 1979).

Iron and Manganese

Iron (Fe) is the fourth most abundant element on earth, but most of it is unavailable to organisms (Lewin 1984). Iron cycling occurs between the ferrous (Fe^{2+}) and ferric (Fe^{3+}) ions. The change between these states generates a large redox potential, and it is this property that makes Fe so vital to cell function (Lewin 1984). The redox potential is used by the electron transport chain in respiration and by ribonucleotide reductase used in the manufacture of DNA (Jones 1986, Lewin 1984). Iron is also important in many other enzyme systems and biological functions. Manganese (Mn) is essential in small amounts for plants, animals, and microorganisms (Nealson *1983)*. It is cycled between the reduced manganous (Mn^{2+}) state and the oxidized manganic (Mn^{2+}) state much as is iron, but the spontaneous oxidation of the Mn^{2+} ion only occurs under aerobic conditions at pH values greater than eight (Atlas and Bartha 1987). Mn^{4+} ions form an insoluble dioxide.

Because Fe is so important to cell function, yet is not readily available in most environments, organisms have developed elaborate systems for obtaining and transporting Fe (Jones 1986, Lewin 1984, Loper and Buyer 1991). Bacteria and other soil organisms excrete low molecular weight Fe-chelating molecules called siderophores. Because siderophores have such a high affinity for Fe, they can not only bind ferric hydroxide at its minute solubility at neutral pH, but can also remove ferric ions from soil minerals. Siderophores vary greatly in chemical structure, and are produced by many bacteria (Loper and Buyer 1991). Most are produced extracellularly (Jones 1986). Coupled with these Fe carriers are membrane receptor molecules on the cell surface which recognize and bind the siderophore-Fe complex and either transport the Fe or the whole complex into the cell (Jones 1986, Lewin 1984, Loper and Buyer 1991). The production of the siderophores and the enzymes responsible for making the receptor molecules is regulated by Fe availability and is repressed in the presence of adequate Fe.

9) Iron and Manganese Oxidizers

In the presence of oxygen, Fe^{2+} is unstable and spontaneously oxidizes to Fe^{3+} (Atlas and Bartha 1987, Jones 1986). Only under acidic conditions can bacteria such as *Thiobacillus ferrooxidans* carry out chemolithotrophic oxidation of Fe^{2+} (Atlas and Bartha 1987). Iron bacteria in non-acidic conditions appear to catalyze the oxidation of Fe^{2+} and become encrusted with ferric iron particles, but they do not appear to derive energy from this process (Atlas and Bartha 1987, Jones 1986). The precipitated Fe may stabilize cell walls, it may protect the cell from oxygen, or it may detoxify heavy metals by binding them (Jones 1986).

Ferric ions precipitate as ferric hydroxide, oxide, phosphate, or sulfate (Ehrlich 1981). Manganese oxidation is catalyzed by many bacteria and fungi (Atlas and Bartha 1987, Nealson 1983), and there is some evidence that bacteria can obtain energy for CO_2 fixation from Mn oxidation (Kepkay and Nealson 1987).

10) Iron and Manganese Reducers,

Under anaerobic conditions, Fe^{3+} may be reduced to the more soluble Fe^{2+} form by a wide variety of heterotrophic bacteria including species of *Bacillus* and *Pseudomonas* (Jones 1986). In lakes, most of the Fe-reducing bacteria are found in sediments, and release Fe^{2+} into the water above (Jones 1986) . In soils anoxic due to water logging or high clay content, Fe reduction occurs and gives the soil a greenish-grey color and sticky texture termed gleying (Atlas and Bartha 1987). Many bacteria can metabolically reduce manganese dioxide, releasing the more soluble Mn^{2+} ions (Atlas and Bartha 1987, Jorgensen 1989, Nealson 1983).

Phosphorus, Calcium and Potassium

Several elements are cycled in soil and water with the help of microorganisms, including bacteria, but are not usually oxidized and reduced. These include phosphorus (P), calcium (Ca), and potassium (K). Phosphorus is not an abundant element on earth but is required by all organisms for nucleic acids, ATP, and other cellular constituents (Atlas and Bartha 1987). Elevated P levels in water bodies have become a concern because of phosphates from detergents, human wastes, and agriculturalproducts (Chapra and Robertson 1977, Cosgrove 1977). These phosphates lead to excessive plant and algal growth which in turn leads to eutrophication. Calcium is an important solute in the cell cytoplasm and is required for the function of many enzymes (Atlas and Bartha 1987). It is also important in cell wall structure and in the bones and teeth of vertebrates. Potassium plays a role in the ionic balance of cells and is a cofactor for several enzymes (Keeton 1980). In general, these elements are cycled between organic and inorganic forms through breakdown of organic matter and mineralization, and uptake of ions and immobilization. They can also be solubilized and precipitated through bacterial activities.

11) Phopyhorus, Calcium and Potassium Solubilizers

Phosphorus is often found in insoluble phosphates which are unavailable to plants. The major forms of primary rock phosphate are apatites, which are calcium phosphates with varying amounts of other ions (Tiessen and Stewart 1985). Many heterotrophic and

chemolithotrophic organisms are capable of solubilizing phosphates through the production of organic or inorganic acids or chelators (Atlas and Bartha 1987, Cosgrove 1977, Ehrlich 1981). When calcium phosphate is solubilized in this way, Ca as well as P is released. Calcium is also biologically cycled between insoluble calcium carbonate and soluble calcium bicarbonate. The balance between these is affected by pH and dissolved CO_2. Bacterial ammonification, nitrate reduction, and sulfate reduction all increase alkalinity and can contribute to carbonate precipitation. The removal of CO_2 through photosynthesis by phototrophic bacteria results in a shift from bicarbonate to carbonate. Potassium is solubilized from precipitated forms through the production of inorganic and organic acids by bacteria such as *Thiobacillus, Clostridium* and *Bacillus* (Berthelin 1983).

PLANT AND ANIMAL ASSOCIATED BACTERIA

12) Plant Growth-Promoting Rhizobacteria

Many bacteria are intimately associated with plants roots. In a zone surrounding the root known as the rhizosphere, the populations of microorganisms differ from those in the surrounding soil both in total number and in species distribution (Atlas and Bartha 1987). The plant alters rhizosphere populations through root exudation and the sloughing of root cells. Most plants also interact with specific fungi to form associations known as mycorrhizae, and these also have considerable effects on populations of rhizosphere bacteria (Meyer and Linderman 1984). Some of the bacteria in the rhizosphere act through direct contact with plants either by causing disease, or by setting up mutualistic associations such as the nitrogen fixing nodules of legumes. Other bacteria can either inhibit or promote plant growth less directly. Some may compete with plants for essential nutrients and cause deficiencies by immobilizing those nutrients (Atlas and Bartha 1987, Barber 1978). Many rhizosphere bacteria are capable of promoting plant growth and are known as plant growth-promoting rhizobacteria (PGPR). Some increase the availability of essential nutrients through solubilization and other nutrient cycling activities (Atlas and Bartha 1987). Allelopathic or antagonistic substances which allow plants to compete for space with other plant species are released by some rhizobacteria. other bacteria release vitamins, amino acids, or growth hormones which increase plant growth (Arshad and Frankenberger 1991, Lynch 1976). Some bacteria increase symbiotic legume nodulation by *Rhizobium* (Kloeper et al. 1991), while others are antagonistic to plant pathogens (Defago and Haas 1990, Weller 1988). Some bacteria limit the ability of plant pathogens to invade plants by

inducing resistance in the plants (Kloepper et al. 1991, Kloepper et al 1993, Tuzun and Kloepper 1994, Weller 1988). Still others appear to promote plant growth through mechanisms not clearly understood. Most PGPR strains do not have a single mechanism which completely accounts for the beneficial effects on the plant (Kloepper et al. 1993, Tuzun and Kloepper 1994). While many PGPR will be active naturally, there is considerable interest in manipulating or applying them, and there is some evidence that application of some strains of bacteria could be very beneficial in aiding the establishment of forest seedlings in new plantings (Chanway et al. 1994).

Bacteria that inhibit the activity of plant pathogens are known collectively as antagonists (Defago and Haas 1990). Pathogens encounter antagonism from rhizosphere bacteria before and during primary infection and also during secondary spread on the root (Weller 1988). Fluorescent pseudomonads appear to be the most importantant antagonists (Alabouvette 1993, Defago and Haas 1990), but bacteria in many diverse genera have been implicated in the biological control of plant diseases (Weller 1988). Soils where populations of antagonists act together to control disease are known as suppressive soils (Alabouvette 1993, Defago and Haas 1990, Weller 1988). There appear to be several, modes of action of antagonism, including competition for nutrients and colonization sites on the root surface (Weller 1988), competition for iron using siderophores (Defago and Haas 1990, Loper and Buyer 1991, Weller 1988), production of lytic enzymes such as cellulases, hitinases, and proteases (Kloepper et al. 1993, Weller and Thomashow 1993), production of HCN (Kloepper et al. 1993), and production of antiobitics (Defago and Haas 1990, Sikora and Hoffmann-Hergarten 1993, Weller 1988, Weller and Thomashow 1993). The "mopping up" of nutrients released from roots may prevent the stimulation of spore germination of pathogenic fungi (Weller 1988), and inhibit plant pathogenic nematodes (Sikora and Hoffmann-Hergarten 1993). Each antagonist may act through more than one mechanism to suppress pathogens. Abiotic factors such as soil type, pH, moisture, and temperature may influence the activity of antagnonists (Alabouvette 1993, Tuzun and Kloepper 1994).

13) Ice Nucleating Bacteria

Some bacteria are able to grow epiphytically on the aerial portions of plants. These are directly exposed to climatic changes and are often pigmented and have special cell walls to protect them from light and periods of dessication (Atlas and Bartha 1987). Some of these bacteria are important in the formation of ice on plants. Two groups, those that produce fluorescent pigments (strains of *Pseudomonas syringae* and *P.fluorescens*) and those that produce yellow pigments (strains of

Erwinia herbicola), have been shown to have ice nucleation activity at temperatures as high as -2C (Lindow et al. 1982a, Maki et al. 1974, Yankofsky et al. 1981). Individual bacterial cells appear to be able to induce the formation of ice (Yankofsky et al. 1981). Other than ice itself, these bacteria are among the most efficient freezing nuclei yet found in natural environments (Vali et al. 1976). Although some of these bacteria are pathogens on some plants, most can be found growing epiphytically on plant surfaces. Plant surfaces themselves do not have ice nuclei active above -8 to -11 C (Lindow et al. 1982b), and in the absence of bacteria, supercooling of water occurs (Lindow et al. 1978). The presence of ice nucleating bacteria limits supercooling, and the formation of ice on and in the leaves of frost-sensitive plants results in irreversible damage (Lindow et. al. 1982a).

The ice nuclei on bacteria fall into three groups; those that are active at -2 to -4 C, which are associated with the surfaces of intact normal cells, those that are active at -5 to -7 C, and those that are active at -8 to -10 C (Yankofsky et al. 1981). The latter group has been associated with lysed and chemically altered as well as intact cells (Maki et al. 1974, Yankofsky et al. 1981). The first group of nuclei are not found in every cell of a population. The proportion of cells expressing ice nucleation varies with the bacterial strain, growth stage of the cells, the conditions under which they were grown, and time (Lindow et al. 1982b, Maki et al. 1974, Yankofsky et al. 1981).

Ice nucleating bacteria are found in widely distributed locations, and on many species of plants, with the notable exception of most conifers (Lindow et al. 1978, Yankofsky et al. 1981). These bacteria are capable of causing frost damage on many species of plants (Lindow et al. 1982a). Because ice nucleating bacteria are so widespread, they may also be an important source of atmospheric nuclei and have meteorological significance in the formation of rain from clouds (Schnell and Vali 1976, Vali et al. 1976, Yankofsky et al. 1981).

14) Plant Pathogens

The surfaces and even the interior of plants are host to many microorganisms, including bacteria. Some of these are pathogenic or can become pathogenic under appropriate conditions. Other bacteria which are not recognized as pathogenic can have deleterious effects on plants through competition for nutrients or production of inhibitory compounds. About 80 species of bacteria have been found to cause diseases of plants (Agrios 1988). Bacterial diseases tend to be favored by warm and moist conditions. Most phytopathogenic bacteria have a parasitic phase on the plant and a saprophytic phase in soil or on plant debris.

Species vary considerably in their ability to survive in the saprophytic phase (De Boer 1982). Bacteria are spread from plant to plant by water, aerosols, insects, animals, and human activities. There has been very little study of bacterial diseases of noncultivated plants. Of the diseases of economically important plants that are also found on wild hosts, little is known of their epidemiology in natural systems, or their effect on plant populations. Much more research is needed on the importance of plant pathogens in natural ecosystems.

Bacterial diseases of plants fall into four main categories (Billing 1987). Blights and cankers start as local areas of. necrosis and proceed to the death of plant parts (blights) or to the formation of stem lesions (cankers). These diseases can remain localized near the site of infection or spread systemically through the plant. Vascular wilts are caused by the invasion of xylem vessels which are either plugged by extracellular polysaccharides or are degraded by enzymes. Wilting of the plant is the main symptom. Soft rots occur when host cells are separated by bacterial enzymatic activity, leading to tissue collapse. Gall-forming bacteria stimulate host cell division, leading to cancer-like growth of root, shoot, or stem tissue.

Many bacterial leaf spots and blights on many hosts are caused by species of *Pseudomonas* and *Xanthomonas* (Agrios 1988). The bacteria cause necrotic spots on leaves and stems, and these spots may coalesce resulting in blighted tissue. In humid or wet weather, infected tissue often exudes masses of bacteria which may be spread to other plants. Penetration can occur through natural openings or wounds, and is greatly favored by water soaking of plant tissues in heavy rain. Pathogenic ice nucleating bacteria may enter through the wounds caused by ice formation (Lindow 1982).

Fire blight can be considered both a bacterial blight and canker disease and a wilt disease. It is caused by *Erwinia amylovora* and is very destructive on apple and pear trees, but can attack many wild species in the rose family and even some nonrosaceous hosts (Agrios 1988). The bacterium can invade through blossoms or wounds and multiplies in host tissues, resulting in death of blossoms, leaves and twigs. Cankers in the bark develop, and larger branches and trunks can be girdled, resulting in wilting and death of the branch or entire tree. Under humid conditions infected parts exude sticky ooze which can be transferred to other plants by water, wind, or insects. The bacterium can also be transmitted in flower nectar by bees and other insects.

Soft rots usually occur on thick fleshy tissues such as fruits and vegetables (Agrios 1988). Soft rot bacteria have been found in the rhizosphere of noncultivated plants in nonagricultural areas (Stanghellini 1982), but are probably not important as plant pathogens in natural ecosystems.

The best known example of a gall-forming bacterium is *Agrobacterium tumefaciens,* which causes crown gall on many species of plants, including willows, brambles, pome fruits, stone fruits, and grapes (Agrios 1988). The bacterium enters the plant through wounds and stimulates the host cells to divide by. inserting a piece of plasmid DNA into the host genome. The plant will then continue to exhibit the symptom (gall growth), even if the bacteria die (Kemp 1982). Galls usually occur just below the soil surface. Plants often grow poorly and may die. The bacteria overwinter in galls and in the soil and are spread by soil water and rain splash.

15) Animal Pathogens

Many bacteria are capable of living on and within animals. They can have little or no effect on the host, they can be beneficial or even vital (eg. mutualistic bacterial associations in the digestive tract), or they can be pathogenic. There are several bacteria which cause diseases of wildlife in the Columbia River Basin. A few representative bacterial diseases are brucellosis, coliform, enteritis, and septicemic pasteurellosis of elk, bacterial pneumonia of bighorn sheep, clostridial diseases, anaplasmosis, and paratuberculosis of wild ruminants, bubonic plague of rodents, and bacterial cold-water disease and bacterial kidney disease of salmonids. There are also bacteria which cause diseases of insects (e.g. *Bacillus thuringiensis),* and these may be important in controlling populations of insects in the wild.

Brucellosis is caused by *Brucella abortus* and occurs in domestic cattle and bison as well as in elk (Smits 1991, Thorne and Herriges 1992). It causes abortion and the birth of stillborn and nonviable calves (Smits 1991). The bacterium is transferred through oral contact with aborted fetuses, or the consumption of feed recently contaminated with fetal or vaginal fluid. It is most prevalent in elk in the winter feeding grounds of western Wyoming, where animals are in unnaturally close proximity (Smits 1991, Thorne and Heriges 1992). The disease is thought to have originated with cattle, but now through monitoring, culling, and vaccination, the cattle in many states are designated free of brucellosis. Although the disease does not appear to threaten the populations of wild elk and bison, its existence in wild herds poses a threat to the cattle industry, as the bacterium can be transferred if elk and cattle feed on the same grounds in late winter and early spring (Thorne and Heriges

1992). Wildlife vaccinations, reducing the number of elk and the time they spend on winter feeding grounds, and separation of cattle and wildlife, appear to be the best control strategies, as eradication from wild populations is probably not feasible (Thorne and Herriges 1992).

The bacterium *Escherichia coli* causes diarrhea and enteritis and is a major cause of mortality among neonatal elk (Smits 1991). The pathogen destroys the gastrointestinal lining. Other coliform bacteria such as *Salmonella, Proteus, Klebsiella,* and *Arizona* may also cause similar symptoms (Robinson 1981). *E. coli* is ubiquitous and is also implicated in some cases of miningitis, footrot, and nephritis (Smits 1991). Animals that are stressed by their environment or by infection with viral or parasitic agents are more susceptible to the disease (Robinson 1981, Smits 1991).

Septicemic pasteurellosis is an uncommon disease in North America, but was responsible for the deaths of 38 elk in the National Elk Refuge in western Wyoming in 1986 and 1987 (Franson and Smith 1988). The disease can occur in all wild and domestic ruminants. The causal agent is *Pasteurella multocida.* Symptoms of the disease include fever, profuse salivation, severe depression, and death in about 24 hours. The bacterium is found in the throats of many animals, and the disease is thought to be brought on by adverse conditions such as poor weather and crowding (Franson and Smith 1988, Rosen 1981). Transmission is probably through saliva and feces (Rosen 1981).

Another species of *Pasteurella, P. haemolytica, is* responsible for pneumonia in Rocky Mountain bighorn sheep. The bacterium is carried in the tonsils and nasal passages of healthy domestic sheep, and has been found in the upper respiratory tract of some healthy bighorn sheep (Dunbar et al. 1990), but can cause severe pneumonia and often death in bighorn sheep (Foreyt 1989, Onderka and Wishart 1988). It is thought that invasion of the lower respiratory tract and subsequent disease occur when other pathogens or environmental stresses reduce the normal protective mechanisms of the repiratory tract (Jaworski et al. 1993). The bacterium has been shown to produce an antiphagocytic principle which may cause immunosuppression of infected animals (Newton and Ward 1992). Transfer from domestic sheep to bighorn sheep has been demonstrated (Foreyt 1989, Onderka and Wishart 1988), and is speculated to be the major cause of respiratory disease in Idaho, where the disease is the primary cause of death of bighorn sheep (Jaworski et al. 1993, Ward and Hunter 1992). Contact between domestic and bighorn sheep should therefore be avoided.

All ruminants show various degrees of susceptibility to infection by clostridial organisms (Smits 1991). *Clostridium perfringens* can cause enterocolitis and enterotoxemia.

Clostridial infections in wounds can cause blackleg, malignant edema, and other diseases. Young animals are thought to be most susceptible. Anaplasmosis is caused by *Anaplasma marginale,* and is primarily a disease of cattle (Kuttler 1984, Smits 1991). Isolations of *Anaplasma* have been made from mule deer in anaplosmosis endemic areas of Wyoming and Idaho (Kuttler 1984), and may act as a nonbovine reservoir of the disease. Pronghorn antelope, elk, and bighorn sheep can be infected with the bacterium, but probably do not maintain it long enough to be a reservoir for infection to cattle (Kuttler 1984). All ruminants are probably susceptible to infection by *Mycobacterium paratuberculosis,* which causes paratuberculosis (Smits 1991). The disease is most acute in deer, and results in inflamation of the intestinal tract, with failure to gain weight and poor shedding of hair (Smits 1991, Williams et al. 1983). The disease has also been found in bighorn sheep and mountain goats (Williams et al. 1983). It also affects domestic cattle, sheep, and goats, and transfer between species may occur.

Bubonic plague is a flea-transmitted bacterial disease of rodents that can be spread to humans and other animals either by fleas or through direct contact (Barnes 1982). The disease is caused by *Yersinia pestis,* and occurs in periodic but unpredictable outbreaks in rodents in a few defined areas of the United States, including southern Oregon. In Oregon the disease is found in the California ground squirrel, several species of chipmunks, and golden-mantle squirrels. The disease can be devastating to their populations. In acute plague, rodents die in 3 to 5 days with hemorrhagic swollen lymph nodes (Olsen 1981). During peak plague years, epizootics move through tens of thousands of square kilometers, making control difficult (Barnes 1982). During plague outbreaks, insecticide spray programs can be used to control the flea vectors. The main concern about bubonic plague is its transmission from the rodents to wildlife, domestic animals, and humans. Throughout history, bubonic plague epidemics have killed millions of people (Boyd 1984). Although human cases are now rare, the mortality rate is still high in spite of available antibiotic treatments.

There are many bacterial diseases of fish. Two of importance in the Columbia Basin are bacterial kidney disease caused by *Renibacterium salmoniarum* (Pascho et al. 1993), and bacterial cold-water disease caused by *Flexibacter psychrophilus* (Inglis et al. 1993). Bacterial kidney disease is a systemic infection that slowly progresses and is frequently fatal (Inglis et al. 1993). It is found in both salmon and trout. Diseased fish may exhibit no external symptoms, but internally show abdominal hemorrhaging and lesions in the kidney. The disease can be transmitted from fish to fish and from fish to progeny via the egg. Because the bacterium can survive and multiply in host phagocytic cells and eggs, control of the disease is difficult.

Bacterial cold-water disease is a serious septicemic infection of hatchery-reared salmonids, especially young coho (Inglis et al. 1993). Mortality in alevins can be as high as 50%. Fish that have begun to feed usually develop lesions if infected and mortality is rarely higher than 20%. The mode of transmission of the disease is uncertain. Control is difficult because the most serious cases occur in fish which have not begun to feed.

LAND USE CONSIDERATIONS

Bacteria inhabit most available habitats and perform vital ecosystem functions. Because bacteria occupy so many niches,disturbances will probably lead to the replacement of species with different species, or simply in shifts of relative abundance, rather than the loss of all bacteria from a habitat, but this can still lead to changes in biochemical processes and ecosystem functions. A disturbance detrimental at one level (e.g. population) may be beneficial at a higher level (e.g. ecosystem) (Odum 1985). Natural stresses such as drought or freezing can mask smaller effects of human activities (Visser and Parkinson 1992). In general, disturbances tend to lead to increased repiration per unit microbial biomass, increased turnover and decreased cycling of nutrients which may be then lost from the system, and an increase in oppurtunistic, rapidly growing species (Odum 1985) . Small scalen disturbance usually increases system heterogeneity, while catastrophic events result in functional homogeneity of the system (Zak et al. 1992) .

Management practices which affect macrofauna and flora will obviously have effects on microorganisms as well, and alterations of the microbial community will in turn affect plants and animals. Alterations of plant communities making then more uniform could favor the activity of plant pathogens. Similarly, the crowding of wildlife into refuges can lead to disease problems as has been, observed in the elk herds of Wyoming. The use of pesticides and the dumping of sewage and toxic wastes can have profound effects on bacteria, both through the loss of sensitive species and theincrease of those species able to utilize the new substrates. It is particularly important to consider bacteria in the dumping of wastes because many proposed waste sites are in arid areas such as southeastern Idaho, where heterotrophic bacteria are found at depths of 70 m (Colwell 1989). While bacterial communities may be altered by any type of disturbance, the specific effects of three management practices relevant to the Columbia Basin, logging,grazing, and mining, will be considered here.

Forestry practices strongly influence the soil community. Summer temperatures are increased by the removal of trees (Fowler et al. 1988), and will stimulate microbial activity. The amount of water reaching the ground, snow accumulation, and runoff are all increased (Bell et al.), and these factors influence soil moisture

which in turn affects all soil bacteria. Losses of nutrients and sediments in runoff may also stimulate the activity of bacteria in streams and lakes. Clear-cutting and road building can lead to soil compaction and erosion, which alters or destroys soil microsites. The removal of trees and the subsequent growth of other plant species also affects soil bacteria through thedestruction of mycorrhizal communities often dominant in forest soils.

Clear-cutting impacts the soil biota for many years following harvest (Paul and Clark 1989). The duration and severity of the impact depend on site quality, climate, and the plant species involved in revegetation. Most studies indicate large microbial biomass increases in the first few years following clear-cutting (Bell et al. 1975, Lundgren 1982, Paul and Clark 1989). This phenomenon has been attributed to the availability of slash and dead roots for decomposition, alterations in temperature and moisture status of the soil, and increased input of more easily degradable plant litter from regrowth of herbaceous plants (Paul and Clark 1989). Increased soil respiration and N mineralization usually also follow logging (Paul and Clark 1989, Vitousek and Melillo 1979). Populations of *Nitrosomonas* and *Nitrobacter* have been found to increase (Smith 1968, Smith et al. 1968). N and other minerals are often lost in stream runoff before plants regrow and take up the excess (Paul and Clark 1989, Smith 1968, Smith et al. 1968). These losses are not always observed, however, and many biological, physical, and climatic factors interact to determine the balance of nutrient turnover in a logged forest (Fowler et al. 1988, Vitousek and Melillo 1979).

Controlled burning of forests usually leads to decreases in the soil microflora, particularly in surface layers (Bell et al. 1975, Paul and Clark 1989). Populations recover rapidly as new plant growth and litter accumulation occurs and is recolonized by bacteria from air, rain, and subsurface soil. This rapid recovery may explain why some studies have indicated an increase in bacterial populations following burning (Fuller et al. 1955, Wright and Tarrant 1957). Controlled burning is usually conducted to mimimize destruction of the duff layer, while the heat of uncontrolled burning consumes the duff layer and exposes the. mineral soil to adverse climatic effects (Fuller et al. 1955). Burning increases soil pH, as well as exchangeable bases and soluble salts (Bell et al. 1975, Fuller et al. 1955, Wright and Tarrant 1957). Organic matter in the upper part of the soil is reduced (Bell et al. 1975). Burning also changes soil structure to decrease permeability to water. All of these chemical and physical factors will influence soil bacteria.

Grazing can have both beneficial and deleterious effects on soil microorganisms. Removal of the tops of grasses stimulates root exudation and the growth of microorganisms which utilize those exudates, particularly bacteria such as *Pseudomonas* spp. which are

capable of rapid growth under ideal conditions (Sherwood and Klein 1981). The return of organic matter in the form of feces will stimulate microbial activity in localized areas. Overgrazing can compact soil, affecting aeration and moisture retention. Excessive grazing pressure will cause shifts from the native perennial grasses to alien species (Franklin and Dyrness 1988), altering the populations of rhizosphere bacteria associated with each species. Annual decomposition of litter in a grassland normally roughly equals productivity. Increasing intensity of grazing reduces the amount of litter available for decomposition (Clark and Paul 1970). Overgrazing can eventually destroy vegetation cover, leading to desertification. Cyanobacteria may then be important in stabilizing and reclaiming these areas.

Because mining usually involves the removal of the soil, it is obviously devastating to the soil community. Mining can also affect surrounding areas through leaching or dust deposition of toxic materials. When mining is finished, the area is usually filled in and a layer of soil may be replaced. Attempts are made to reestablish vegetation and a functioning soil community. Microorganisms are critical for the changes to mine spoils required for plant growth. These include the accumulation of soil organic matter, increases in available plant nutrients such as N and P, improvements in soil texture, water holding capacity and soil pH. Although soil building activities on mine spoils can be hastened with additions of organic matter and topsoil, and by the planting of species which form associations with N2 fixing bacteria, the natural steps of plant and microbial succession must occur for effective reclamation (Cundell 1977). In semiarid regions mine spoils may be initially colonized by cyanobacteria and lichens. Their photosynthetic and N_2 fixing abilities will result in accumulations of organic matter and N which will stimulate other microorganisms and finally plants. The presence of the plant rhizosphere will then allow more species of bacteria to colonize the site.

Bacteria have been found to be capable of surviving and growing under the low nutrient regimes and environmental extremes found in soils disturbed by mining. While soil respiration, microbial biomass C, ATP, actinomycete numbers, hyphal lengths and N_2 fixing potential were found to be significantly lower in mined soil compared to an adjacent undisturbed prairie site, bacterial numbers were greater in the mined soil (Visser et al. 1983). In a forest mine site, bacterial numbers were higher in disturbed soil than in undisturbed soil, but not as high as in undisturbed organic material on the forest floor (Visser et al. 1979). *Arthrobacter* increased in the disturbed site, possibly because of its ability to withstand starvation, freezing and thawing, and drying (Visser et al. 1979, Robinson et al. 1965). Nitrification can increase insoils disturbed by mining (Parker et al. 1987), although this is not always found (Parkinson 1979).

Varous practices have been found to increase the rate of establishment of plants and microorganisms on mined sites. Incorporation of organic matter appears to provide an initial carbon source to stimulate the growth of bacteria, including the N_2 fixing *Azotobacter* (Parker et al. 1987, Visser et al. 1979). In mine sites where toxic metals are found, the addition of organic matter speeds the establishment of plants and nutrient cycling bacteria by chelating the metals and reducing their availability for uptake (Palmer 1992). Additions of decomposer and symbiotic species of bacteria to soils may encourage revegetation (Parkinson 1979). Intermittent inputs of N fertilizer can lead to rapid growth of grasses, but these have a high C:N ratio and are resistant to decomposition and further nutrient cycling when N again becomes limiting (Palmer 1992). The encouragement of a. legume, which hosts N_2 fixing bacteria, is thought to be preferable because N is available in a limited but steady supply throughout the growing season.

In the eastern U.S., mine spoils can contain high levels of S-bearing pyritic components which are oxidized by species of Thiobacillus, resulting in acid production (Olson et al. 1981, Visser et al. 1983) . Spoils in the western U.S., however, are usually neutral to alkaline. S oxidizers may still be present, but under arid conditions little oxidation occurs (Olson et al. 1981) . High numbers of Thiobacillus have been found in wells in mining areas and may contribute to the presence of iron, manganese, cadmium, sulfate and hydrogen sulfide in the wells (Olson et al. 1981).

MONITORING BACTERIA IN SOIL

The Columbia Basin covers a very large area and many diverse habitats. Although representatives of the functional groups discussed will undoubtedly be found, information regarding the presence of particular species and their distribution and abundance is lacking. To determine the effects of management practices, microbial communities should first be characterized and then monitored during and after disturbances. Bacteria can be monitored in soil on several different levels. Assessments of single species, communities of species, total bacterial biomass, total microbial biomass, and bacterial activities, all will provide different information, and careful consideration of the questions being asked is required to choose the most appropriate level to study. Within each level, the different techniques available each offer advantages and disadvantages, and these must also be considered within the context of the time, facilities, and expertise available. Because bacteria are strongly affected by different soil conditions, comparisons between study sites can only be made in properly replicated experiments. Monitoring of

bacterial numbers and activities can be used to assess changes at the same site over time.

Species and Communities

Determining the presence and abundance of specific groups of bacteria can provide useful insight into ecosystem functions. Identification of which species representing a functional group is/are present could enable the choice of indicator species to be monitored during ecosystem disturbances. Species diversity can also be an indicator of soil quality because of its obvious relationship to functional diversity (Visser and Parkinson 1992). Unfortunately, most of the methods available for identifying and quantifying bacteria involve their isolation and culture. The removal of bacteria from their natural medium prevents us from obtaining knowledge about their microsites or their associations with other microorganisms (Parkinson and Coleman 1991). Perhaps more importantly, many types of bacteria are very difficult or, impossible to grow in culture.

Despite the difficulties mentioned, culturing on selective media is a useful method for quantifying some types of bacteria. These media contain substrates which enhance the growth of the desired organism and compounds which inhibit the growth of others. Differences in bacterial colony color and morphology are also used to separate species. Once isolated, the identity of a bacterium can usually be confirmed by morphological characteristics and various biochemical tests, including Gram staining, and utilization of specific, substrates. These tests have traditionally been performed on slides, Petri plates and in test tubes, and are often time-consuming and costly.

Recently various identification kits have become available for rapid identification of some bacteria. An example is the GN MicroPlate introduced by Biolog, Inc. (Hayward, CA), which is used to identify Gram-negative bacteria (Bochner 1989, Jones, Chase and Harris 1993). A series of 95 carbon sources, including alcohols, polymeric chemicals, sugars, organic acids, and amino acids, are present in wells in a microtitre plate. Oxidation of these compounds by bacterial suspensions added to the wells results in the reduction of an indicator dye tetrazolium violet to a purple formazan. The resulting color changes form a carbon source utilization profile, or metabolic fingerprint, which can be analyzed with a computerized microplate spectrophotometer. The use of this indicator dye can be combined with virtually any biodegradable compound under either aerobic or anaerobic conditions. Biolog has developed a systematic process for selecting sets of substrates that can be used to identify and characterize unknown bacterial and manufactures microplates with preselected sets of substrates loaded and dried in the wells (Bochner 1989) . A large data base is available to match the

metabolic fingerprints of unknown isolates with those of known bacteria. The data base is being constantly expanded but does not contain all the bacteria of interest in soil, and bacteria which cannot be cultured cannot be identified with this technology. The accuracy of identification using this system is very high for some groups of bacteria, but very low for others (Jones, Chase and Harris 1993). Improvements can be made by expanding the database with standards identified by other methods. Some groups of bacteria may be too diverse or variable to differentiate.

Another diagnostic tool for bacteria utilizes whole-cell fatty acid (FA) profiles (Roy 1988). FAs in bacterial cells are saponified, methylated, extracted into hexane/ether, and analyzed using a gas chromatograph (GC). FA profiles are compared with those of known standards. FA profiles have been found to be highly diagnostic for some species of bacteria, regardless of geographic source of the isolates. Over 200 FAs are used for identification purposes. Using an automated GC system with an automatic sampler, an integrator, and a computer, over 17,000 samples per year can be analyzed. As with the Biolog test plates, a data base of known standards is being constantly expanded. The software allows the user to add relevant FA profiles.

Identification of bacteria by direct observation is not usually possible. Bacteria in soil smears or thin sections can, however, be probed with antibodies to known bacteria. If these antibodies are labelled with fluorescein isothiocyanate, the bacteria to which they attach will fluoresce when observed with fluorescence microscopy (Newell et al. 1986). Because of the requirement for specific antibodies, this technique is restricted to bacteria that have been cultivated as pure populations. Fluorescence immunoassay techniques enable specific counts of particular species such as *Rhizobium* spp. and nitrifying bacteria (Parkinson and Coleman 1991, Paul and Clark 1989). Because of their sensitivity, these techniques are particularly useful for bacteria which are difficult to grow, grow slowly, or are present in low numbers (Newell et al. 1986). Production of the labelled antibodies, however, can be difficult and time consuming. Live and dead bacteria cannot be distinguished unless the fluorescent antibodies are combined with an indicator of cell activity.

In recent years molecular techniques have been applied to studies on microbial communities. Analysis of DNA and RNA can provide very accurate identifications of organisms. Bacteria can be identified from cultures or from soil. Use of the polymerase chain reaction (PCR) can be used to amplify minute quantities of genetic material to levels allowing analysis. Several approaches have been taken to studies of soil communities and new methods will undoubtedly emerge as the technology develops.

Gene probes offer the ability to identify bacteria in mixed populations directly from soil (Holben et al. 1988). Bacterial

cells are dispersed and separated from soil particles, collected by centrifugation, and lysed. Total bacterial DNA is purified from the cell lysate by equilibrium density gradient. The DNA is then either denatured and directly blotted onto cellulose nitrate filters (for dot/slot blot analysis), or size fractionated by electrophoresis in agarose gels and transferred to cellulose nitrate filters (for Southern blot analysis) . Using hybridizations with single-stranded ^{32}p-labeled DNA probes, the presence of aspecific microbial population in the soil can be detected by the presence of a DNA sequence unique to that organism. RNA probes can also be used and are found to hybridize more efficiently (Brooker et al. 1990). Advantages of using gene probes are that no culturing is required, a specific DNA sequence is detected so gene expression (which may be environmentally controlled) is not required, and multiple organisms can be monitored in a single sample (Holben et al. 1988). The disadvantages include the time and equipment involved, and the need for specific DNA probes for each organism of interest.

Other molecular approaches use ribosomal RNA (rRNA) sequences (Pace et al. 1986). One technique uses direct isolation of RNA from bacteria in soil. The RNA is then sorted by gel electrophoresis and individual 5S rRNA types are sequenced and compared to libraries of 5S rRNA sequences of known species. This approach can be used to study communities of limited diversity (less than about 10 different organisms). Another more complex approach which can be used to study more diverse communities uses the larger 16S rRNA which is too large for traditional RNA sequencing. Total DNA is isolated from soil bacteria and 16S rDNA genes are cloned. These genes can then be sequenced, and these sequences used for identification purposes. These methods allow the direct analysis of soil communities without the need for culturing. Rapid gene sequencing services are available. Identifications are limited by the size of the sequence libraries available.

Biomass

Some of the problems of species and community level studies include the difficulties in defining individual species as indicators of soil quality, in determining the total species complement of a given soil, in accurately identifying species, and in relating laboratory data on biochemical functions to what occurs in the field (Visser and Parkinson 1992). In many cases an estimate of the total soil microbial or bacterial biomass can provide useful information regarding soil health and in particular the effects of soil disturbances. The proportion of total soil C that is in microbial biomass has also been considered useful in soil monitoring. Several methods have been developed for making biomass estimates.

The soil dilution plate technique has long been used to isolate bacteria and estimate their numbers. An agar medium which supplies the needs of as many diverse groups of bacteria as possible is used, and soil dilutions are spread on plates of the medium and resultant bacterial colonies counted. Plates can be incubated under either aerobic or anaerobic conditions. Based on bacterial numbers and average cell biomass, an estimate of total bacterial biomass can be made. The method is relatively quick and easy, but has many drawbacks. Many bacteria can not be cultured using standard methods, and therefore biomass estimates are too low. Cells may be clumped together and appear as single colonies on plates. Because relatively small amounts of soil are used and. bacterial populations vary widely between microsites, large numbers of samples are needed to control variability. Cell mass also varies widely between species and with different growth conditions, and biomass estimates based on an average cell mass can be. inaccurate (Paul and Clark 1989).

Bacterial counts based on direct observation overcome many of the problems of culturing, but not those of sample and cell mass variability. The general method involves the preparation of soil smears or thin agar films on slides which are then stained (Parkinson and Coleman 1991). Early work using stains such asphenolic aniline blue indicated that bacterial numbers in soil were 10 to 100 times higher than estimated by plate counts, although live and dead cells could not be distinguished. More recently, the use of fluorochrome stains which make cells fluoresce under. ultraviolet light has improved the direct counting method. Some difficulties still exist in distinguishing live bacteria from dead bacteria and from stained or autofluorescent particles in the sample. One fluorochrome stain, fluorescein diacetate (FDA), only fluoresces when cleaved by an esterase, and should therefore distinguish active from inactive cells (Newell et al. 1986, Paul and Clark 1989) . Many bacteria, however, are unable to take up FDA (Karl 1986, Paul and Clark 1989).

Several physiological methods have been developed for determinations of total soil microbial biomass. One of these is the fumigation-incubation technique (Jenkinson 1966, Parkinson and Coleman 1991). Microbes in a soil sample are killed with chloroform, and then the soil is reinoculated with fresh soil and the $C0_2$ evolved over 10 days at 25 C is measured. The value obtained is corrected for basal respiration obtained from untreated control samples, and divided by a factor for the percent of total biomass C released as $C0_2$ in a 10 day period. The final value is a measure of microbial biomass C. The method has been found to be unsuitable for waterlogged, acid, or recently amended soils. Care must be taken to ensure complete kill with the chloroform fumigation. The correction factor for the percent of C released can also be a source of error if not appropriate for the soil being tested.

One of the drawbacks of the fumigation-incubation technique is the time required to perform it. Fumigation-extraction was developed as a quick alternative (Parkinson and Coleman 1991, Vance et al. 1987). The soil is fumigated as before but then organic carbon is extracted using K_2S0_4. The method can be used for a wide variety of soils, but the extraction efficiency can vary with different soils.

Substrate-induced respiration (SIR) was also developed as a rapid estimate of soil microbial biomass (Anderson and Domsch 1978). The respiratory response of a soil to glucose addition is measured in the form of $C0_2$ released. Using the fumigationincubation method, SIR performed at 22 C has been calibrated to microbial biomass (1 ml $C0_2$ = 40 mg microbial biomass C) . When SIR is combined with the use of selective inhibitors, an estimate of the proportions of fungal and bacterial biomass can be made.

Because ATP is used by all living cells, it can be extracted from soil as a measure of the total soil biomass (Parkinson and Coleman 1991). ATP does not persist in soil in a free state (Paul and Clark 1989). ATP can be measured in several ways. In the luciferin reaction, the ATP reacts with luciferin and luciferase in a series of steps which result in an emission of light, which can be measured with a photometer. Equations have been developed for transforming ATP values to total biomass, and the relationship between ATP and biomass estimates obtained by other methods , is strong. ATP has also been found to be well correlated with other measures of soil microbial acitivity (Hersman and Temple 1979). The extraction of ATP is not always consistent, however, and the method may not be useful for all types of soils and conditions.

Activity

In some cases it may be more useful to focus on the activity of the soil microbial community rather than on the organisms themselves. The processes measured can be general such as respiration or the breakdown of common substrates, or more specific such as the steps involved in the nitrogen cycle or the production of specific enzymes.

One of the most common methods of assessing soil respiration is to measure the evolution of $C0_2$, either in the field or in the laboratory under controlled conditions (Parkinson and Coleman 1991). Field estimates include $C0_2$ evolved by soil microbes, microfauna, and plant roots. It is often very difficult to separate these components. In laboratory experiments respiration can also be estimated based on 0_2 uptake.

The amount of $C0_2$ produced per unit microbial biomass, ormetabolic quotient (q $C0_2$) has been considered a useful parameter in

assessing soils (Anderson and Domsch 1986, Visser and Parkinson 1992), and a good approximation of overall system recovery and stability following disturbance (Zak et al. 1992). It can be easily determined by performing basal respiration determinations followed by SIR on the same soil sample. Various studies indicate that the q $C0_2$ increases in systems under stress and decreases with ecosystem succession or soil maturity (Odum 1985, Parkinson and Coleman 1991, Visser and Parkinson 1992).

Heat evolution from soil can also be used to assess soil microbial activity (Karl, 1986, Parkinson and Coleman 1991). Microcalorimetry can allow continuous recording of soil activity over long periods of time without soil disturbance.

Rates of organic matter breakdown (mass loss) in soil can be used to measure soil microbial activity. Materials such as wood, paper, or plant debris, often enclosed in mesh bags, are placed on or in the soil, and are later removed for measurement of loss through decomposition (Parkinson and Coleman 1991). Because factors such as temperature and moisture are very important in the rate of organic matter decomposition, and vary considerably in the field, comparisons of decomposition rates are most accurately made in the laboratory, where the soil decomposer community is the only variable (Visser and Parkinson 1992). The activity of more specific groups of organisms can also be assessed using specific substrates such as chitin or different types of cellulose. Materials can be radiolabelled to allow more accurate determinations of decomposition of specific components.

Enzymes are indicative of various soil processes. Unfortunately enzymes are found in both living and dead soil components and can be of microbial, plant, or animal origin. Only a few enzymes have proved useful for studies of soil microorganisms (Parkinson and Coleman 1991). Dehydrogenase activity has correlated well with other measures of microbial activity in some studies but has been poorly correlated in others. Amylase has been used successfully in some studies.

Some specific soil processes can be analyzed by various chemical means. N_2 fixation can be assessed using acetylene reduction or using 15N. Other assays exist for nitrification, S oxidation, and other important steps in nutrient cycles. Processes which involve only a few microbial species, such as N_2 fixation and nitrification, are considered to be most sensitive to environmental disturbances, and may therefore be most useful in assessing soil quality. Nutrient losses through leaching and volatilization can also be monitored as a means of determining imbalances in nutrient cycling (Visser and Parkinson 1992).

CONCLUSION

With growing awareness of the importance of microorganisms to healthy ecosystems comes the need to consider the effects of land use practices on microbial activities. The study of microorganisms is different from that of larger organisms because microorganisms are affected not only by macro-scale influences such as soil type and vegetation cover, but also by the physical and chemical constraints of microsites, which can be very different from the soil average and are very difficult to measure. Bacteria can also have different metabolic activities under different conditions, making inferences based on their presence alone questionable. As a broad group, bacteria have proven to be adaptable to almost any situation, but effects of disturbances on the presence and function of specific functional groups are in most cases poorly. understood. Interactions with microfauna and plants in nutrient cycling also require further research. The application of new study techniques should help to clarify the impact of human activities on the microbial community and the subsequent effects of microorganisms on their altered environment.

FUNCTIONAL GROUP:	photoautotrophs
KEY ECOLOGICAL FUNCTIONS:	aerobic photosynthesis anaerobic photosynthesis food source for higher organisms
EXAMPLE SPECIES:	*Nostoc* spp. *Anabaena* spp. *Chromatium* spp. *Chlorobium* spp.
KEY ENVIRONMENTAL FACTORS:	light availability aerobic (cyanobacteria) or anaerobic (sulfur bacteria) environment H_2S availability (sulfur bacteria) moisture temperature

FUNCTIONAL GROUP:	methanogens
KEY ECOLOGICAL FUNCTIONS:.	production of methane removal of H_2
EXAMPLE SPECIES:	*Methanobacterium* spp. *Methanococcus* spp. *Methanobacillus* spp.
KEY ENVIRONMENTAL FACTORS:	anaerobic environment H_2 availability other bacteria moisture temperature

FUNCTIONAL GROUP:	heterotrophs
KEY ECOLOGICAL FUNCTIONS:	decay organic matter release $C0_2$ improve soil structure
EXAMPLE SPECIES:	*Pseudomonas* spp. *Bacillus* spp. *Erwinia* spp. *Arthrobacter* spp.
KEY ENVIRONMENTAL FACTORS:	organic matter availability pH aeration moisture temperature

FUNCTIONAL GROUP:	nitrogen fixers
KEY ECOLOGICAL FUNCTIONS:	fix atmospheric N_2 release combined N to other organisms
EXAMPLE SPECIES:	*Rhizobium* spp. *Frankia* spp. *Azotobacter* spp. *Nostoc* spp
KEY ENVIRONMENTAL FACTORS:	organic substrates (heterotrophs) Light (cyanobacteria and plant-associated heterotrophs) nitrogen status of environment presence of host (plant associated) moisture temperature

FUNCTIONAL GROUP:	nitrifyers
KEY ECOLOGICAL FUNCTIONS:	increase N availability to plants increase N leaching
EXAMPLE SPECIES:	*Nitrosomonas* spp. *Nitrobacter* spp. *Nitrospira* spp.
KEY ENVIRONMENTAL FACTORS:	ammonia availability aerobic environment PH moisture temperature

FUNCTIONAL GROUP:	denitrifyers
KEY ECOLOGICAL FUNCTIONS:	loss of N from ecosystem N_2O emissions
EXAMPLE SPECIES:	*Pseudomonas* spp. *Alcaligenes* spp.
KEY ENVIRONMENTAL FACTORS:	nitrate availability anaerobic environment organic substrates moisture temperature

FUNCTIONAL GROUP:	sulfur oxidizers
KEY ECOLOGICAL FUNCTIONS:	increase S availability to plants remove toxin H_2S
EXAMPLE SPECIES:	*Beggiatoa* spp. *Thiovulum* spp. *Thiothrix* spp. *Thiobacillus* spp.
KEY ENVIRONMENTAL FACTORS:	H_2S availability aerobic environment light availability (photosynthetic S bacteria) moisture temperature

FUNCTIONAL GROUP:	dissimilatory sulfur reducers
KEY ECOLOGICAL FUNCTIONS:	remove SO_4^{2-} from system produce toxin H_2S
EXAMPLE SPECIES:	*Desulfovibrio* spp. *Desulfotomaculum* spp.
KEY ENVIRONMENTAL FACTORS:	SO_4^{2-} availability H2 or organic acid availability anaerobic environment moisture temperature

FUNCTIONAL GROUP:	iron and manganese oxidizers
KEY ECOLOGICAL FUNCTIONS:	removal of available Fe and Mn from system formation of insoluble Fe and Mn deposits
EXAMPLE SPECIES:	*Thiobacillus ferrooxidans* *Galionella* spp. *Metallogenium* spp. *Pseudomonas* spp.
KEY ENVIRONMENTAL FACTORS:	Fe^{2+} and Mn^{2+} availability aerobic environment pH moisture temperature

FUNCTIONAL GROUP:	iron and manganese reducers
KEY ECOLOGICAL FUNCTIONS:	convert Fe and Mn to more soluble forms formation of gleyed soils
EXAMPLE SPECIES:	*Bacillus* spp. *Pseudomonas* spp. *Alcaligenes* spp.
KEY ENVIRONMENTAL FACTORS:	anaerobic environment $Fe^{3+}$and Mn^{4+}availability inhibited by nitrate pH moisture temperature

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FUNCTIONAL GROUP:	calcium, potassium and phosphate solubilizers
KEY ECOLOGICAL FUNCTIONS:	increase Ca, K and P availability to plants and other organisms bioweathering of mineral surfaces
EXAMPLE SPECIES:	*Thiobacillus* spp. *Nitrosomonas* spp. *Clostridium* spp. *Bacillus* spp.
KEY ENVIRONMENTAL FACTORS:	organic substrates (heterotrophs) presence of reduced S or N (chemolithotrophic) moisture temperature

FUNCTIONAL GROUP:	plant growth -promoting rhizobacteria
KEY ECOLOGICAL FUNCTIONS:	produce plant growth-promoting substances inhibit plant pathogens increase nutrient availability
EXAMPLE SPECIES:	*Pseudomonas* spp. *Bacillus* spp. *Enterobacter* spp.
KEY ENVIRONMENTAL FACTORS:	presence of appropriate plant nutrient status of soil and rhizosphere competition with other rhizosphere inhabitants moisture temperature
FUNCTIONAL GROUP:	ice nucleating bacteria
KEY ECOLOGICAL FUNCTIONS:	frost damage on plants possible induction of precipitation
EXAMPLE SPECIES:	*Pseudomonas syringae* *P. fluorescens* *Erwinia herbicola*
KEY ENVIRONMENTAL FACTORS:	presence of appropriate plant incidence of subzero temperatures moisture temperature
FUNCTIONAL GROUP:	plant pathogens
KEY ECOLOGICAL FUNCATIONS:	kill plants directly predispose plants to damage by adverse environmental conditions reservoir for crop diseases
EXAMPLE SPECIES:	*Pseudomonas* spp. *Erwinia amylovora* *Agrobacterium tumefaciens*
KEY ENVIRONMENTAL FACTORS:	presence of host plant plant density moisture temperature presence of vectors

FUNCTIONAL GROUP:	animal pathogens
KEY ECOLOGICAL FUNCTIONS:	kill animals directly predispose animals to predation reservoir for domestic animal and human disease
EXAMPLE SPECIES:	*Brucella abortus* *Pasteurella haemolytica* *Yersinia pestis* *Renibacterium salmoniarum*
KEY ENVIRONMENTAL FACTORS:	density of host presence of other pathogens and environmental stresses presence of other hosts presence of vectors

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Niwa - Review of Bacteria Report by Andrea Muehlchen 9/2/94

I do not have a copy of Andrea Muehlchen's contract specs in front of me, so please take this into consideration as you read my comments. In the absence of this, I will use our current contract specs as a measure for comparison.

My general feeling is that the report is a good general review of bacteria, but may not go into the detail that is necessary for use in resource planning and management.

Regarding points that are specifically asked for in current contract specs:

Species of special concern, particularly indicators, are not discussed.

Differences between habitats (cover type, successional stage, tree size class, soil type, etc.) are described in very general terms in the narrative; but are not recognized in the models, which are only constructed for each functional group as a whole.

Representative species are rarely listed at species level. This is particularly important for those genera are in more than one functional group.

Special habitats, hot spots of diversity and areas of high endemism are not discussed. This may be a difficult thing to do for bacteria.

As stated by others, the section on management implications needs to be expanded and deal with more specifics.

As an example of the type of information I hope we will be acquiring in our contracts, next week I will FAX you a copy of a preliminary introduction that Elaine Ingham sent to me to critique to make sure she is on the right track. Her discussion of food webs and their responses to habitat and succession is the level of information that I believe can be used in the development of ecosystem management policy.

CGN

Reviewer:

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Comments: An outstanding overview of the different functional groups of bacteria found in natural habitats was presented. It is clear that the author spent a great deal of time researching topics presented in this review. Again, great synthesis of the information! Very comprehensive.

Aside from my comments on the manuscript, I offer the following suggestions.

General suggestions:

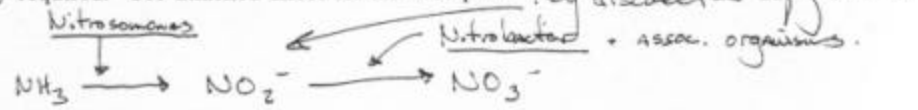
1. The word "some" was overused. Especially as the first word of sentences.
   this is do as I say - not as I do weeks :)
2. Avoid using the same word multiple times in the same sentence. For example on page 1, second sentence of the second paragraph. "Different species have very... and utilize many different substrates."

3. Use chemical formulas consistently through the nutrient cycling section of the text (pages 3-12.) I suggest introducing the chemical formula for a given compound in parentheses ~~the~~ after the first time it is mentioned and then using the chemical formula thereafter. This will make these sections flow smoother for the reader.

4. A description of the various terms you used to describe the different groups of bacteria would be helpful prior to discussing the nutrient cycles. Nothing fancy or complicated. Perhaps a paragraph simply stating that microbiologists use the following terms to define groups of bacteria based on their nutritional requirements or capabilities. I don't know who the intended audience is for this report, but if it is general, I'd be tempted to spell out what you mean by a "chemolithotroph" for example... Having this up front might be useful to your readers.

5. Consider adding brief figures showing the different nutrient cycles. The old adage that a picture is worth a thousand words holds true in this case. I think I would have gotten a more clear picture about the cyclical nature of the nutrient cycles if they were presented in a diagrammatic fashion. Nothing fancy required. See attached sheet for an example. Very discorrected copy makes

Specific comments:



1. I think you did an excellent job presenting the "science" of the functional groups. However, I think there is some room for making a strong argument about the microbial ecology of the ? systems. It is hard not knowing whom is going to read this or how they are going to use the information you compiled, but I would add two short paragraphs-one right at the beginning of the review and another at the beginning of the "Management Considerations" section. In the first paragraph, I would really stress the fact that it is impossible to make sound management strategies concerning the microbiology of a given natural habitat if no scientific evidence is available. In this light, you have compiled a fairly comprehensive description of the major functional groups of bacteria commonly found in a variety of habitats. I would go on to stress, that although it is impossible to know the exact bacterial species composition or degree of diversity that exists in their given ecosystem, that it is likely to contain some subset of the functional groups presented in your review.

In the second paragraph,

I would reiterate the fact that without scientific evidence, it is impossible to predict which particular subset of bacterial functional groups are present in their ecosystem and that you have merely presented the major functional groups that MAY be present in their system. I would also reemphasize your statement that just about any major perturbation to the ecosystem will most likely also affect the natural balance of the microbial ecosystem. And that some of these shifts may result in detrimental effects above the ground. I would also suggest to those using this information that some type of effort be made to monitor shifts in bacterial species diversity if this something they are really concerned about. I might ~~stress~~ the use of the rapid identification systems such as the GC-fame, the Biolog, and the API along with several refereed journal articles to show that this is a plausible way to look for shifts in their system.

add a few sentences describing or simply stating that it is possible - use these types of systems to monitor or look for changes in their ecosystems?