Nutrients in Fire-Dominated Ecosystems

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Abstract.—Fires can produce a wide range of changes in nutrient cycles of forest, shrub, and grassland ecosystems depending on fire severity, fire frequency, vegetation, and climate. These changes can be beneficial when fires increase the availability of plant nutrients, and deleterious when they volatilize, entrain ash in smoke columns, increase runoff of mineralized nutrients, or accelerate leaching from soil systems. This paper examines the effect of fires on nutrient cycling and flux pathways with special emphasis on Madrean-type ecosystems. Most of the best information on fire impacts on these ecosystems comes from research done in interior and coastal chaparral ecosystems north and west of the Madrean floristic province.

INTRODUCTION

Fire is a physical-chemical process that occurs as a continuum of intensities and severities across small areas and whole landscapes. The severity of its impacts depends upon the interactions of fire temperature, duration, combustion phase, fuel load, vegetation, climate, slope, topography, soils, and area burned. Thus the impact of forest, shrub, and grass fires on nutrient resources varies over a continuum. Our ability to describe those impacts is a function of scientific information obtained over a rather limited range of fire intensities, knowledge of nutrient cycling processes, and understanding of fire as a physical-chemical process.

Fire intensity refers to the rate at which a fire produces thermal energy in the fuel-climate environment in which it occurs. It can be measured in terms of temperature, heat yield, and rate of spread. Temperatures can range from 50 to 1,000° C, and heat yields can be as little as 2 BTU/kg or as high as 2,000 BTU/kg. Rates of spread can vary from 0.5 m /week in peat fires to as much as 7 km/hr in large wildfires. The intensity produced by any fire is an integration of the fuel conditions and climatic conditions that precede ignition. Fuel loadings range from <1 Mg/ha in grasslands to 400 Mg/ha in denser old-growth tree stands. Fuel moistures and organic constituents play a prominent role in the rate at which fires release thermal energy. Finally, fire intensity is determined by the interactions of climate conditions such as air temperature, relative humidity, antecedent rainfall, and wind. Slope, topography, altitude, soils, and fire size may further modify intensity.

The facet of fire intensity that results in the most damage (fire severity) to site nutrient resources is duration. Because fast moving fires in fine fuels, such as grass, do not transfer as much heat to a forest floor or mineral soil as do slow moving fires in heavy fuels, their impacts on nutrient cycling processes are much less severe. Severity is a qualitative measure of the effects of fire on soil and site resources (Hartford and Fransen 1992).

Heavy fuels with loads of >100 Mg/ha can produce temperatures in excess of 1,000° C. On the other end of the fuel spectrum, grass fires usually have temperatures of 80 to 160° C. Fire-prone vegetation types, such as chaparral, burn at temperatures of 350 to 370° C (Woodmansee and Wallach 1981). At temperatures above 300° C, the entire forest floor is usually consumed. In the range of 180 to 300° C, 50% of the litter layer is burned. Litter is only scorched at temperatures under 180° C.

Soil temperature effects on nutrient cycling processes are particularly important since they quickly

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affect the ability of forest ecosystems to recover and sequester nutrients released by the combustion of above ground organic matter (Hungerford 1996). Disruption of soil nutrient cycling processes is then a function of the severity of burning. Temperature profiles in the mineral soil depend on the intensity of the fire, fuel loads, duration of the burning, and antecedent soil moisture (Hartford and Franson 1992, Hungerford 1996). With less severe soil heating, mineral soil temperatures usually do not exceed 50 Co at 1 cm. However with severe soil heating, temperatures can reach temperatures >250° C at depths of 9-16 cm, causing considerable mortality to soil organisms and volatilizing nutrients. Disruptions begin in the 40-70° C range with plant tissue death. At soil temperatures of 50-56° C, roots are killed; seed mortality occurs in the 70-120° C range. Although most microorganisms die off between 50-160° C, fungi are less resistant to thermal effects than bacteria and hyphal mortality happens at the lower end of this temperature range. Organic matter distillation starts in the 200-315° C range, and volatilization begins when temperatures climb to 350-400° C.

An important component of understanding the effects of fire on nutrient resources is knowledge of nutrient cycling. This includes not only nutrient pools, but also key fluxes, transformations, and losses. Figure 1 is a generalized cycling diagram for nitrogen (N) in a forest ecosystem. The arrows indicate fluxes between pools (square boxes) and losses from the ecosystem (circles or ovals). The arrows indicating

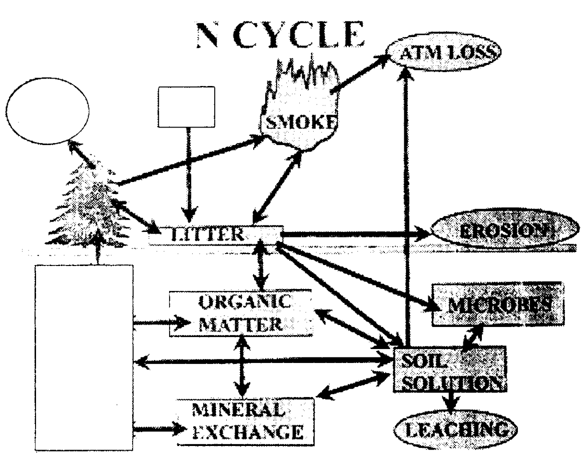

Figure 1. Major pools and flux pathways for nitrogen in fire-dominated forest ecosystems.

fluxes do not indicate their magnitude. Other major nutrients in the organic pool, such as phosphorus (P), sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg) follow the same pathways except that direct loss to the atmosphere from the soil does not occur.. The discussion that follows utilizes Figure 1 as a framework.

Information on the effects of fire on nutrients in Madrean ecosystems is limited and incomplete. Much of the best information on nutrients comes from research in interior chaparral ecosystems to the north of the Madrean floristic province, elsewhere in North America, Australia, and the Mediterranean region. So, some fire effects information from these other regions is incorporated into this analysis to provide a more complete picture of nutrient processes and dynamics in fire-dominated ecosystems like the Madrean floristic province.

NUTRIENT POOLS AND FLUXES

Atmosphere

Global Implications

Burning of fuels in the Madrean floristic province certainly has localized impacts on nutrient cycling. However, it is also part of the annual global biomass burning, which consumes 8,680 million metric tons and produces atmosphere-wide and ecosystem-wide ecological effects (Levine 1991). Of this amount, relative distribution is 42% grass, 18% forest, 23% agricultural waste, and 17% fuelwood. The majority of biomass burning is human caused, and appears to be on the increase. Biomass burning is a major contributor to greenhouse gases, producing 40, 38, 32, 39, and 20% of the world's annual production of carbon dioxide, ozone, carbon monoxide, particulate organic carbon, and other greenhouse gases (hydrogen, nonmethane hydrocarbons, methyl chloride, and nitrogen oxides), respectively. Burning in the Mexican portion of the Madrean province significantly exceeds that of the United States portion (Fule and Covington 1995).

Ash Convection and Wind

Nutrient-rich ash materials remaining after a fire can be removed from or redistributed within a burned area by convection in a smoke column or surface wind transport. These processes account for a small portion of atmosphere-related nutrient losses during and immediately after small, low-intensity fires, but are a more important consideration after large wildfires and in windy regions. For low-intensity fires, ash lost in convective smoke plumes can amount to 1-4% of the mass of the burned fuel (Raison et al. 1985a). With higher intensity fires, ash losses in convective columns can exceed 11 %. Data on nutrient losses in wind-borne ash after fires are very scarce, but losses are estimated to be low because of the relatively low mass transport of soil and ash in wind from most burned areas (Baker and Jemison 1992).

Volatilization

Nutrients are volatilized directly into the atmosphere if temperatures are high enough. Nitrogen is the element most prone to this type of loss since it starts to vaporize at 300° C. At temperatures above 500° C, over half the N in organic matter can be volatilized. Hotter temperatures are needed to vaporize K (760°+ C), P (774°+ C), sulfur (S) (800°+ C), Na (880°+ C), Mg (1107°+ C) and Ca (1240°+ C) (Weast 1988).

Harwood and Jackson (1975) reported nutrient losses to the atmosphere from low intensity slash burning of 10-17% of total nutrients (P, K, Ca, and Mg) in the fuel. Raison et al. (1985b) measured higher, non-particulate elemental transfers to the atmosphere from low intensity slash burning of 54-75% (N), 37-50% (P), 43-66% (K), 31-34% (Ca), 25-49% (Mg), 25-43% (manganese -Mn), and 35-54% (boron - B). Grier (1975) documented nutrient losses to the atmosphere through volatilization and ash convection from the Entiat wildfire in Washington (mixed conifer forest). Most of the N loss (39%) was volatilization, as expected, but much of the monovalent cation losses (35% for K and 83% for Na) could have also been through volatilization due to the high fire intensity.

Litter

The litter layer is an important component of forest ecosystems in that, among other things, it provides a cover to forest soils to mitigate the erosive effects of rainfall, and is a source of mineralizable nutrients. It consists of the organic rich horizons L, F, and H horizons, collectively designated the "O" (organic) horizon. The L layer consists of freshly fallen plant material. Beneath this is the F (or fermentation) layer of partially decomposed, but mainly recognizable plant material. The final litter layer above the first mineral soil horizon is the H (humus) layer of highly decomposed plant and animal-derived organic matter consisting of carbohydrates, amino acids, proteins, nucleic acids, lipids, lignins, humus, and minerals, listed in order of resistance to decay (McColl and Gressel 1995). Prior to incorporation in the mineral soil through animal activity, organic matter is particularly susceptible to combustion in fires and loss of key nutrients. Depending on variations of fire severity, litter consumption can range from scorching to complete ashing.

The amount of litter in an ecosystem and its importance in nutrient cycling are dependent on the plant type (grass-shrub-forest), productivity, climate, and decomposition rates. Tiedemann (1987) contrasted biomass and nitrogen on a shrub-grass-forb to sagebrush-grass to pinyon-juniper ecotone in the intermountain region of the West (Table 1). Across this

Table 1. Biomass and N distribution: shrub-grass, sagebrush, and pinyon-juniper ecosystems (from Tiedemann 1987).

Component	Biomass (mg/ha)	Nitrogen (mg/ha)	N %
LOW SHRUB			
Overstory	—	—	—
Understory	0.600	0.006	0.1
Litter	0.300	0.002	0.1
Soil (0-22 cm)	—	4.200	99.6
Roots	1.200	0.012	0.2
TOTAL	2.100	4.220	
SAGEBRUSH			
Overstory	11.400	0.059	1.3
Understory	1.100	0.032	0.7
Litter	5.450	0.039	0.8
Soil (0-60 cm)	—	4.527	94.1
Roots	16.800	0.150	3.0
TOTAL	34.750	4.768	
PINYON-JUNIPER			
Overstory	97.000	0.425	5.2
Understory	0.400	0.004	0.1
Litter	100.000	1.000	12.4
Soil (0-30 cm)	—	6.615	81.9
Roots	36.000	0.030	0.4
TOTAL	233.400	8.074	

gradient, the amount of litter increased from 0.3 to 100.0 Mg/ha. Pase (1972) documented slope-dependent litter layers of 9.2 to 16.4 Mg/ha on north and south slopes, respectively, in unburned chaparral of central Arizona. Wienhold and Klemmedson (1992) found litter masses of 33 Mg/ha under unburned chaparral stands in the Bradshaw Mountains north of Phoenix, Arizona. Litterfall rates of 0.192 to 0.176 Mg/ha/yr were measured. Covington and Sackett (1992) reported litter layer buildups of 27.1, 35.9, and 123.4 Mg/ha in unburned ponderosa pine stands on the Mogollon Rim of Arizona that had not burned in over 106 years.

Thus, as ecosystems transition from grass-dominated to woody plant systems, the litter layer increases substantially and the percent of ecosystem elements, particularly N, tied up in litter and susceptible to loss by fire increases. In the ecosystems referenced by Tiedemann (1987) that amount ranged from 0.1 to 12.4%. DeBano and Conrad (1978) reported a similar figure for ecosystem N in litter (10%) in California chaparral (Table 2). In Arizona chaparral, Wienhold and Klemmedson (1992) found that the N component of litter amounted to 16.7% of the ecosystem N prior to a prescribed fire. Likewise, DeBano and Klopatek (1987) reported that 12% of the N in an Arizona pinyon - juniper ecosystem was tied up in litter (Table 3).

Although the main pool for P, a critical plant nutrient, is in the soil not the litter (94 to 98%, Tables 2 and 3), organic forms of P in the litter are more available to plants. So, severe burning of vegetation and litter doesn't necessarily have the same potential impact on P pools as on N. Thus the impact of complete litter combustion on P cycling can be more

Table 2. Nitrogen and phosphorus distribution in California chaparral and loss due to prescribed fire (from DeBano and Conrad 1978).

	Nitrogen			Phosphorus		
Component	mg/ha	%	Fire loss mg/ha	mg/ha	%	Fire loss mg/ha
Plants	0.134	9	0.101	0.010	2	0.009
Litter	0.147	10	0.008	0.022	4	+0.009
Soil: 0-2 cm	0.337	24	0.036	0.120	21	0.102
Soil: 2-10 cm	0.806	57	*1	0.416	73	*
TOTAL	1.424		0.145	0.568		0.030

[1] *Not determined*

Table 3. Nitrogen and phosphorus distribution in Arizona pinyon-juniper (from DeBano and Klopatek 1987).

	Nitrogen		Phosphorus	
Component	mg/ha	Percent	mg/ha	Percent
Plants	0.425	5	0.036	1
Litter	1.000	12	0.044	1
Soil	6.615	82	3.963	98
TOTAL	8.040		4.043	

severe than what is indicated by the size of the individual nutrient pools. Also, P in soils with high Ca levels can be complexed into non-available forms with detrimental consequences for ecosystem productivity. Since the cycling of P is primarily through the organic-P pools, removal of vegetation all at one time by burning results in depletion of the aboveground P pool at a rate greater than mineral weathering can replace it.

Litter layer consumption can be highly variable within and between fires. Amounts consumed by fires have been reported to be 21 to 50% (prescribed fire, Pase and Lindenmuth 1971), 34 to 80 % (prescribed fire, Covington and Sackett 1992), and 45% (prescribed, DeBano and Conrad 1978). Campbell et al. (1977) described the effects of moderate and severe burning within a ponderosa pine wildfire on the Mogollon Rim of Arizona. Whereas the moderately burned areas still contained 38% vegetation and litter, the severely burned areas had less than 23% vegetation and litter.

Nutrient losses from the litter layer during fires is a function of fire severity. Grier (1975) noted nutrient losses from the litter layer after the intense Entiat wildfire that amounted to 19 (Ca), 21 (K), 31 (Mg), and 97% (both N and Ca) of pre-burn conditions. DeBano and Conrad (1978) measured N and P changes in the litter layer after a prescribed fire in California chaparral. While the N loss totalled 5% of the preburn litter N, the P pool in litter increased 43% due to the accretion of ash from the burned vegetation. For the system as a whole, the N loss was 10% (half coming from the litter), and the P loss was 2% (mainly from reductions in soil P in the top 2 cm)

Soils

The process of soil formation involves the transformation of parent material (rock, colluvium, or alluvium) over time and under the influence of climate, topography, biological processes, and disturbances. Soils develop into distinct profiles and horizons (such as O, A, E, B, C) depending on the combination of soil-forming factors. Many of the key processes involved in nutrient cycling occur in the soil (Figure 1), and the soil is the most important nutrient reservoir in most ecosystems (Table 1).

Physical Processes

Several soil physical processes and properties are affected by fire. These effects can impact both the nutrient status and cycling in Madrean ecosystems. Consumption of litter and soil organic matter by fire can seriously affect infiltration, the moisture holding capacity of soils, and the ability of soil systems to process rainfall. Removal of vegetation and litter by burning can also alter the post-fire thermal regime in the soil that controls microbial processes. Changes in microbial processing of organic matter ultimately affect the plant-available nutrient pool.

When fires burn off vegetation and litter layers that mitigate the impact of rainfall on the soil, the result often is increased runoff, soil dewatering, and ultimately watershed drying. Bare soil surfaces can seal off under the impact of raindrops, resulting in greatly higher rates of surface runoff. The net effect is a reduction in soil moisture and erosion of nutrient-rich ash and A horizon sediments. Apart from the physical removal of nutrients in runoff (discussed in a following section), the drying of soils diminishes the ability of recovering and colonizing microorganisms and plants to cycle nutrients. Adequate soil moisture is necessary to support microbial processes and to maintain a sufficient flow of nutrients to the roots of growing plants (Neary et al. 1990). Desiccation of the soil can then in turn create a negative feedback on nutrient cycling by decreasing plant cover and increasing surface erosion of nutrient-rich sediments.

Another physical response to fires in soils that is linked to the process just discussed above is water repellency (DeBano 1981). This condition develops in the presence of high intensity fires and certain types of organic matter. Water repellency in flat terrain just contributes to soil desiccation, but in steep terrain it can significantly accelerate erosion. It produces both long term effects (mass wasting, soil erosion, site degradation, etc.) and short term effects (increased runoff, ash and soil transport, etc.) that affect nutrient cycling processes. On a large-area basis, nutrients lost in mass wasting and surface erosion related to water repellency (<0.001 Mg/ha) may only be 10% of the total plant-litter-soil losses (DeBano and Conrad 1978). However, plant re-establishment is difficult on areas stripped of their nutrient-upper soil layers.

Thermal regimes of soils can be significantly altered by fires. Soils under closed forest canopies can experience large increases in maximum daily temperatures (20° C) and decreases in minimum night temperatures after fires. These changes can affect the physiology of microorganisms involved in nutrient cycling processes (Klopatek 1995). Thermal properties of soils (as well as other properties) can be altered when high fire temperatures (700-800° C) destroy mineral particles.

Chemical Processes

Heating during fires can significantly alter the nutrient status and nutrient cycling of forest, shrub, and grass ecosystems (DeBano et al. 1979, Dunn and DeBano 1977). Forest soils are more susceptible to alterations in their chemical state since more of the nutrient capital is aboveground and larger biomass accumulations can produce hotter temperatures during wildfires. However, the bulk of their nutrients still reside below the soil surface (Tables 2 and 3). Some of the effects of fire on soil chemistry and nutrient cycling processes include reduction in cation exchange capacity due to organic matter combustion or displacement, changes (both positive and negative) in nutrient availability as a result of increases in soil pH, direct nutrient volatilization, loss of nutrients due to ash and soil particle erosion, changes in nutrient forms to less or more available forms, and increases in leaching due to the disruption of nutrient uptake (Hungerford 1996).

The effects of fire on elemental cycling, particularly N, can be either minor or profound. Apart from the ability of fire to convert N immobilized in surface organic matter (plants and litter) to N gases, most of the N cycling processes in the soil are directly affected by fire. Some of the main processes affecting nitrate N (NO_3-N), for example, are:

a. Immobilization by decomposers

b. Uptake by growing vegetation

c. Denitrification to N gases (NO_2, NO, N_2)

d. Reduction to ammonia N (NH_4-N)

e. Adsorption on organic matter and clay exchange sites

f. Retention in pore spaces

g. Leaching to groundwater

All of these, except Item f., are directly or indirectly affected, mainly through alterations to plant, soil arthropod, and microorganism populations. Oxidation of litter and surface soil organic matter has important effects on N cycling.

Organic matter losses in the litter layer and A horizon can significantly affect the nutrient status of soils, since organic matter is a long-term source of mineralizable nutrients, and is the major factor controlling total cation exchange capacity (organic and clay mineral). Losses of N in the A horizon associated with organic matter combustion can exceed those of the entire litter layer (Table 2, DeBano and Conrad 1978). Organic matter contents of 4 to 6% in an A horizon, can be reduced to less than 1% organic matter.

A soil chemistry change which typically follows fires, but is most pronounced in fires of high intensity, is increased pH. Complete litter layer consumption increases soil alkalinity by releasing substantial amounts of cations. Most well-developed forest soils have pH's of 5.5 to 6.5, but may be higher where parent material (limestone, dolomite, etc.) is a strong factor. Elements such as Ca, Mg, K, S, and N generally become more available at a pH of 7.0, while copper (Cu), cobalt (Co), Mn, and zinc (Zn) are more available at pH's of <6.0. Nitrogen often becomes more available with light fires when it is shifted from organic forms and NO_3-N to NH_4-N (Hungerford 1996).

Specific changes in soil chemistry have been documented by investigations in ponderosa pine, chaparral, and pinyon-juniper in Arizona at the northern edge of the Madrean floristic province. Overby and Perry (1996) measured significant increases in soil NH_4 in the 0 to 10 cm depth, changing from 5.2 mg/kg before a prescribed fire in chaparral to 48.7 mg/kg immediately after the fire. A smaller but significant response was also measured for P (5.4 to 14.6 mg/kg). The soil pH declined slightly but not significantly, and soil organic carbon increased from 4.7 to 5.6%. Similar, but low magnitude, responses were documented in the 10 to 20 cm soil depth. Covington and Sackett (1992) measured substantial increases in inorganic N (mainly NH_4-N) in the upper 15 cm of soils after prescribed fire in ponderosa pine stands. Old growth stands exhibited the largest response, going from 0.002 to 0.036 Mg/ha due to high litter loads.

Recovery of soil nutrient levels can be fairly slow in some ecosystems, particularly those in the southwestern United States and northern Mexico where decomposition rates are slow. Klopatek (1987) determined that N and P concentrations beneath pinyon-juniper canopies, 35 years after a wildfire, had not recovered to levels found in stands that had not burned in 300 years (Table 4). In addition, when contrasting soils beneath burned and unburned stands, two-fold differences were noted in the percent of total N that was mineralized. This difference indicates that mineralization and nitrification may be enhanced by fire disturbance.

Table 4. Nitrogen and phosphorus time trends and mineralization in northern Arizona Pinyon-Juniper 300 and 35 years after burning (from Klopatek 1987)

Site - Years since burn	Sample	PO_4-P mg/kg	NO_3-N mg/kg	NH_4-N mg/kg	Mineralized %
300	Canopy	38.0	4.4	20.1	2.2
	Interspace	6.2	1.1	9.4	4.8
35	Canopy	23.4	0.5	12.1	4.6
	Interspace	10.1	0.7	8.9	10.6

Soil Biota

These organisms play very important roles in the processing, storage, and transformation of nutrients. Their occurrence and population sizes are influenced by a variety of environmental factors such as aeration, pH, moisture, temperature, energy sources, vegetation type and distribution, and by disturbances, such as fire, that affect these factors (Wells et al. 1979). Klopatek and Klopatek (1987) determined that interspace areas within an ungrazed northern Arizona pinyon-juniper stand contained 213,000 nitrifying bacteria/g of soil, while under the tree canopy nitrifying bacteria were found in numbers of only 35,000/g of soil. Conversely, they found more vesicular-arbuscular endomycorrhizae under the canopy than in interspace areas. Whitford (1987) studied microarthropods, another component of soil fauna, in soils of pinyon-juniper stands in the Chiricahua Mountains of southern Arizona. He found that pinyon pine litter contained 21,550 microarthropods/m^2, juniper litter contained 11,400 microarthropods/m^2, and soils from interspace areas contained 4,064 microarthropods/m^2.

Microorganisms

There is a scarcity of information available about soil microbial populations within ecosystems of the Madrean Archipelago, and how they are influenced by fire. However, fire effects on soil biota can be inferred from research elsewhere. Under the influence of fire, soil microorganism populations and species composition can increase or decrease depending on the intensity of the fire, maximum temperatures, soil water content, duration of heating, and depth of heating (Hungerford 1996). Site conditions (fuel loadings, aspect, elevation, etc.) and weather conditions pre- and post-fire are important since they can influence the nature of the fire and site recovery. Microorganism responses within and between fires on any given site and between sites within the Madrean ecosystem will fall along a continuum determined by factors mentioned above (DeBano et al. 1995). Low intensity, rapidly moving fires, such as in low fuel load grass understories or grasslands, do not have a major effect on microbial populations. High intensity fires with long durations, such as in mixed conifers with high fuel loads, cause the greatest impact on soil microbes.

Fire effects on microorganisms are greatest in the surface 1-2 cm where microorganism populations are most abundant and heating effects are the greatest. The general trend is for microorganism populations to decline significantly after fires, but then expand dramatically above pre-fire levels as nitrifier populations explode with altered nutrient, thermal, and moisture regimes, and regrowth of vegetation.

Soil heating can kill microorganisms directly (50-210° C) or alter their reproductive capabilities (Covington and DeBano 1990). Where temperatures as high as 210° C are needed to kill bacteria in dry soils, moisture in the soil can reduce lethal levels to around 110° C (Wells et al. 1979). Microbial population changes can also be related to changes in the soil environment; for example, heterotrophic bacteria would be impacted by loss of the organic matter food base after a fire (Barbour et al. 1980). Fire can indirectly affect microbial populations by totally or partially oxidizing organic carbon in and above the soil surface. Organic carbon is needed as a substrate and nutrient source by heterotrophic organisms. Soil pH can also increase after a fire in some forest types, affecting many microorganisms that are sensitive to pH changes. However, fire-related pH changes most likely would be minimal in the near-neutral pH soils commonly found in most of the Madrean region (Covington and DeBano 1990).

The reduction or loss of microorganisms will affect nutrient cycling. For example, both *Nitrosomonas spp.* and *Nitrobacter spp.* groups, which are involved with nitrification, are very sensitive to heat (Dunn and DeBano 1977). Increases in nitrification observed in chaparral soils following fires may be related to heterotrophic nitrification by fungi (Wells et al. 1979), and to increased available NH_4-N resulting from mineralized vegetation and litter N (Overby and Perry 1996).

In general, the effect of fire on soil microorganisms in the short-term is to reduce fungi, but increase populations of bacteria and actinomycetes (Barbour et al. 1980). Actinomycetes are, however, less sensitive to heat and desiccation than are bacteria. Species characteristics are important since some organisms can develop spores or other resting stages that are more resistant than the vegetative stages.

Mycorrhizae are soil fungi that form mutualistic relationships with plant roots. They obtain nutrients from host plants and contribute to plant nutrition, particularly P, and water absorption. They also provide some degree of resistance to plant pathogens and enable their host plants to become established and grow in severe habitats (recently burned areas) where they might not normally survive (Atlas and Bartha 1981). There are two main types of mycorrhizae, the endomycorrhizae that penetrate plant roots, and the ectomycorrhizae that form sheaths around plant roots. The latter are usually associated with conifers, oaks, and other angiosperms. Vesicular-arbuscular mycorrhizae (VAM) are a type of endomycorrhizae that are most commonly found in association with plant roots (Atlas and Bartha 1981).

Klopatek et al. (1988) indicated that colonization of VAM was moderately affected at soil temperatures <50° C, significantly reduced between 50 and 60° C, and severely reduced when burning temperatures reached 80 to 90° C. At 94° C there was a total loss of VAM . Although moisture generally aggravates heat damage in soils during fires, they found that damage was greater when the soils were dry than when they were wet. The duration of a fire in the surface organic debris, as well as the temperatures achieved, affects survival of mycorrhizael. In a pinyon-juniper stand, recovery 5 years after a prescribed fire was greater in interspace areas where initial fuel loadings were relatively light than under canopy areas where fuels were heavier (Klopatek 1995). Several studies in the grasslands, where fires may generate less heat and have a short duration, have not demonstrated long-term declines in mycorrhizae (Klopatek 1995). The time period for below ground ecosystems to recover after fires and the long-term consequences on nutrient availability and site productivity after repeated fires are not well known.

Vegetation

Above Ground Biomass

Nutrients in aboveground biomass pools are most obviously and easily affected by fire. Most of the nutrients lost from burned sites originate in vegetation as well as litter, although in some cases the surface layers of soils can contribute significantly to off-site losses. As indicated in Table 1, forests and woodlands have higher biomass loads than shrub-grass ecosystems so they are more sensitive to nutrient losses in fires. Disruptions to root systems can also affect nutrients on burned sites, since slow recovery of vegetation due to destroyed root systems delays root uptake of fire-mobilized nutrients and increases leaching losses.

Roots

A major role in nutrient cycling of forest, shrub, and grassland ecosystems is played by plant roots. Not only do roots take up and store nutrients while plants are active, but they also are sources of organic matter and nutrients and function as important substrates for microorganisms. Davis and Pase (1977) measured root masses of 172.6 kg/m3 in the upper 1.8 m of soil in chaparral - live oak communities in Arizona, at the northern end of the Madrean province. About 75% of this root biomass was in the upper 0.6 m of the soil. Roots of oaks can penetrate to depths of 9 m in some soils and have been measured as deep as 21 m. Although roots are protected somewhat from the heat of fires, intensive fires can kill entire root systems and smolder in roots underground for a year or more. Cessation of uptake due to plant and root death after fires can have a major impact on the cycling of nutrients, particularly N (Vitousek and Melillo 1979). In Arizona chaparral, significant NO_3-N increases have been measured after fires due to release of this form of N from extensive, decaying root systems that were killed by the fires (Davis 1989).

OFF-SITE TRANSPORT

Erosion

The amount of nutrients lost off-site after fires by surface runoff or debris flows is highly variable. Factors such as fire intensity, slope, watershed condition, storm timing, rainfall amount, precipitation intensity, topography, elevation, and slope affect nutrient loss from this process. The Madrean floristic province is probably the most susceptible ecosystem in North America to this type of post-fire nutrient loss because of the geomorphic sensitivity of the landscapes (high mountains, intense rainfalls, shallow soils, intense and frequent fires, slow vegetation recovery rates etc.). Therefore, sediment and nutrient losses after prescribed fires or wildfires are highly variable. Sediment losses from fires in Arizona chaparral have been reported to range from 3.8 to 204.0 Mg/ha (Neary 1996).

Data on erosion loss of nutrients after fires in the Madrean ecosystem are fairly scarce and difficult to

Table 5. Sediment loss, runoff, and organic matter loss from a prescribed fire in California chaparral (from DeBano and Conrad 1976).

Condition	Slope (%)	Debris (mg/ha)	Runoff (m^3/ha)	Organic matter (mg/ha)
Burned	50	7.340	786	0.410
	20	2.848	584	0.312
Control	50	0.210	25	0.007
	20	0.000	3	0.000

Table 6. Nutrient loss in sediment form a California chaparral prescribed fire (from DeBano and Conrad 1976).

Condition	Slope (%)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)
Burned	50	15.1	3.4	19.3	47.4
	20	7.5	1.0	7.6	18.5
Control	50	0.3	0.1	0.5	0.5
	20	0.0	0.0	0.0	0.0

estimate given the highly variable and episodic responses of watersheds to climatic events. DeBano and Conrad (1976) provided some fairly complete information from California chaparral that can be used to illustrate potential Madrean ecosystem responses. They measured significant slope-related watershed responses to prescribed fire in terms of debris production, runoff, and organic matter lost (Table 5). Nutrient losses in mineral sediments and organic debris were 34 to 94 times background levels on the steeper slopes which responded more to the combination of fire and rainfall event (Table 6).

Leaching

Losses of nutrients from burning in the Madrean system are set up by both the mineralization of large amounts of nutrients at one time as well as temporary termination of uptake by plants (Vitousek and Melillo 1979). The magnitude of nutrient losses after fires in the Madrean floristic province is difficult to gage because of the highly variable nature of both fires and climatic events. However, where data do exist, they indicate that Madrean and other southwestern United States ecosystems have the potential for larger leaching responses than elsewhere in terms of concentrations, but not necessarily total mass (Neary 1996).

SUMMARY AND CONCLUSIONS

Prescribed fires and wildfires can produce a considerable range of changes in nutrient cycles of forest, shrub, and grassland ecosystems in the Madrean floristic province, depending on fire intensity, fire frequency, vegetation, and climate. Grassland ecosystems are less susceptible to disruption in nutrient cycling due to generally lower intensity of fires and smaller amounts of nutrient capital in aboveground pools. These changes can be beneficial where prescribed fires increase the availability of plant nutrients and deleterious when severe wildfires produce nutrient volatilization, ash entrainment in smoke columns, increased runoff of mineralized nutrients, and accelerated leaching from soil systems. More information on the effects of fire on ecosystem nutrients is most available in the smaller United States portion of the Madrean province, where fire frequency currently is lower than the Mexico segment.

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