

Soil and Nutrient Cycling in Mediterranean-Type Ecosystems: A Summary and Synthesis¹

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The presentations at this session addressed the detailed aspects of nutrient cycling processes in Mediterranean ecosystems. Although many of these processes are reasonably well understood, some areas need further study before our current knowledge can be applied confidently by the land manager. This summary highlights some of the nutrient cycling processes discussed, points to obvious gaps in our knowledge, and lists the concerns having the most important management implications.

NUTRIENT INPUTS

Nutrients are added to Mediterranean ecosystems in several ways, including precipitation, dry fall, biological fixation, and rock weathering. Some of these processes have been discussed in detail by speakers at this Symposium. The importance of the different input mechanisms varies with the nutrient.

The cations, phosphorus, and sulfur are introduced into the ecosystem principally by precipitation, dry fall, and rock weathering. Nutrient inputs by precipitation and dry fall are well documented and vary widely, depending on the local and regional meteorological conditions, as discussed by Schlesinger (these Proceedings). The quantities of nutrients arriving in dry fall are usually greater than those contained in precipitation. Local air quality, nearby wildfires, and proximity to oceans can all influence the chemical composition of the precipitation.

¹Presented at the Symposium on Dynamics and Management of Mediterranean-type Ecosystems, June 22-26, 1981. San Diego, California.

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The weathering of parent rock may be an important source of some nutrients. The rates of weathering of the different parent rock materials vary and affect the inherent fertility and productivity of a site. Little is known about the nutrient additions to southern California soils by rock weathering although some research on granitic soils in Idaho indicates that substantial amounts of some nutrients can be added by weathering (Clayton 1979).

Nitrogen additions to the Mediterranean ecosystems have received much attention recently because nitrogen is most susceptible to loss by leaching and volatilization and is the nutrient most likely to be limiting in Mediterranean ecosystems. Nitrogen can be replaced by both physical and biological mechanisms (table 1). Physically it is replaced by both wet and dry fall from the atmosphere (Schlesinger, these Proceedings). Dry fall is more important and contributes 1.63 kg/ha/yr as compared to 0.42 kg/ha/yr for wet fall. In areas having high levels of air pollution, such as the Los Angeles air basin, up to 6.75 kg/ha/yr may be added as wet fall (Morgan and Liljestrand 1980). The effect of additional nitrogen enrichment in heavy smog areas is not known, but nitrogen could possibly be leached from the soil and contribute to the high nitrate levels observed in the groundwater in the foothill areas of the San Gabriel Mountains in southern California.

Dinitrogen fixation by bacteria and actinomycetes is a major source of nitrogen replacement (table 1). The free-living bacteria do not seem important, however, although only a few measurements have been made. Preliminary studies have shown free-living dinitrogen fixation in chaparral soils can be stimulated by adding a carbon source such as sugar (J. Kummerow, pers. commun.), or by incubating soils for a week under moisture conditions near field capacity (Dunn, unpubl. data). Although dinitrogen-fixing bacteria present in chaparral soils are capable of rapid reproduction and can readily fix nitrogen under certain conditions, their role in natural systems is unknown.

Symbiotic dinitrogen fixation by legume-*Rhizobium* symbiosis is much better understood than the other mechanisms. Although legumes are present in abundance after a fire, they do not fix the amounts of nitrogen expected (Poth, these Proceedings)--probably because the legumes are competing with the nonleguminous plants for available nitrogen in the soil instead of satisfying their own needs by fixing nitrogen from the atmosphere (Dunn and Poth 1979; Nilsen, these Proceedings). The legumes replace less than 15 percent of the nitrogen lost from a stand by fire and only 30 percent of the nitrogen contained in their own biomass.

Nitrogen is probably also replaced by the *Ceanothus-Frankia* symbiosis and possibly the

Table 1--Amounts of nitrogen gained and lost from chaparral by different mechanisms (kg/ha/25 yr).

	Losses	Gains
Fire (volatilization)	¹ 146- ² 419	Dinitrogen fixation
Postfire erosion		Legumes ³ 15- ⁴ 75
Sediment	¹ 10- ² 181	Shrubs ⁵ 2.5- ⁶ 1225
Water	¹ 0- ² 12	Free living ⁷ 25
Type conversion	¹⁰ 97	Atmospheric ⁸ 25- ⁹ 200
Denitrification	?	

¹Data from DeBano and Conrad (1978).

²Unpublished data from a prescribed burn done on the Buckhorn east of Santa Maria, Calif.

³Data collected on the San Dimas Experimental Forest after the 1976 Village fire on areas occupied by *Lupinus* spp.

⁴Fixation by *Lotus scoparius* (Poth, these Proceedings).

⁵Data from Kummerow and others (1978).

⁶Nutrient accumulations reported by Zinke (1969) on the San Dimas lysimeters and elsewhere in southern California.

⁷Unpublished laboratory data (P. H. Dunn).

⁸Data from Schlesinger (these Proceedings).

⁹Data from Los Angeles County air pollution (Morgan and Liljestrand 1980).

¹⁰Data on nitrate losses from disturbed chaparral watersheds (Davis, these Proceedings).

Cercocarpus betuloides-*Frankia* symbiosis in shrubs; the exact amounts are not known but are suspected to be high (table 1; Poth, these Proceedings). The *Ceanothus*-*Frankia* symbiosis seems to have poor dinitrogen fixation ability in 1-year-old stands and in mature stands older than 20 years (Kummerow and others 1978; Poth, these Proceedings). Studies of seedlings in the San Gabriel Mountains showed few nodules were developed the first 2 years after fire, but a large increase in nodular biomass occurred in the third, fourth, and fifth years. Lack of nodulation during the first year may have been related to nitrogen availability on the site. Postfire soils have high levels of available nitrogen (Christensen and Muller 1975, DeBano and others 1979a, Dunn and others 1979), which may suppress nitrogen fixation. After the large amounts of available nitrogen are immobilized it may be advantageous to the *Ceanothus*-*Frankia*

symbiosis to fix nitrogen again.

The relation between seed dormancy, in legumes and other nitrogen-fixing plants, and soil heating during a prescribed fire is not fully understood. Fire breaks the dormancy and is the principal mechanism inducing germination and establishment of these plants on a site after a fire. However, prescribed burning over a moist soil may adversely affect seed germination in the soil. Data by Westermeyer (1978) showed that in seeds from some species, seed mortality was higher in moist than in dry soils heated to the same temperatures. However, the differences in heat sensitivity among species were not great enough to explain the differences in seedling crops observed on moist soils under prescribed burns and adjacent dry soils under wildfires. These contradictory seedling responses must be better understood before major prescribed

burning programs are implemented. The failure to establish seedlings capable of fixing nitrogen may lead to a long-term decline in site fertility and productivity after repeated burning over moist soils.

NUTRIENT LOSSES

Nutrients can be lost from Mediterranean ecosystems by volatilization (DeBano and Conrad 1978, Ralston and Hatchell 1971), erosion (DeBano and Conrad 1976), leaching (Davis 1980; Vitousek and Melillo 1979; Riggan and Lopez),³ and harvesting (Boyer and Dell 1980). Not all nutrients are lost at the same rates because different processes of loss are important for different elements. It is important to recognize these differences when assessing the impact of different management alternatives on a site (DeBano, these Proceedings).

Volatilization

Nitrogen is one of the nutrients most sensitive to loss by volatilization. It can be lost by heating during a wildfire or a prescribed burn (DeBano and Conrad 1978), by ammonia volatilization in acid soils (Vitousek and Melillo 1979), and possibly by denitrification under anaerobic conditions (Swank and Caskey 1980). The amount of nitrogen volatilized during a fire can be estimated reasonably well if the litter and soil temperatures are known (DeBano and others 1979b). The estimated nitrogen losses from chaparral during prescribed fires have varied from 146 to 419 kg/ha (table 1). Currently no simple method of measuring litter and soil temperatures continuously is readily available to the land manager for routine measurements for use in assessing nitrogen losses. Although maximum temperatures can be determined more easily and inexpensively than continuous measurements, they are not completely satisfactory for characterizing biological changes produced by soil heating. Research studies are needed to quantify and model soil and litter temperatures and heating during different intensities of burning (DeBano, these Proceedings). Losses of nitrogen by ammonia volatilization are not well known in Mediterranean ecosystems although some losses have been detected during chaparral fires (Dunn, pers. commun.). Ammonia losses from acid soils under coniferous forests in a Mediterranean climate have not been studied, although nitrogen could be lost in this way. It is also possible to lose nitrogen by denitrification, particularly

³Riggan, Philip J., Lopez, Ernest. Nitrogen cycling in the chaparral ecosystem. In Proceedings of the symposium on the ecology and management of chaparral ecosystems; Western Society of Naturalists annual meeting, December 27-29, 1979. Pomona, CA. Manuscript in preparation.

from poorly drained, nutrient-rich soils and sediments in riparian zones. Denitrification losses have been reported from second-order mountain streams draining logged deciduous forest watersheds in the eastern United States (Swank and Caskey 1980).

During fires, sulfur volatilizes in much the same way as nitrogen, but probably at higher temperatures. Tiedemann and Anderson (1980) reported up to 6g percent of the total sulfur was lost at 11750 C; nitrogen is completely volatilized at 500° C (White and others 1973). Data on sulfur losses at different temperatures need refining and the significance of these losses for short- and long-term productivity should be established.

Unlike nitrogen and sulfur, most nutrients are not lost into the atmosphere as gases. Instead, significant amounts of calcium, magnesium, potassium, phosphorus, and sodium are transported as particulate material in smoke (Clayton 1976). This is a local or regional (in large wildfires) redistribution rather than an irreversible loss, such as the loss of nitrogen to the atmosphere.

Erosion

The quantity of nutrients lost from a site also depends on the amount and type of erosion. Accelerated erosion commonly occurs after wildfires (Rowe 1941, Sinclair 1954) when much of the eroded material is produced by surface erosion and rilling (Wells 1981). Poor infiltration and surface erosion can be caused by a water repellent soil condition formed during a fire (DeBano 1981). More nutrients are lost from the site by this surface erosion than might be expected, because large quantities of highly soluble nutrients are deposited on the soil surface during a fire. The largest nutrient losses following fire seem to be associated with the mineral sediment and organic debris rather than with water (DeBano and Conrad 1976, Campbell and others 1977). Water serves primarily as a transporting medium. The amounts of nitrogen lost in sediments and water presented in table 1 illustrate the difference in magnitude of these different erosional losses.

In assessing erosional losses of nutrients, a careful distinction must be made between on-site movement and the loss from the entire watershed. Losses from on-site movement, as measured by troughs or other small scale collection devices, may differ considerably from those measured in debris basins constructed at the mouths of larger watersheds. These relationships need to be better defined.

Leaching Losses

High concentrations of some nutrients, notably nitrates, have been reported to be lost from

some disturbed watersheds (Davis 1980; Vitousek and Melillo 1979; Riggan and Lopez).³ The losses are most noticeable after timber harvesting and brush-to-grass conversions. Although the total nitrogen lost from a watershed as nitrates following disturbance probably does not significantly affect site productivity and fertility, it may alter downstream water quality.

Several mechanisms may be responsible for nitrate release. The most popular explanations are (1) higher nitrification rates following disturbance, (2) greater rates of mineralization and decomposition of organic litter material, and (3) the inability of new shallow-rooted vegetation occupying the site to retain the nitrate nitrogen previously cycled by deep-rooted plants (Vitousek and Melillo 1979). It is important that the dominant mechanisms contributing to nitrate production and loss from these disturbed watersheds be better understood so possible remedial measures can be developed.

Harvesting

The amount and type of biomass harvested and the postharvest residue treatment all influence nutrient removal and loss (Boyer and Dell 1980). Also, the distribution of nutrients in the leaves, stems, small twigs, boles, and litter affect the amounts removed by a given treatment. For example, removing only the boles of trees during logging would have a much different effect on nitrogen than removing both the leaves and small stems. The effect on short- and long-term site productivity of removing different amounts of nutrients is not known. Data on nutrient distributions in chaparral (Zinke 1967; Zinke, these Proceedings) and in forests (Zinke and Stangenberger 1980) may provide a basis for establishing threshold values for different plant nutrients. Also, this total nutrient distribution must eventually be expressed in terms of availability to be useful for assessing site productivity.

ACCUMULATION AND MINERALIZATION OF ORGANIC MATTER

Litter Production

Litter production is directly controlled by primary productivity, as discussed by Alexander (these Proceedings). The quantity of leaves on a plant that becomes litter each year depends partly on the amount of rainfall a site receives 2 years earlier, during bud formation (Riggan, pers. commun.). The length of time leaves remain on chaparral shrubs is shortened by drought and lengthened by more favorable climatic conditions. Some of the nutrients are translocated back into the plant stems and roots before the leaves fall; the amount varies among species. About 9 percent of the total above-

ground biomass seems to be deposited in the litter each year (Gray, these Proceedings).

Decomposition

After the leaves and small twigs die they become part of the standing dead and litter biomass, and decomposition depends on several factors. First, placement of the material is important. The material remaining in the canopy (standing dead material) decomposes very slowly compared with the buried material. Material deposited on the mineral soil surface has an intermediate decomposition rate (Yielding 1978). A second factor in decomposition is moisture, particularly in young, open canopy stands where the aboveground material and litter held in the canopy dry out quickly. Temperature is a third factor. Rate of decomposition of litter on the soil surface depends on whether the canopy is open or closed, because this condition controls both temperature and moisture (Winn 1977). Moisture fluctuations are more influential than temperature fluctuations (Marion, these Proceedings). The role of stand age (Winn 1977), possible allelopathic effects (Rice and Panchoy 1973), and nutrient content of the litter (Rundel and Parsons 1980) in decomposition are still controversial points.

It is unclear whether a steady state is reached between litter deposition and decomposition. Kittredge's data (1955) support a steady-state condition, whereas Winn's results (1977) were not definitive. Schlesinger and Hasey (1981) concluded that the forest floor reached a steady state in 11 to 13 years. Decomposition rates also seem to vary among plant species. Schlesinger and Hasey (1981) found the overall decomposition rate fast, with evergreen material decomposing slower than deciduous leaves; Yielding (1978) found both rapid and slow decomposition rates for different species.

Fire as a Mineralizing Agent

Most Mediterranean ecosystems are burned regularly by either wildfires or prescribed burns, which act as active mineralizing agents (St. John and Rundel 1976). Fire is particularly influential in those ecosystems where a large portion of the nutrient pool is contained in the biomass, and where the decomposition rates of the unburned plant material between fires regulate the productivity of the system (Raison 1980). The accumulated undecomposed litter and plant material is suddenly combusted and the plant nutrients contained in it are released. This "pulse" nutrient addition may play an important role in the rapid reestablishment of vegetation following fire (Marion, these Proceedings).

Fire has variable effects on nutrient availability--it may mobilize the nutrients, induce a

deficiency, or have no effect (Wells and others 1979). Although some of the nutrients contained in the plants are volatilized, or lost as airborne particulates, most of the combusted material is deposited on the soil surface. Some of the nitrogen remaining after the fire is in a highly available form as ammonia- and nitrate-nitrogen (DeBano and others 1979a, Christensen and Muller 1975). The nitrogen remaining in the uncombusted organic matter after burning is readily mineralized by microorganisms so that the level of available inorganic nitrogen is kept high (Dunn and others 1979).

Conflicting results on phosphorus availability have been reported after a fire (Wells and others 1979). In most soils the availability of phosphorus may be increased by burning (Vlamis and Gowans 1961, Vlamis and others 1955). However, some soils presumably contain significant amounts of soluble iron and aluminum, which may tie up the phosphorus and cause a phosphorus deficiency after repeated burning (Lunt 1941, Vlamis and others 1955). The basic cations (Ca, Mg, K, Na) contained in the plant material are released by burning and generally reduce soil acidity. The more frequent the burning the more pronounced the increase in pH (Wells and others 1979). The increased plant growth or "ash bed" effect observed after fire seems also to include a heating of the soil as well as greater nutrient availability (Bruce 1950, Renbuss and others 1973). The presence of highly available nutrients in the "ash bed" usually makes fertilization of freshly burned watersheds ineffective (DeBano and Conrad 1974, Vlamis and Gowans 1961).

Nutrient Availability and Uptake

Nutrient availability and uptake from burned and biologically decomposed plant material is only partly understood. Nitrogen compounds have received more study than the other plant nutrients. Decomposition plays the most important role in nitrogen release and availability--particularly during the interval between fires (Marion, these Proceedings). Although fire releases large amounts of available nitrogen, and nitrification rates are stimulated (Arianoutsou-Faraggitaki and Margaris, these Proceedings; Christensen and Muller 1975; Dunn and others 1979), more nitrogen is probably made available by decomposition during the interval between fires (Marion, these Proceedings). Decomposition and pyrolysis during fires are equally important processes for the release of potassium, calcium, and magnesium. Little is known about the factors affecting mineralization and availability of phosphorus and sulfur.

Both nitrogen mineralization and nitrification are important biological processes affecting nitrogen availability. Nitrogen mineralization is controlled largely by substrate quantity and quality, temperature, and moisture. Carbon is frequently the most limiting factor for microbial

activity and the presence of highly resistant organic compounds (phenolics and lignins) may restrict the energy source available to microbes responsible for nitrogen mineralization (Marion, these Proceedings). The ammonia released by mineralization may be immobilized by decomposers, taken up by vegetation, fixed by clays, volatilized, adsorbed on cation exchange sites in the soil, or undergo nitrification (Vitousek and Melillo 1979). Nitrification can be carried out by both chemotrophic and heterotrophic microorganisms (Dunn and others 1979) which may be inhibited by parent rock material (Nakos 1981) or tannins (Rice and Pancholy 1972). The nitrates produced are highly soluble, and if not immediately immobilized by microbes (El-abyad and Webster 1968) or taken up by plants (Vitousek and Melillo 1979), may be lost to streamflow by leaching (Davis, these Proceedings).

The role of mycorrhizae in nutrient uptake by plants in Mediterranean ecosystems has not been fully clarified. Preliminary studies in chaparral show that mycorrhizae are present in all shrubs (Dunn, pers. commun.). *Quercus dumosa* has been found to have many hypogenous mycorrhizal fruiting bodies (Dunn 1980). It is possible that mycorrhizae may reduce the need for microbes in recycling nutrients before the nutrients are taken up by plants. Immediately after fire the available nutrients are probably immobilized by living microbes. As nutrient stress increases, between fires, mycorrhizae probably play a more important role in plant nutrition and site productivity. For example, in South Africa the growth rate of pine seedlings was 50 times greater on soils inoculated with mycorrhizae as compared to native untreated fynbos soils (Miller, these Proceedings). Mycorrhizal responses may also involve nutrient-water stress relationships which have evolved as features of the Mediterranean-type ecosystems (Miller, these Proceedings). Basic information on moisture stress relationships for different plant species is limited, although some information is now available for several chaparral species (Roberts, these Proceedings).

MANAGEMENT IMPLICATIONS AND KNOWLEDGE GAPS

Several of the nutrient cycling processes and mechanisms have strong management implications in addition to being intellectually enticing to the researcher. The papers presented pointed out the need to:

1. Define the trade-offs among nitrogen losses, soil wettability, and biological damage to roots, seeds, and soil microbes in burning over wet and dry soil.
2. Quantitatively assess the impacts of burning or permanent type conversion on steep slopes having different types of soils.
3. Establish spatiotemporal treatment patterns that reduce the amounts of nitrate nitrogen released from disturbed or converted watersheds.
4. Establish criteria for postfire fertili-

zation.

5. Relate on-site nutrient movement to losses from the entire watershed so realistic assessments of nutrient losses can be developed.

Many of the concerns expressed by the managers can be addressed or satisfied with existing information, but this must be prepared in a format that will be useful to the land managers when making on-the-ground decisions and assessments. Probably this task can be accomplished most effectively in handbooks and guidelines developed jointly by the managers and researchers. Additional research is needed in some areas before parts of these guidelines can be quantitatively established. Until such information is available, judgment and experience will have to fill the gaps.

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