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Lodgepole Pine Ecosystems

Biotic processes play a critical role in regulating material flux in Rocky Mountain lodgepole pine forests

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The study of water and nutrient fluxes through ecosystems provides many opportunities for learning about the biology of organisms and acquiring information relevant to land management. In this paper we present some results for the lodgepole pine (*Pinus contorta* ssp. *latifolia* [Engelm. ex Wats.] Critchfield) forest ecosystem, a relatively simple but widely distributed forest type in western North America. Our results from Wyoming add to the growing body of literature that illustrates how biotic processes play a key role in regulating various aspects of ecosystem structure and function.

New environmental stresses demand a more complete understanding of biological activity and ecosystem structure and function

Lodgepole pine forests dominate much of the montane environment from Colorado to northern Alberta, often forming monospecific stands. Commonly classified as intolerant of environmental conditions beneath the forest canopy, the species usually depends on recurring disturbances for successful reproduction. While bark beetle epidemics, wind storms, or timber harvesting may create the necessary openings, perhaps the most prevalent prehistoric disturbances were the hot, stand-replacing fires that occurred at 100- to 400-year intervals throughout most of its range (Arno 1980, Romme 1982, Romme and Knight 1981). Biomass accumulation after a fire (and perhaps a clearcut) follows predictable patterns for the major forest components (live plant, forest floor, and dead wood biomasses), with the maximum rate of biomass accretion occurring in the fourth or fifth decade of development (Figure 1). Biomass accumulates until the next fire, as annual net primary productivity appears to continually exceed annual respiration by heterotrophic organisms (Yavitt and Fahey 1986),[1] a different situation from some other forests where an equilibrium in total biomass at maturity is hypothesized (Bormann and Likens 1979).

Because of environmental gradients and the fact that different parts of the landscape are in varying successional stages, lodgepole pine forests exhibit considerable structural variability. For example, in a series of eight mature (> 80 year old) stands that we studied in the Medicine Bow Mountains, southeastern Wyoming, tree density ranged from 400 to 15,000 stems per ha; total tree biomass from 120 to 180 Mg per ha; canopy height from 7 to 25 m; and leaf area index (LAI, all surfaces) from 4 to 10 (Pearson et al. 1984). This structural variation can also affect the productivity and species composition of the forest understory (Romme et al. 1986). Indeed, lodgepole pine habitats can be classified using understory composition for purposes of guiding forest management practices (Wirsing and Alexander 1975).

Variation in water and nutrient fluxes may be strongly linked to differences in species composition (Gorham et al. 1979, Waring et al. 1981), but other factors must account for the variation in the usually monospecific lodgepole pine forests. To evaluate the importance of such factors, we analyzed the fluxes of water, nitrogen, and other major ions in several contrasting stands of lodgepole pine forest located in the Medicine Bow Mountains. We observed that water yield from these stands is highly variable and controlled by the amount of leaf area and soil water storage capacity; that mineralized nitrogen is retained tenaciously in the forest floor; that nitrogen leaching from the soil rooting zone occurs in organic forms and is probably related to soil texture; and that three classes of anions—strong acids, bicarbonate, and organics—are important for cation

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[1] J. A. Pearson, D. H. Knight, and T. J. Fahey. 1986. Patterns of biomass and nutrient accumulation during ecosystem development in *Pinus contorta* forests, southeastern Wyoming. Submitted.

leaching. The organic anions' mobility also depends on soil texture, which thereby exerts an additional influence on cation leaching.

Hydrology

Each spring, when skiers are packing away their equipment, the creeks and rivers draining the Rocky Mountains swell, carrying torrents of water to the communities below. The need for a reliable supply of water limits economic development in the Intermountain West, and several management plans for increasing water availability have been implemented. The manipulation of montane forests is a critical component of some of these plans.

The annual hydrologic pattern in the Rocky Mountains can be divided into three intervals: 1) an extended period of snow accumulation, usually from October until April, with little movement of water in the liquid state; 2) a rather brief interval in May and June during which the accumulated snow melts, saturating the soil and contributing to groundwater and streamflow; and 3) a relatively dry summer during which evapotranspiration reduces soil water content, often leading to tree water stress. Most summer rains are inadequate for soil moisture recharge or nutrient leaching beyond the rooting zone (Reynolds and Knight 1973). Predicting quantitatively the fluxes of water throughout the year, and how variation in biotic, climatic, and soil conditions affects those fluxes, depends on understanding the hydrophysiology of lodgepole pine. Potentially much more water can move via transpiration than via direct soil evaporation.

Besides the diurnal response of stomata to soil radiation, the most important factors inducing stomatal resistance to water vapor flux in lodgepole pine are drought and cold temperature stresses. Stomatal opening is impaired in the spring and autumn by subfreezing overnight temperatures (Fahey 1979) that create a lag, limiting transpiration even when daytime temperatures are warm. Stomatal closure is also induced by low atmospheric humidity and by internal tree water deficits that arise when root uptake does not meet transpirational demand (Running 1980), particularly when cold soil (<5° C) lowers the permeability of root membranes to water (Kaufmann 1982). When soil water potential declines below a particular limit (about −1.2 MPa), as may occur during late summer (Fahey and Young 1984), stomata remain closed throughout the day, reducing transpiration rates to nearly zero (Fetcher 1976). Because stomatal closure also prevents uptake of carbon dioxide for photosynthesis, primary productivity is limited by cold temperatures in the fall, winter, and spring, and often by dry soils in late summer.

The capacity of the soil to store melting snow water during the spring depends directly on the soil pore space emptied of water by evapotranspiration during the previous summer and fall. The primary variable affecting this feature is the total leaf area from which transpiration occurs. For mature, closed-canopy stands in droughty environments, the amount of leaf area per unit land area (i.e., leaf area index, LAI) appears to vary with the degree of water stress that usually develops during the growing season (Grier and Running 1977; Knight et al. 1981, 1985). In lodgepole pine ecosystems, LAI is closely related to soil storage capacity, as most of the water available to the trees each year is that retained in the soil during snowmelt. In young forests or low-density stands lacking canopy closure due to disturbances, where LAI is low, trees are unable to reduce soil water potential to −1.2 MPa during most growing seasons and proportionately more snow water leaves the ecosystem via streamflow (Table 1). Forest managers use this principle to increase water yields from Rocky Mountain watersheds.

The hydrologic patterns described above are complicated by the ability of the evergreen lodgepole pine to transpire during the snowmelt period. Because the atmospheric conditions that cause thawing also stimulate the opening of stomata (i.e., warm nights and days), we expected that water uptake by the trees could limit the magnitude of water outflow beyond the rooting zone. Utilizing a simulation model based on lodgepole pine physiology (Knight et al. 1985), we estimated that about 5 to 20% of the snowpack water could be diverted from potential streamflow by vernal transpiration (VT, i.e., transpiration during the snowmelt/drainage period), and that water yield from some stands could be reduced to nearly zero under certain conditions. The highest VT values would be associated with high LAI, partly because of the large surface area for transpiration but also because of more shading, which prolongs the snowmelt period, thereby providing more days for VT. Furthermore, the shading also extends the VT period later into the spring when conditions are warmer and the potential for transpiration is higher.

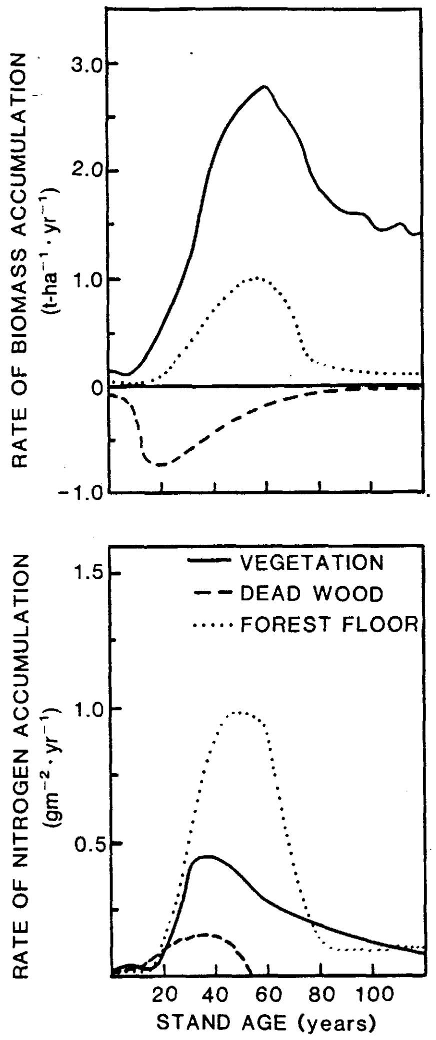

Figure 1. Generalized patterns of biomass accumulation (above) and nitrogen accumulation (below) in three major biomass compartments during ecosystem development after a stand-replacing fire in lodgepole pine forest, Medicine Bow Mountains, Wyoming.

One primary effect of timber har-

Table 1. Water fluxes (in cm of water) during the 1980 snowmelt drainage period in four contrasting stands of lodgepole pine forest, as predicted by a hydrologic simulation model.[a] Note the great differences in subsurface outflow even though water inputs were about the same.

Stand description	Leaf area index[b]	Soil water storage	Water input[c]	Vernal ET[d]	Subsurface outflow
1) 110-year-old forest on well-drained glacial till	9.9	16	49	20	13
2) 110-year-old forest on poorly drained glacial fluvium	7.1	20	48	19	9
3) Uneven-aged forest on a coarse granitic soil	3.9	6	48	6	36
4) Simulated clearcut of stand 1 above	0.5	5	49	2	42

[a] Adapted from Knight et al. (1985)
[b] m^2 leaf area per m^2 ground area
[c] Maximum water equivalent of snowpack plus rain during the drainage period
[d] Evapotranspiration during the drainage period

vest, fire, or insect epidemics is a lower LAI, which can lead to an earlier and shorter snowmelt period and higher streamflow. This effect is compounded by the possibility of snow redistribution by wind from the forest into small openings (Leaf 1975, Troendle 1983). Differences in the dominant tree species composition could be important also. For example, water outflow beyond the rooting zone in the spring would be much greater in a stand dominated by the deciduous aspen (*Populus tremuloides* Michx.) because essentially no VT occurs when the trees are leafless. In contrast, some lodgepole pine forests can change through succession to a spruce-fir forest capable of developing up to twice the amount of evergreen leaf area (Kaufman et al. 1982).[2]

Clearly, different parts of the montane landscape supply different proportions of the total water yield during the spring snowmelt period. Variation in meteorologic conditions, snow accumulation, soil water storage, and stand LAI must be estimated by land managers wishing to maximize water yields. New ways of rapidly assessing these critical variables over large areas would greatly facilitate the ongoing efforts of watershed scientists.

The importance of nitrogen

The low productivity of the lodgepole pine ecosystem is commonly attributed to the short, cool, sometimes dry growing season, but the limited availability of nitrogen may be equally important. Less nitrogen is deposited in Rocky Mountain precipitation than in many areas, partly because total precipitation is relatively low but also because two-thirds of the annual precipitation usually comes as snow, which is lower in nitrogen than rainfall (Fahey et al. 1985). Furthermore, there are few nitrogen-fixing species in lodgepole pine forests (Fahey et al. 1985). Nitrogen concentrations in lodgepole pine leaves from our study area (0.7% dry mass) are among the lowest reported for vascular plant leaves, probably a reflection of the low nitrogen inputs as well as periodic losses associated with volatilization during fires (Raison 1979). Such low levels of tissue nitrogen may limit photosynthetic rates.

Mature forests in general seem to derive much of the mineral nutrients required for continued growth and maintenance by translocation from senescing tissues and recycling through detrital food chains (Cole and Rapp 1981). This would explain the ability of forest stands to supply much larger amounts of nitrogen to new growth than enter the ecosystem annually via the various input vectors. When detritus reaches the ground as litterfall, high carbon: nitrogen ratios may favor microbial immobilization. Therefore, it is not surprising that nitrogen concentrations in leaf litter usually increase during the initial stages of decay in forests (Bocock 1963). We found that nitrogen accumulates in decaying lodgepole pine leaves for up to seven years (Figure 2), and that during this interval nearly as much nitrogen is added to decaying leaves as was present originally (Fahey 1983). Detrital wood also accumulates nitrogen, but only in a state of advanced decomposition (Fahey 1983). Some researchers have proposed that the nitrogen accumulating in decaying detritus could be supplied by precipitation (e.g., Gosz et al. 1973). However, the quantity added by this source in our area is insufficient to account for the accumulation rates that we observed.

Although inorganic nitrogen (NH_4^+ and NO_3^-) is almost entirely removed from precipitation as it passes through the litter layer, we have measured a net leaching flux of organic nitrogen from the forest floor (Yavitt and Fahey 1984). To balance the resulting deficit, other sources of nitrogen must exist for litter microbes. One possible source is fixation by free-living bacteria, a source that apparently is quite large in some forests (Gordon and Wheeler 1983). However, Fahey et al. (1985) detected only small amounts of nitrogen fixation in decaying detritus (<ten percent of annual precipitation inputs), probably because of the cold and/or dry conditions that prevail during much of the year.

At this time we believe that the most likely source for the high nitrogen accumulation in decaying lodgepole pine litter is fungal translocation from the humus and upper mineral soil layers where the lower carbon: nitrogen ratio is conducive to nitrogen mineralization. To estimate the rates of this transfer, Fahey et al. (1985) constructed a flux diagram for nitrogen in the forest floor of a 110-year-old forest (Figure 2). The calculations suggest that large quantities of nitrogen ($0.4\ g \cdot m^{-2} \cdot yr^{-1}$) move from humus to the surface litter layer, but direct tracer studies are needed to confirm this estimate.

We also determined that nitrogen flux to the mineral soil occurs primar-

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[2] H. E. Haemmerle and D. H. Knight. 1986. Coniferous forest leaf area in relation to stand age and site index in the Medicine Bow Mountains, Wyoming. Unpublished.

ily as soluble organic compounds (about 0.8 $g \cdot m^{-2} \cdot yr^{-1}$). After passage into the mineral soil horizons, most organic solutes were lost from solution, presumably as precipitates onto soil colloids. In general, more organic nitrogen was lost from solution as the proportion of soil colloids increased (i.e., with finer soil texture), suggesting that the outflow of nitrogen from undisturbed stands appears to decrease with increasing clay content.

How then do the plants obtain the large amounts of nitrogen required for the production of additional leaves and other tissues during growth? Because the carbon:nitrogen ratio of organic matter in the soil mineral horizons is relatively low (35 compared to 70–130 for litter), microbial oxidation must release some NH_4^+, which can be absorbed by roots. We measured peak rates of nitrogen mineralization in early summer when soils are moist and relatively warm, and when nitrogen demands of plants are probably highest. During the phases of rapid biomass and forest floor accumulation 30 to 60 years after disturbance, substantial "mining" of soil organic matter probably occurs, creating a deficit that is, however, replenished in older stands with net accumulations of soil organic matter and nitrogen. The soil appears to accumulate nitrogen during later stages of ecosystem development that can nourish new tree growth following a disturbance. Decaying wood may serve much the same function as soil organic matter (Fahey 1983), and together they comprise a "big, slow compartment" that may be critical for facilitating ecosystem persistence following disturbance (O'Neill and Reichle 1979). As in agriculture, plans for intensive forest management must consider potential impacts on this often-ignored detrital compartment of the ecosystem.

Inorganic nitrogen appears to be in high demand, judging from the very low concentrations of NH_4^+ and NO_3^- we measured in soil solutions of undisturbed forest. Under these conditions, the bacteria that convert NH_4^+ to NO_3^- (autotrophic bacteria) probably are not active, in part because these nitrifying bacteria are known to be poor competitors for NH_4^+ in soils (Belser 1979). Even

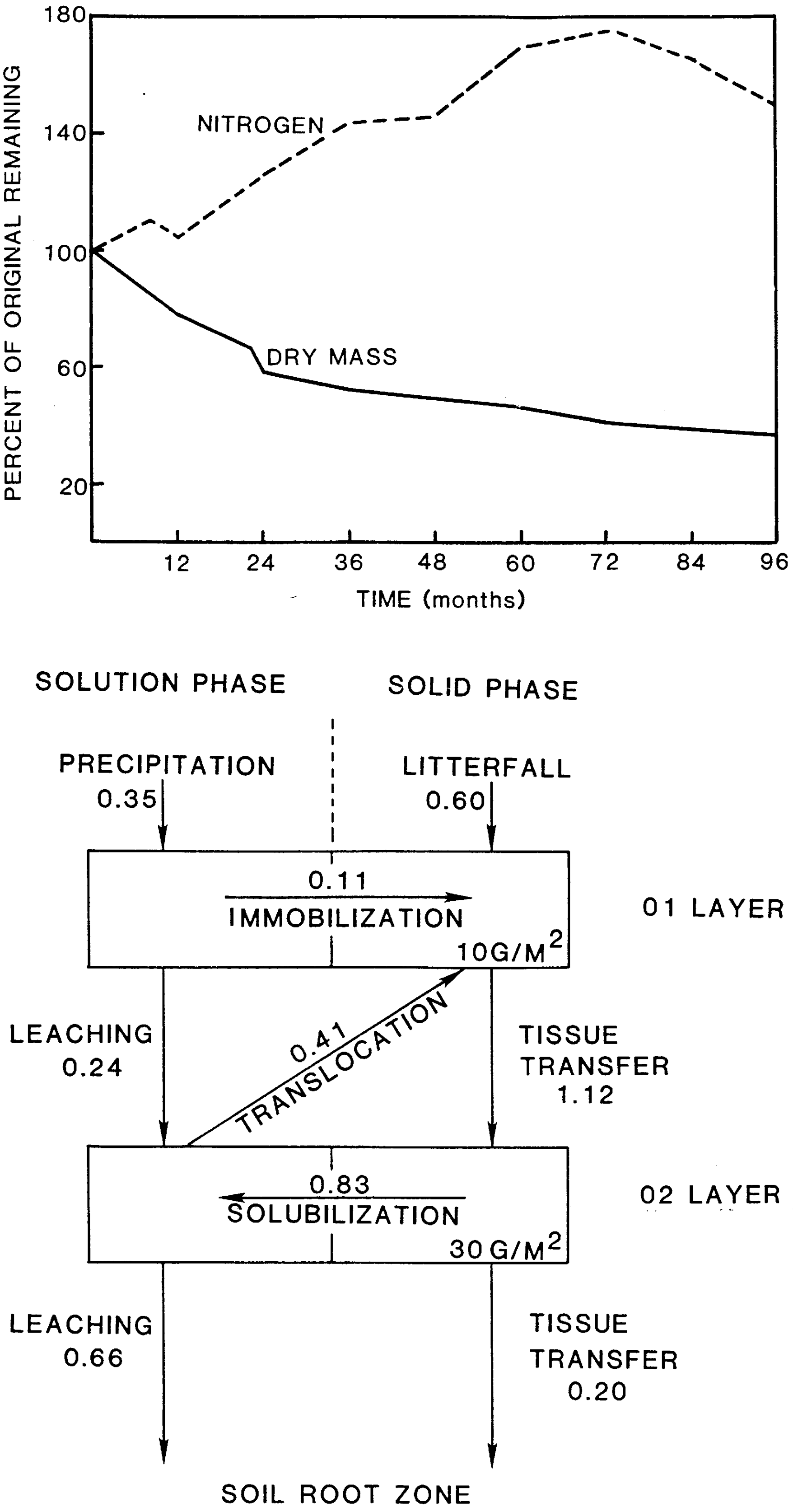

Figure 2. Nitrogen fluxes in the forest floor of a mature lodgepole pine forest ecosystem, Medicine Bow Mountains, Wyoming. Dry mass loss and changes in nitrogen content of decaying leaves are shown above, and annual nitrogen fluxes ($g \cdot m^{-2} \cdot yr^{-1}$) between major solution and solid phase compartments are shown below (adapted from Fahey et al. 1985).

following elimination of root uptake, we observed a considerable lag (> 1 year) in the generation of NO_3^-, which is consistent with results from other nitrogen-deficient forests (Vitousek et al. 1982). The most intense competition for mineral nitrogen may occur between roots and the decomposers, especially litter fungi. This scenario suggests a positive feedback whereby limited nitrogen uptake by trees results in litter with a high carbon:nitrogen ratio, stimulating greater microbial immobilization of nitrogen during litter decay (Vitousek 1982). Eventually this cycle is broken by tree mortality, whether due to pest and disease outbreaks, timber harvest, or fire.

Fluxes of major ions

The forest ecosystem can be depicted as a series of subsystems composed of biotic and abiotic solid phases that are the sources and sinks of soluble materials and that are coupled by hydrologic fluxes. Predominant components in the lodgepole pine ecosystems are plant tissues, forest floor detritus, and soil colloids.

As described previously, ionic concentrations in precipitation are low in our study area. Precipitation collected with gauges open to the atmosphere only during rainfall was considerably more acidic than bulk rainfall (mean pH = 4.6 and 5.2, respectively), suggesting the importance of wind-blown soil particles from adjacent intermountain basins (Gosz et al. 1983) that neutralize the acidity. Total wet and dry precipitation (bulk precipitation) is dominated by Ca^{2+} and SO_4^{2-} ions, with smaller amounts of NO_3^-, HCO_3^-, Mg^{2+}, K^+, Na^+, and NH_4^+ ions.

Contact with the forest canopy modifies the chemical composition of precipitation further. This is especially true for rainfall, which increased in ionic strength by an average 2.3 times over bulk rain. Although large differences in canopy surface area should result in variation among sites in throughfall composition, we were unable to detect significant differences in four contrasting stands because of high within-stand variation. Snow appears to be affected much less, as differences in total cation concentration between snow from the forest and that from adjacent openings were less than 15%. The low temperatures that prevail during most snowfalls probably limit dissolution and evaporation processes.

Three processes could increase the ionic concentration of throughfall: 1) evaporation of rain intercepted by the canopy, 2) dissolution of solids deposited on canopy surfaces, and 3) leaching of substances from the canopy tissues. By measuring throughfall quantity during 86 storms we have estimated that 27% of the increase results from the first process, evaporation. This proportion varies markedly between rainstorms (from <10% to >50%) depending on the intensity and duration of the event. The second process, dry deposition, also is important in many Rocky Mountain ecosystems because of upwind deserts and large amounts of surface area on which to trap the material, and this may explain much of the addition to throughfall of sodium and sulfate. The third process, foliar leaching, probably explains most of the increase in levels of highly mobile plant nutrients like potassium.

The increase in throughfall cation concentration was not balanced by equivalent increases in the measured anions (i.e., SO_4^{2-}, NO_3^-, Cl^-, and HCO_3^-), implying the importance of some as-yet unmeasured anions to balance the cations. This apparent anion deficit probably represents anionic-functional groups of organic acids, which were, in fact, highly correlated with dissolved organic carbon concentrations ($r^2 = 0.76$, $n = 184$).

Because most anions are not adsorbed by the negatively charged humic colloids, the supply of anions and also hydrogen ions regulates net cation leaching from forest floor to mineral soil. In general, one or two of the three major groups of anions—bicarbonate, organic, and strong acid—usually predominate in forest floor solutions. For example, the warm, moist climate of some tropical regions allows nearly complete oxidation of organic matter, leading to a predominance of bicarbonate derived from respiratory carbon dioxide, whereas soluble organic acids are more important products of decomposition in northern conifer forests (Johnson and Cole 1980). Many temperate forests are subject to wet and dry anthropogenic deposition of strong mineral acids (sulfuric and nitric), which may lead to the increased importance of strong acid anions.

In lodgepole pine ecosystems we observed a situation in which all three major groups of anions were important for nutrient transport (Figure 3). Because free acidity was almost entirely neutralized by base cations in the forest floor, dissociation of carbonic acid was enhanced and large amounts of organic solutes were mobilized (Yavitt and Fahey 1986). The highest concentrations of all the chemical species in forest floor leachate were observed when snowmelt began, apparently because decomposition beneath it (Fahey 1983) led to the generation of carbon dioxide and soluble organic compounds that appeared as neutral bicarbonate and "fulvate" salts. Although the soil solution pH values (5.5–6.0) in our study area allowed dissociation of carbonic acid, low respiration rates in the cold and often dry soils limited carbon dioxide concentrations so that carbonic acid levels were rather low and bicarbonate leaching less pronounced than expected. Soil carbon dioxide concentrations in the lodgepole pine soils did not differ significantly between stands and were 0.3 to 0.6%, nearly one-tenth that in typical agricultural soils (Buyanovsky and Wagner 1983).

The high sulfate levels at the beginning of snowmelt probably represented, in large part, delayed transfer of neutral salts deposited in wet and dry precipitation during the previous summer. Some evidence for this assertion was obtained during two years when unusually heavy rains occurred in late summer, wetting the soil to the depths of our soil water collectors. Samples collected during both periods had unusually high ionic strength, with calcium, magnesium, and sulfate being the major ions present. Whether collected in the summer or during the spring snowmelt period, the sulfate levels were higher than would be expected from decomposition.

We collected soil water samples from near the base of the rooting zone for five years in six contrasting lodgepole pine stands. Multiplying the ionic concentrations of these solutions by the daily water flux, estimated with a hydrologic model developed for our

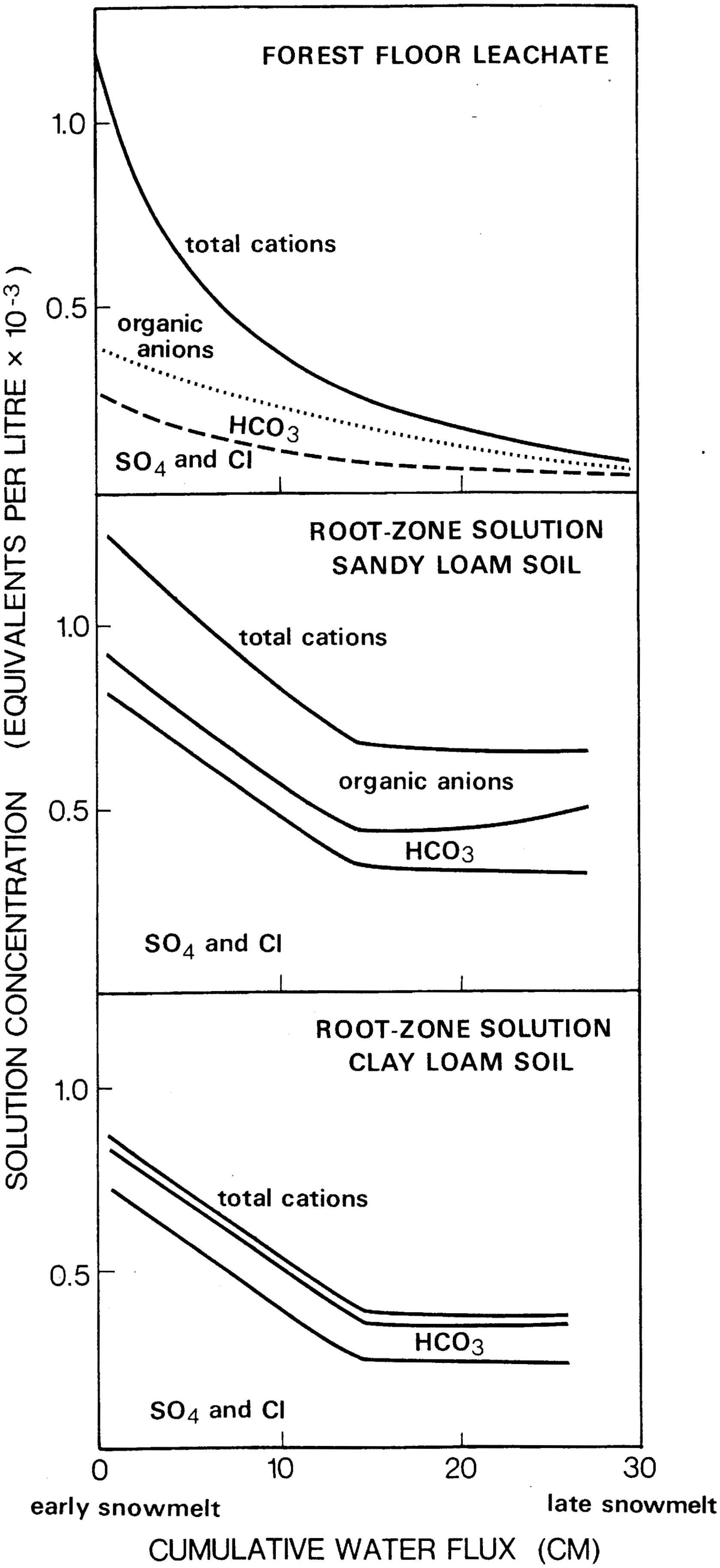

Figure 3. Concentrations of major ionic constituents in forest floor leachate and in the major rooting zone for two contrasting mineral soils during the snowmelt period of mature lodgepole pine forest ecosystems, Medicine Bow Mountains, Wyoming (adapted from Yavitt and Fahey 1986).

stands, we were able to estimate element fluxes beyond the rooting zone (Knight et al. 1985). Cation flux to the mineral soil from the forest floor consistently exceeded leaching beyond the rooting zone. Again, variation among stands seemed most directly related to colloid or clay content (soil texture), probably because of its effect on the mobility of organic anions. Of the cations leached from the forest floor, the proportion retained in the rooting zone ranged from about 90% in two fine-textured soils on glacial till to about 30% on a soil derived from coarse granitic bedrock. Although roots undoubtedly play an important role in regulating elemental fluxes through the soil profile, the effect of soil texture on the mobility of organic solutes appears to be very important in causing between-stand differences.

The strong biotic control exercised for nitrogen also is reflected in the patterns for one of the major cations, potassium, which appears to be in similar high demand in lodgepole pine forests. For example, we observed a large decline in the mass ratio of K/(Ca + Mg) along the water flux pathway in mature stands: with the throughfall value of 0.45, forest floor leachate value being 0.39, the root-zone soil solution being 0.25, and the subsoil solution being 0.06. Thus, as demonstrated elegantly by Stone and Kszystyniak (1977), some pine forest ecosystems very effectively conserve their potassium stores.

As discussed by Sollins et al. (1980), the most important biological mechanism influencing ionic fluxes in our study area may be the release of hydrogen ions during root uptake. Because roots absorb larger amounts of cations than anions, they must release hydrogen ions to maintain a charge balance. These protons are consumed in ion exchange reactions and primary mineral weathering in the soil adjacent to the roots, releasing the base cations for uptake or leaching from the soil. We have calculated that about 250 milliequivalents $\cdot m^{-2} \cdot yr^{-1}$ of hydrogen ions are released into the soil by the root system of a 110-year-old stand of lodgepole pine, all of which are consumed within the soil because the flux of free acidity is very small (<1 mEq $\cdot m^{-2} \cdot yr^{-1}$). The root system efflux also far exceeds the hydrogen ion inputs via precipitation (7 mEq $\cdot m^{-2} \cdot yr^{-1}$).

Summary

Despite the low productivity of forests in the Rocky Mountain environment, biological activity plays a critical role in regulating the fluxes of water and major ions. Moreover, although much of the landscape is dominated by monospecific stands of lodgepole pine, these fluxes vary markedly among sites. Concomitant differences in soil texture and forest structure appear to be important factors that induce this variation, a result of their influence on soil water storage capacity and the mobility of ionic solutes in mineral soil. Water and nitrogen availability, along with a cool, short growing season, limit the amount of leaves and roots that can develop, which in turn regulate water flows, the generation of protons consumed in soil weathering reactions, and the supplies of organic matter for heterotrophic organisms. New environmental stresses and increasing pressures for intensive forest management dictate that a more complete understanding of the controls of material fluxes in natural and man-dominated ecosystems is needed. The lodgepole pine ecosystem, while relatively simple, provides a representative example of the complexity that can be involved.

Acknowledgments

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