# ECOSYSTEM STUDIES IN THE SUBALPINE CONIFEROUS FORESTS OF WYOMING

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# Ecosystem Studies in the Subalpine Coniferous Forests of Wyoming

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**Abstract**--An overview is presented on recent ecosystem studies in the Medicine Bow National Forest and Yellowstone National Park. Most of the research has focused on lodgepole pine forests. Hydrology, leaf area development, decomposition, nutrient dynamics, soil chemistry, landscape ecology, and the effects of tree harvest, fire, and mountain pine beetles have been emphasized.

The subalpine elevations of Wyoming mountain ranges are characterized by a mosaic of meadows, lakes, and forests dominated by various mixtures of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and aspen (*Populus tremuloides* Michx.). As in other parts of the Rocky Mountains, vegetation patterns are determined by environmental factors associated with elevation, topographic position, soil characteristics, and the history of disturbances including fire, logging, and outbreaks of the mountain pine beetle (*Dendroctonous ponderosae* Hopk.). On the warmer and drier sites lodgepole pine appears to form a stable community that persists until fuel accumulation makes the next fire inevitable (Romme and Knight 1981, Despain 1983). Elsewhere spruce and fir are the climax species, sometimes developing in the understory of pioneer lodgepole pine or aspen forests but in other cases invading directly following a burn or some other disturbance (Stahelin 1943, Romme and Knight 1981).

For many years research on the subalpine forests of Wyoming was focused on species composition, classification, and succession. Such studies are essential for providing the understanding required for sound resource management, but many questions pertaining to nutrient cycling and water flows were not being addressed. Of course, research at the nearby Fraser Experimental Forest was providing good information on forest hydrology, but more remained to be done. Recognizing the importance of such research for management, my colleagues and I began to study the subalpine forests of Wyoming from an ecosystem perspective. In this paper I will provide an overview of some of our results thus far.

Most of our research thus far has focused on forests dominated by lodgepole pine and has been done at the stand level rather than at the scale of the watershed. Originally we had hoped to find a watershed in Wyoming that could be studied in the manner of the Fraser or Hubbard Brook watersheds, but during the search we concluded that our watersheds were so heterogeneous (in terms of vegetation, soils, and geologic substrate) that it would be difficult to evaluate biotic effects on water and nutrient fluxes -- one of our primary interests. Instead we selected homogeneous stands of a few hectares as our ecosystems. Such stands had the advantage of being closer to the scale of an actual timber sale than whole watersheds, and we hoped that they would provide the opportunity to examine more precisely the effects of vegetation structure on ecosystem processes. Studying stands instead of watersheds has its problems (Knight et al. 1985), but we felt they could be resolved in the relatively simple lodgepole pine forest. Most of the research has been done in the Medicine Bow National Forest, 50 km west of Laramie, but several studies were conducted in Yellowstone and Grand Teton National Parks as well.

Many individuals have helped in the development of our research, including colleagues at neighboring universities and with federal agencies, but the following individuals deserve special recognition: James F. Reynolds, Ned Fetcher, William H. Romme, Steven W. Running, Timothy J. Fahey, John A. Pearson, Joseph B. Yavitt, and Howard E. Haemmerle. These graduate students, listed in order of degree completion, worked long hours for little reward other than a chance to make a contribution to forest science. To a very large extent, it is their results that are highlighted in this overview. I am also especially grateful for the cooperation extended to us by the staff of the Medicine Bow National Forest. Our research has been funded by the National Science Foundation, Wyoming Water Research Center, University of Wyoming - National Park Service Research Center, Department of Interior (Office of Water Research and Technology), and the Department of Agriculture (U. S. Forest Service, Rocky Mountain Forest and Range Experiment Station).

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## Stand Hydrology

The streams draining Wyoming watersheds are important as sources of water for the semiarid basins below, as habitat for a popular sport fishery, and as sources of nutrients and sediments in downstream reservoirs. Everyone recognizes that streamflow is affected by watershed vegetation, but little was known about the hydrology of lodgepole pine forest at the scale of single stands. Reynolds and Knight (1973) calculated the importance of forest floor interception following summer rains, concluding that in most years winter snowfall is the only source of water adequate to cause water outflow beyond the rooting zone. Normally, only one pulse of outflow occurs each year. Moreover, the primary source of water for the lodgepole pine is from snowmelt, as most rains are completely intercepted by the canopy and forest floor.

The amount of spring outflow from a stand is dependent on the storage capacity for snowmelt water created by evapotranspiration (ET) during the previous year. Transpiration is known to be a substantial part of ET, but few data were available for stands of Rocky Mountain coniferous forest. Fetcher (1976) found that lodgepole pine stomatal resistance could be an important factor reducing transpiration towards the end of the growing season and that the degree of control was greater on drier sites. This information added to a growing body of information on the water relations of lodgepole pine (Swanson 1967, Owston, et al. 1972, Johnston 1975). With the assistance of better instruments for measuring transpiration in the field, Fahey (1979) and Running (1980a, 1980b) were able to accomplish a more detailed analysis of lodgepole pine stomatal behavior in relation to environmental conditions. Kaufmann (1984a, 1984b) conducted similar research on lodgepole pine, subalpine fir, and Engelmann spruce in Colorado.

Understanding stomatal physiology is important for hydrologic studies, but extrapolating to the whole tree or forest is difficult. Our initial attempt to resolve this problem for lodgepole pine was with the use of whole-tree potometers (Knight, et al. 1981). Entire 100-yr-old trees, up to 26 cm d.b.h., were cut and suspended in reservoirs of water for periods of several days. Careful monitoring suggested that the rate of water loss from the reservoir was a reasonable estimate of tree transpiration. Tree diameter and maximum observed 24-hour uptake were highly correlated, with the largest trees transpiring 40-44 L on clear days in early summer. Maximum observed hourly uptake for the larger trees was 2.5 to 3.5 L, with total nighttime uptake being about 12% of 24-hour uptake. On overcast days potometer uptake was reduced by 30-34%. Transpiration data for trees of different sizes were used to estimate a total clear-day transpiration from the forest of 3.3 mm. Interestingly, a very dense "dog-hair" stand, with 14,000 trees/ha, had about the same leaf area index (7) and transpiration rate as an adjacent more open stand with 2,000 trees/ha and a much higher basal area/ha.

Our most recent analysis of lodgepole pine forest hydrology involved more detailed measurements and a stand-level computer simulation model (Knight et al. 1985). Eight contrasting stands were compared over a 3-year period. Estimates of actual ET for the period from early spring to late fall ranged from 21 to 53 cm, which was 33-95% (x= 73%) of total annual precipitation. For all stands and years, transpiration accounted for 50-61% of ET, and 9-44% of the transpiration occurred during the spring drainage period while snow still covered the ground (vernal transpiration, VT). Estimated VT and outflow varied considerably among the stands (fig. 1), with VT accounting for 4-20% of the snow water. We estimated that outflow beyond the rooting zone occurred only during the snow melt period and accounted for 0-80% of the snow water.

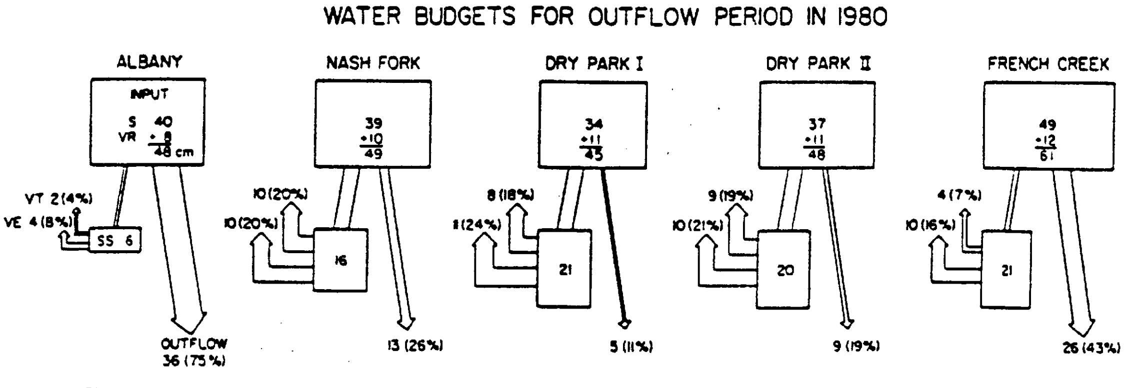

Figure 1.–Diagrams depicting the water budget of five contrasting stands of lodgepole pine forest during the 1980 outflow period (from the initiation of snow melt until the end of drainage). Units are cm-$H_2O$. See figure 2 for a generalized annual budget. The amount added to the value for the maximum snow water equivalent (S) is vernal rainfall (VR), i.e., rainfall that occurred during the snow melt period. The smaller boxes represent soil storage (SS) and are full at the end of the outflow period. Percentages in parentheses indicate the proportion of S + VR flowing via outflow, vernal transpiration (VT), and vernal interception (VE) during the outflow period (as estimated with a computer simulation model). From Knight et al. (1985); reprinted with permission of the Ecological Society of America.

Outflow could be reduced to zero under conditions of high VT, high soil storage capacity, high LAI, relatively slow snowmelt, and average or below snow water equivalent. The hydrology of deciduous aspen forests should be considerably different because they lack the potential for VT, but we have not yet studied this kind of vegetation in detail. Figure 2 contrasts the hydrology of a typical stand of Wyoming lodgepole pine to a stand of Douglas fir in Oregon.

In sum, our results are helping to quantify the generally accepted concept that stands differing in structure and environmental conditions experience different rates of water outflow at different times during the snow melt season, contributing differentially to stream hydrograph shape.

## Forest Leaf Area

Leaf area, whether evergreen or deciduous, is an important determinant of transpiration rate as well as photosynthesis and aerosol impaction, but until recently little information has been available on this important forest parameter. Usually leaf area is expressed as leaf area index (LAI, $m^2$ leaf surface area/$m^2$ ground surface area). Deciduous forest LAI is often calculated for a single leaf surface while all surfaces are commonly included for the LAI of coniferous forests.

LAI is a stand feature that varies with habitat type and is, of course, affected by silvicultural practices. Utilizing our computer simulation model, which includes LAI as a key variable, we observed that increases in water outflow following any kind of disturbance is proportional to the decrease in leaf area (Knight et al. 1985). Removal of leaf area appears to be more important than reductions in tree density or basal area (Knight et al. 1981).

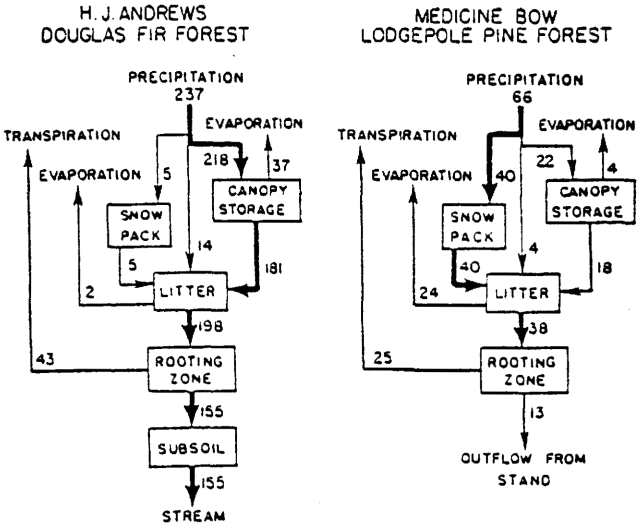

**Figure 2.**–Generalized annual hydrologic budgets for the H. J. Andrews Douglas fir forest in Oregon and a typical stand of lodgepole pine forest in the Medicine Bow Mountains. Numbers are cm-$H_2O$ per year. The figure for Douglas fir is redrawn from Sollins, et al. (1980), and is used with permission of the Ecological Society of America.

These observations led to a study designed to determine how LAI changes with site quality and forest age (Haemmerle et al., submitted). Forty-three stands in the Medicine Bow Mountains were divided into two series, one in which lodgepole pine appeared to be the long-term dominant and another where subalpine fir was common. A maximum LAI of 16 was calculated for a stand from the pine series, while 39 was the maximum LAI for the fir series. Maximum leaf area in the pine and fir series is reached in 125-200+ and 200-300+ years, respectively, with more time required as site quality declines. Differences in maximum leaf area and the timing of this maximum probably are caused by tree establishment patterns, physiological differences among species, and site water balance. The relationship of LAI to important ecosystem processes and the fact that LAI is now being estimated more easily (Pearson et al. 1984, Haemmerle et al., submitted), even from satellites (Running 1986), suggests that it can and should be used more frequently in forest management decisions.

## Nutrient Conservation and Outflow

Water passing through the soil profile, beyond the root zone, carries dissolved nutrients which are losses to the terrestrial ecosystem but inputs to ground and surface water systems. Considering that a large proportion of litter decomposition occurs during the winter under snow (Fahey 1983), and that the only pulse of water adequate for leaching occurs in the early spring before vigorous tree growth, we wondered if each year there is a "spring flush" of nutrients beyond the rooting zone that tends to maintain the soils in a nutrient-deficient state. Nutrient outflow/atmospheric input ratios were estimated, with the results being consistently < 1.0 for N; consistently > 1.0 for Ca, Na, and Mg; and ranging from 0.3 to 2.0 for P and 0.2 to 3.3 for K. These results suggest that N usually is accumulating in lodgepole pine forest ecosystems, even during years of heavy snowpack and and large volumes of outflow, probably due to microbial or vascular plant uptake; and that P and K may accumulate on some sites. Weathering, another input for elements other than N, could not be estimated for our analysis and, therefore, the ratios for these elements are difficult to interpret.

Simple estimates of nutrient inputs and outputs are useful for ecosystem studies, but they ignore the processes involved. To improve our understanding, several studies were initiated on litter decomposition, nutrient retention, and other factors affecting soil water chemistry. The nutrient dynamics of aboveground detritus were studied by Fahey (1983), who found that decaying leaves and wood actually increase in N, P, and Ca during some stages of decomposition. For example, nitrogen content of decaying boles doubled between 30 and 55 years following tree death before beginning a slow decline after the C/N ratio of the wood drops to a critical level (Fahey and Knight 1986). This and other research suggests that N is one of several limiting factors for the lodgepole pine ecosystem, whether for the microbes or vascular plants, and that decaying logs may be an important source of N for sustained site productivity. Dead wood resulting from the last disturbance, usually a fire in the case of our stands, was a major nutrient storage compartment, sometimes exceeding other forest floor components by several-fold in 80-100 yr old stands. Silvicultural practices that lead to significant reductions in the amount of woody detritus may be detrimental to long-term site productivity.

Ecologists and managers commonly focus on aboveground biomass, but Pearson et al. (1983) estimated the amount of root biomass as well in Wyoming lodgepole pine forest. They found that the average proportions of biomass in boles, branches, foliage, woody roots, and fine roots were 61, 7, 6, 20, and 6%, respectively, with root/shoot ratios ranging from 0.27 to 0.50. The highest ratios were in the more dense stands. Interestingly, the proportion of biomass in fine roots was about equal to the proportion in leaves. Ninety percent of the root biomass was within 40 cm of the surface in lodgepole pine forests, though tap roots were observed down to a depth of 2 m or more. Whereas Fahey (1983) studied detrital decomposition above ground, Yavitt and Fahey (1982) estimated rates of root decomposition. Despite being in closer proximity to soil moisture and soil microbes, woody roots appeared to decompose no more rapidly than aboveground boles of comparable size. Both may last a century or more. Complete mineralization of leaves requires 12-22 years, depending on site conditions (Fahey 1983).

As decomposition occurs, the soil solution is enriched in a variety of ions that could be leached beyond the rooting zone. For a time we thought that N was retained within the forest floor, due to the extremely low concentrations of $NH_4^+$ and $NO_3^-$ in forest floor leachate, but subsequent studies revealed that the major transfer of N from detritus to mineral soils occurred in soluble organic compounds (Yavitt and Fahey 1985, Fahey et al. 1985, Yavitt and Fahey 1986). However, despite relatively high N fluxes to the mineral soil in organic compounds, little N of any kind could be detected in water samples collected near the bottom of the rooting zone. Observing that finer textured soils had lower N concentrations than more coarse soils, Fahey and Yavitt hypothesized that adsorption onto colloids was an important abiotic mechanism for N immobilization.

Annual N inputs from fixation and precipitation appear to be very low in lodgepole pine forests (fig. 3), as are decomposition rates, and consequently N could be an important limiting factor along with the short, cool, sometimes dry growing season (Fahey and Knight 1986). Fahey et al. (1985) found that about 90% of the N pool was in the soil organic matter, with 6% and 4% in aboveground detritus and living biomass, respectively. They hypothesized that some of the N available for microbial growth in the detritus was translocated to the forest floor from the mineral soil by fungal mycelia, and that a portion of the N required for tree growth was obtained by translocation from senescing leaves to twigs (as reported for other conifers, Gosz 1980). Of course, the slowly decomposing forest floor and soil organic matter are important sources as well. David Coleman and his associates, from the University of Georgia and Colorado State University, are studying the interspecific microbial interactions affecting decomposition in one of our Medicine Bow study areas.

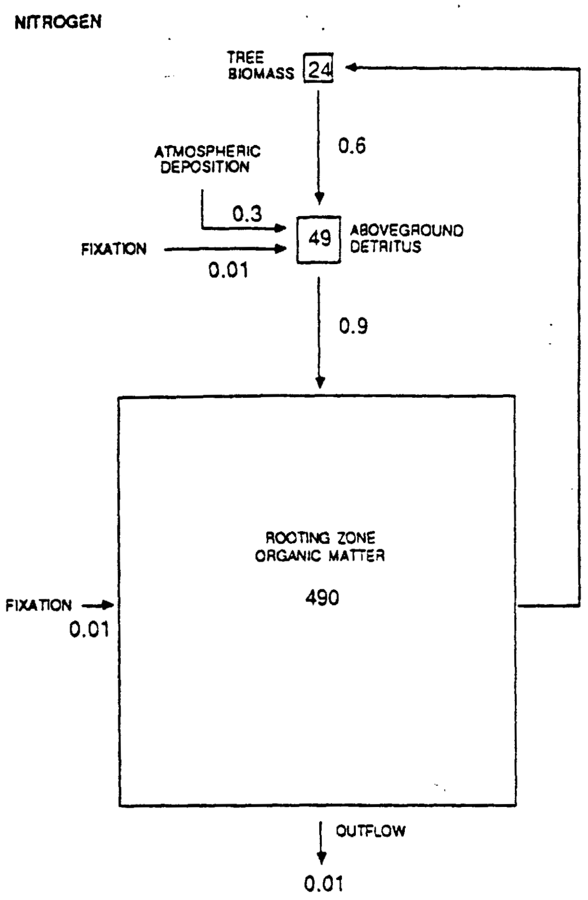

**Figure 3.**–Generalized annual nitrogen budget for a typical 100-yr-old stand of lodgepole pine forest in the Medicine Bow Mountains, drawn from data presented in Fahey et al. (1985). Numbers in boxes and by arrows are $g/m^2$ and $g/m^2/yr$, respectively. Much of the N in the rooting zone compartment is in organic matter that apparently is not readily decomposable, as the mean tissue N concentration of the foliage is low (0.7%) compared to other coniferous species. Note (1) that N inputs to the ecosystem are larger than N losses, suggesting that N is accumulating, probably due to being a limiting factor for the biota; and (2) that the tree uptake estimate is larger than the sum of the input estimates to the rooting zone, which suggests that the soil N pool is gradually being depleted in this aggrading forest. Replenishment of the soil N pool may occur as the forest ages further (Fahey and Knight 1986).

Other chemical fluxes have been studied, with the observation that the slightly acidic rainfall (mean pH = 4.6) is commonly neutralized to pH 5.2, probably by basic, microscopic aerosols (dry deposition) from upwind deserts (Fahey and Knight 1986). The neutralizing capacity of forest soils in the Medicine Bow Mountains is substantial due to the accumulation of such aerosols, an observation relevant to concerns being expressed about acid precipitation (Reiners et al., in preparation). Potential nutrient loss via leaching is accelerated by acidic soil water (Fahey et al. 1985), whether natural or anthropogenic, but biotic sources of hydrogen ions appear to be more important than precipitation at the present time (Fahey and Knight 1986).

### Effects of Disturbances and Succession

A widespread technique for studying ecosystems is to monitor changes in energy, water, and nutrient fluxes following disturbances to the biota. Sometimes natural disturbances such as fires or insect outbreaks can be used, but more controlled "treatment" perturbations and computer simulation "experiments" are other options. All three have been used in our research. Most have been done at the scale of a single stand covering several hectares, but others have focused on landscapes.

Our initial studies at the stand level involved simulation of a clearcut using the hydrologic model H2OTRANS (Running 1984, Knight et al. 1985). Computer simulations suggested that the increase in water outflow is, to a large extent, dependent on the amount of leaf area removed. Of course, timber harvesting is a standard tool for increasing streamflow.

Another approach was tree thinning. A 20 x 40 m plot in our Fox Park stand was thinned by tree girdling and another comparable plot was clearcut. A control stand was located within 40 m on the same soil type. The experiment provided an opportunity to examine the effects of removing two levels of leaf area and killing different numbers of trees. The thinning treatment was designed to duplicate, to the extent possible, the effects of a mountain pine beetle outbreak and included painting the exposed sapwood with spores of blue stain fungi -- the type of fungi that are also introduced by the beetles and which are believed to account for the rapid demise of the shoots (we observed that trees that are only girdled may live for 5 years or more). The clearcut and thinning treatments were applied in 1982, with the hypothesis that increases in water and nutrient outflow would be proportional to the amount of leaf area removed (clearcut > thinned > control).

The results for nutrient outflow were not what we anticipated (Knight et al, in preparation). Killing 60% of the trees by girdling, mostly the larger trees (as often occurs following a bark beetle infestation), had very little if any effect on the outflow of N, K, and Ca. In contrast, killing all of the trees via clearcutting increased N outflow by 40 times, K outflow by 3 times, and Ca outflow by 3 times. A similar pattern was observed for the concentrations of nitrate and total nitrogen in soil solutions. Hardly any concentration differences were observed when comparing the control and girdled stands, but nitrate concentrations were commonly > 100 times higher in the clearcut stand.

These results are interesting from at least two perspectives. First, we wondered if the high C/N ratios of the forest floor might negate the importance of N uptake by trees for limiting N outflow beyond the rooting zone. This proved not to be the case, as an abundance of leachable nitrate was observed in the clearcut stand. Apparently nitrification bacteria were able to produce more nitrate when competition for N by the trees was eliminated. While somewhat warmer soil surface temperatures would have existed in the clearcut stand, it seems doubtful that this difference alone could produce the great differences observed.

Secondly, the results of our experiment imply that the surviving trees in a thinned stand are able to absorb the nutrients formerly being used by the "dead trees." Our first inclination was to think that the roots of adjacent trees are so intermingled that as the roots of one tree die, the roots of nearby trees grow to fill any root gaps that are created. This may be the case, but other explanations are possible. For example, the root systems of adjacent trees are commonly grafted in pine forests (Graham and Bormann 1966). Is it possible that the root system of the surviving tree could somehow sustain through grafts, or mycorrhizal connections, the root system of the girdled tree? Do root systems become dysfunctional at the same time as the shoot dies? Are root gaps created at the same time as canopy gaps? Research on these questions is currently underway in one of our lodgepole pine stands. The results should clarify root growth dynamics following disturbances and the importance of root growth for regulating nutrient outflow.

Ecosystem development or change following disturbance is a topic of widespread interest among ecologists. The comparison of stands of different ages but on similar sites is a common approach for addressing this topic, but Pearson et al. (in press) attempted to use the tree ring record in the living and dead trees to examine biomass and nutrient accumulation during the history of the relatively simple lodgepole pine forest in our area. Changes in dead wood, forest floor, and live tree biomass (including roots) were estimated separately. Maximum total biomass accumulation rates of 2.5-3.2 metric tons/ha/yr were reached 40-60 years after fire in even-aged stands, but an uneven-aged stand developing on a former meadow did not achieve a maximum accumulation rate (1.5 tons/ha/yr) until after 80 years. Biomass increment occurred primarily in the living vegetation compartment throughout stand development, except for brief episodes of increment in the dead wood compartment associated with the mortality of large trees. Maximum forest floor biomass increment generally was about 25% as high as maximum living biomass increment. It is difficult to say when biomass accumulation rates will approach zero, i.e., when net primary productivity is balanced by heterotrophic respiration, and indeed the stand may burn before this happens. With sufficient time fuels develop to the point where fires become inevitable, whether the ignition source is lightning or humans.

With regard to nutrient accumulation, Pearson et al. (in press) suggest that the forest floor is the major biomass compartment accounting for the immobilization of N, P, Ca, and Mg, at least during the first 40-80 years of stand development. Living biomass appears to be next most important, especially after 60-80 years, and accounted for most K accumulation throughout stand development. The importance of dead wood is suggested as well, especially while the stand is about 20-80 years old and when dead wood from the previous forest is still an active site for nutrient immobilization. Nutrient increment rates remained positive even in the oldest stand (about 200 years old).

## Mountain Pine Beetle Ecology

As noted, outbreaks of mountain pine beetle are a natural disturbance in many western coniferous forests. A common notion is that older stands become more susceptible to the bark beetles, which create canopy gaps that release the growth of smaller suppressed trees, thereby maintaining a higher level of primary productivity than would occur otherwise. The interaction brings to mind cybernetic systems with feedbacks that control certain processes, in this case photosynthesis. Romme et al. (1986) examined this question in Yellowstone and Grand Teton National Parks, observing that indeed annual wood production per hectare usually returned to pre-outbreak levels or exceeded them within 10-15 years. However, their estimates of annual wood production over the last 70-80 years indicated that the beetle outbreak introduced more variation in productivity than would have existed in their absence. They concluded that the mountain pine beetle do not function as cybernetic regulators, at least in the strict sense. Nevertheless, because of the rapid recovery of annual wood production, they suggested that the effects of the beetles could be considered generally benign or even beneficial in some situations (e.g., increased understory growth may favor certain animals).

Could outbreaks of the mountain pine beetle affect the probability of crown fires? In another study in Yellowstone National Park, Romme et al. (in preparation) concluded that, while flammability may increase during the first year or two after an infestation because of dead leaves still on the trees, the risk of destructive fire during years 2-20 may be lower because (1) the leaves and many twigs fall off, reducing fuel continuity, and (2) the proportionate increase in forest floor fine fuels is small by the time the forest is old enough to be susceptible to a beetle outbreak. Accelerated growth in understory trees may increase fuel continuity and fire risk after 20 years.

Other studies have been done on forest fire ecology in Wyoming (Loope and Gruell 1973, Despain and Sellers 1977, Bartos and Mueggler 1979, Romme and Knight 1981, Romme 1982, Despain 1983, 1985; Knight 1987; Stottlemeyer 1987). Some of these studies focus more on community succession than on energy-, water-, and nutrient-related processes, but all aspects of disturbance ecology are relevant to understanding ecosystems.

## Landscape Ecology

In recent years ecologists have become more conscious of the scale at which their research is being done. Some focus on leaves or other appendages; others focus on whole organisms, and still others on communities, i.e., rather arbitrarily defined assemblages of organisms. As usually addressed, the ecosystem scale is comparable to the community scale. The study of ecosystems always involves addressing community and individual organism characteristics to some degree but, as should be apparent in this paper, the focus is more on energy, water, and nutrient fluxes rather than on species composition. Community and ecosystem research usually involves the study of relatively homogeneous stands that are more or less a few hectares in size, or processes that are important at that scale. At least two other scales can be studied as well, i.e., the landscape scale consisting of a mosaic of communities over an area of a square kilometer or larger (more or less), and the biospheric scale where data are collected for the whole earth.

Landscape studies have great relevance to ecosystem research, and vice versa. Using aerial photos, the tree ring record, and computer simulation techniques, Romme (1982) was able to date and map the occurrence and areal extent of fires during the last few centuries in a 73 km$^2$ tract of subalpine forest and meadows in Yellowstone National Park. He demonstrated how the proportion of this landscape in young, middle, and older stages of succession changed considerably through time (fig. 4). Romme is now working with Don Despain, Park Research Biologist, to determine if larger portions of the Park are in what has been referred to as a "shifting mosaic steady state" (Bormann and Likens 1979). Romme could find no evidence that fire suppression had affected the subalpine forest mosaic that he studied, primarily because large fires have occurred there at long intervals of 300-400 years and fuel accumulation since Park establishment generally has not been sufficient to support large fires. In a subsequent paper, Romme and Knight (1982) speculate on the implications of shifting mosaics for water and nutrient out-

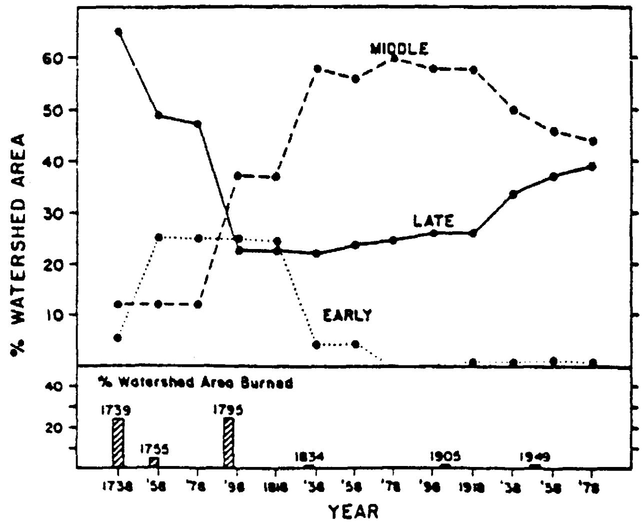

Figure 4.–Percent of a 73-km$^2$ area in Yellowstone National Park covered by forests in early, middle, and late stages of succession, and the percent of the area burned in a series of fires from 1738 to 1978. The shift occurring in the predominant successional stages suggests that the area is not in a "shifting mosaic steady state." From Romme and Knight (1982); reprinted with permission of the American Institute of Biological Sciences.

flow, lake productivity, song birds, and elk. Knight (1987) reviewed the effects of coniferous forest mosaics on flammability and the spread of parasites.

The landscape scale seems highly relevant to the management of National Forests and wilderness areas, since roads, campgrounds, timber harvesting, habitat improvements, and fire suppression are creating new mosaics. In some areas forest fragmentation is occurring (Harris 1984), while elsewhere there is the potential of landscape homogenization due to fire suppression (Habeck 1985). Landscape architects have been employed to design aesthetically pleasing landscapes, but what is the ecological impact of different landscape designs? Is there an ecological rationale for prescribing one vegetation mosaic over another? Optimal mosaics apparently can be designed for water yield (Leaf 1975) and for certain wildlife species (Thomas et al. 1976, Harris 1984), but less is known about the effect of the mosaic on, for example, biotic diversity, maintaining a certain level of primary or secondary productivity, the spread of fire or insect epidemics, and nutrient fluxes that could affect site productivity or streamwater quality. Large National Forests in the Rocky Mountain states provide excellent locations for such research because the landscape mosaics are being manipulated now and will be for many years to come.

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Charles A. Troendle
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