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WATER AND NUTRIENT OUTFLOW FROM CONTRASTING LODGEPOLE PINE FORESTS IN WYOMING[1]

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Abstract. Factors affecting water and nutrient outflow beyond the rooting zone were studied during a 3-yr period, using data from eight contrasting stands of lodgepole pine (*Pinus contorta* ssp. *latifolia*) forest in southeastern Wyoming and the output of a hydrologic simulation model (H2OTRANS) based on tree physiology. Nutrient outflow during a specific time period was estimated by multiplying simulated water outflow times element concentrations in the soil solution, the latter determined from samples collected periodically near the bottom of the rooting zone.

Estimates of actual evapotranspiration (*ET*) for the period from early spring to late fall ranged from 21 to 53 cm, which was 33–95% ($\bar{x}$ = 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 (vernal transpiration, VT). Estimated VT and outflow varied considerably among the stands, with VT accounting for 4–20% of the snow water. Outflow occurred only during the snow melt period and accounted for 0–80% of the snow water. Snow water equivalent varied annually by 300% or more. Nutrient outflow from the different stands also varied greatly. Ratios between simulated annual outflow and atmospheric inputs (bulk precipitation) were consistently >1.0 for Ca, Na, and Mg; were consistently <1.0 for N; and ranged from 0.3 to 2.0 for P and from 0.2 to 3.3 for K. Much of the variability in water and nutrient outflow can be attributed to the degree of biotic control, with water outflow affected by a different combination of factors than nutrient outflow. H2OTRANS was used to simulate the effects on outflow of different snow water equivalents and different total leaf areas. One result of the simulations was that nitrogen appears to be retained even at the highest levels of water outflow. Another was that increases in water outflow following reduction in leaf area were proportional to the leaf area removed.

The results indicate that stands differing in site or habitat type experience different rates of water and element losses at different times during the snow melt season, and contribute differentially to streamwater quality and hydrograph shape. Factors affecting outflow are discussed in the context of successional trends, common perturbations including timber harvest, and hypotheses pertaining to nutrient conservation in terrestrial ecosystems. Nutrient retention in the snow-dominated lodgepole pine ecosystem appears to be primarily dependent on evergreen leaf area, duration of the VT period, and high carbon/nutrient ratios of the forest floor. Net losses of limiting nutrients probably occur primarily in pulses after abiotic perturbations such as fire.

Key words: computer simulation; evapotranspiration; forest biomass; forest hydrology; habitat types; immobilization; leaf area; nitrogen; nutrient input; nutrient outflow; Pinus contorta; *Rocky Mountains; transpiration; Wyoming.*

INTRODUCTION

Many studies on water and nutrient movement in terrestrial ecosystems have focused on outflow, partly because losses can be accelerated by some land uses but also because there are various popular hypotheses concerning the balance between nutrient input and output. For example, nutrient balance has been related to such ecosystem characteristics as successional status and diversity (Odum 1969), transpiration (Bormann et al. 1969), soil respiration and rainfall patterns (McColl 1973), biomass increment (Vitousek and Reiners 1975), microbial uptake (Stark 1972), and certain element-specific processes such as nitrification (Likens et al. 1977). Each hypothesis appears to be correct in certain situations but, as with any ecosystem phenomenon, water and nutrient losses are influenced by many factors that vary through time and space. Our objective was to analyze the factors affecting water and nutrient outflow from small, relatively homogeneous stands of Rocky Mountain forest dominated by lodgepole pine (*Pinus contorta* ssp. *latifolia* [Engelm. ex Wats.] Critchfield). The results are discussed in the context of forest management and current hypotheses on water and nutrient fluxes.

Factors affecting the input-output balance of water and nutrients have often been studied using the small-watershed approach. This approach has been extremely useful where impervious substrata exist. However, it is often more difficult to examine in detail the

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factors regulating nutrient loss from specific areas within watersheds because streams integrate outflow from the patches and gradients that invariably exist (Rutter 1968). Hydrologists, recognizing that runoff from two equal portions of a watershed may be quite different, have developed the concept of contributing area or variable source area (Rawitz et al. 1970). Furthermore, the elemental composition of stream water is affected by stream bank erosion, soil characteristics below the root zone, bedrock composition, and stream organisms, in addition to nutrient loss from the terrestrial ecosystem under study.

We chose to study stands instead of watersheds because of our interest in examining the effects on outflow of varying edaphic and vegetative conditions. The principal problem encountered with the stand approach is accurate estimation of water and nutrient outflow, even from stands that are small and homogeneous. Our approach to this problem has been to develop a stand-level simulation model (H2OTRANS) that calculates water outflow as the difference between hydrologic inputs and the sum of evapotranspiration and storage. The model integrates the effects of air temperature, atmospheric humidity, solar radiation, precipitation, soil storage capacity, and stand leaf area. In this paper we describe the development and validation of this model, and the results we obtained by using the model to examine water and nutrient outflow from lodgepole pine forest stands with contrasting characteristics. Nutrient outflow was calculated as the product of water outflow and nutrient concentrations in the soil solution near the bottom of the rooting zone.

Lodgepole pine forests in the Rocky Mountains have several characteristics that were relevant to the planning of our research. First, snow melt and early spring rain are normally the only sources of water adequate to cause nutrient leaching beyond the rooting zone (Reynolds and Knight 1973). Thus, outflow usually occurs only once during the year, in what can be referred to as the snow melt or spring flush period. Under these conditions, nutrient loss is partly dependent on the quantity of nutrients available for outflow at the end of the winter. Organic matter is mineralized under the snowpack (Fahey 1983), and large amounts of nutrients are potentially available for leaching during the spring flush period, a time when root uptake is probably slow.

Another feature is the great variability in leaf area, stand structure, and soil storage capacity. Tree density may vary from <300 to ≥15 000 trees/ha, and the range in the leaf area index of mature stands is as great as from 4 to 14, or greater (Moir and Francis 1972). We have observed lodgepole pine forests on both deep glacial till soils (>3 m) and coarse, shallow soils derived from a granitic substrate (<0.5 m). Although most of the root system occurs in the upper 0.4 m (Pearson 1982), tap roots extend down to 2 m or more where bedrock permits, and the soil profile dries steadily during the summer to this depth or below (Dahms 1971, Johnston and Doty 1972, Johnston 1975). On many sites soil water is depleted in late summer and trees come under water stress (Fetcher 1976), with the soil remaining dry and usually unfrozen during the winter. Modelling the restriction of transpiration by stomatal control following water stress development has been one of the challenges in developing H2OTRANS.

A third feature of the lodgepole pine ecosystem is the capacity for vernal transpiration (VT), i.e., transpiration during the snow melt period and immediately after, while deep drainage continues. Several studies have shown that sapwood recharge and transpiration occur during this time (Swanson 1967, Owston et al. 1972, Fahey 1979). Our research was designed, in part, to estimate (1) the proportion of the snowpack that can be transpired during the snow melt period, thereby reducing outflow; and (2) the conditions of snowfall, water storage capacity, and VT that reduce the outflow of water and nutrients to zero. Outflow may be an annual event in some stands but less regular in others.

STUDY AREA AND METHODS

Description of study area

Eight stands of lodgepole pine forest in the Medicine Bow Mountains of southeastern Wyoming were selected to represent the variety of stand structure and soil characteristics in the area. Data on water, nutrients, climatic characteristics, and biomass in these stands were collected during the period 1978–1982. Each stand was ≈1–3 ha in area and relatively homogeneous in forest and soil structure. Six of the eight stands were virgin forest. The stands were located at elevations of 2800–3050 m, and represented four ages (17, 70, 110, 240 yr); tree density was 375–14 640 stems/ha, and leaf area indices (LAI, all surfaces) ranged from 1 to 10. Understory vegetation was sparse in all stands except French Creek and Rock Creek (Table 1). In two instances the stands occurred in adjacent pairs on the same soil type: a 20-yr-old stand (Chimney Park I) that had originated after a clearcut, next to a 110-yr-old uncut forest (Chimney Park II); and two adjacent 110-yr-old stands, one very dense (Dry Park II, 14 640 trees/ha) and the other more open (Dry Park I, 2217 trees/ha). These pairs provided the opportunity to study the effect of stand structure on water and nutrient outflow without the variability introduced by different climatic or soil characteristics.

The soils of the eight study areas were variable (Table 2); both Inceptisols (Lithic Cryochrepts) and Alfisols (Typic Cryoboralfs) were observed. Soils at three of the sites (Nash Fork, Rock Creek, and French Creek) were derived from Quaternary glacial alluvium, whereas soils at the other sites were derived from either Precambrian granite (Albany), coarse outwash (Dry Park), or schist (Chimney Park). Soil depth ranged from ≈0.5 m on

Table 1. Vegetation characteristics of the eight study areas in the Medicine Bow Mountains, Wyoming.

Stand feature	Two adjacent stands at Chimney Park		Two adjacent stands at Dry Park		Albany	Nash Fork	French Creek	Rock Creek
	I	II	I	II				
Age (yr)	17	110	110	110	Uneven	110	240	75
Tree density (stems/ha)	4518	9700	2217	14 640	1920	1850	420	1280
Height of canopy top (m)*	2.3	6.1	11.9	5.6	7.3	10.4	15.1	8.6
Tree basal area (m^2/ha)	1	55	42	50	20	64	37	26
Tree sapwood basal area (m^2/ha)*	1	25	25	36	14	28	12	18
Tree sapwood volume (m^3/ha)*	5.0	94.5	161.4	113.9	67.3	187.7	100.5	115.2
Tree biomass (Mg/ha)								
Leaf	1.5	10.0	9.7	8.4	5.6	11.4	6.9	12.2
Total	4.8	170.0	171.7	144.9	76.1	174.8	174.7	98.4
Understory cover (%)	5	2	1	1	2	15	35	32
Leaf area : mass ratio (cm^2/g)†	89.1	87.7	74.9	84.3	69.6	87.2	64.5	73.2
Leaf area index (m^2/m^2)*	1.3	8.8	7.3	7.1	3.9	9.9	4.5	9.0

* Stand parameters for H20TRANS; see Study Area and Methods: Estimating Outflow.
† Kaufmann and Troendle (1981) calculated a value of 95.2 for *Pinus contorta* in Colorado.

the granite at Albany to >2 m on the glacial alluvium, and maximum water storage capacity in the soils ranged from 6 to 22 cm (Table 3).

Climatic characteristics

The climate throughout the Medicine Bow Mountains is characterized by long, cold winters and short, cool summers, with mean daytime temperature and relative humidity in July of ≈20°C and ≈25%, respectively. Snow normally begins to accumulate by the end of October, and usually the stands are not snow-free until early June or later (depending on the amount of snow, elevation, LAI, and aspect). Total precipitation in the stands ranged from 41 to 90 cm with ≈68% of the annual precipitation coming as snow (Table 3).

An instrument tower was placed in each stand. It supported a ventilated shelter (painted white) containing a hygrothermograph mounted at mid-canopy. An actinograph and standard precipitation gauge were mounted either at the top of the tower above the canopy or on a small platform in a nearby, unobstructed opening. Precipitation was measured within 24 h after each rainfall event (>0.2 cm), and the hygrothermographs were serviced and calibrated weekly from late April or early May until mid-October. Temperature and relative humidity readings of the hygrothermograph were rarely in error by more than 2° and 5%, respectively. The actinographs were calibrated once at the beginning of each field season. Data gaps caused by pen skips or clock malfunction were filled with data from the nearest stand (usually 2–5 km distant). Temperature, humidity, and solar radiation data were summarized as mean hourly values, and rainfall was recorded as the sum occurring on a particular Julian date.

Table 2. Some soil characteristics of the eight study areas in the Medicine Bow Mountains, Wyoming.

Soil feature	Two adjacent stands at Chimney Park	Two adjacent stands at Dry Park	Albany	Nash Fork	French Creek	Rock Creek
Depth (m)	1–2	>2	0.5	>2	>2	>2
pH at 0–15 cm*	5.7	5.5	5.5	5.5	5.3	5.0
Organic matter at 0–15 cm (% dry mass)†	6.3	8.3	5.8	7.4	9.3	7.0
Bulk density at 0–30 cm (g/cm^3)‡	1.53	1.47	1.32	1.40	1.22	1.05
Geologic substrate	schist	glacial alluvium	granite	glacial till	glacial till	glacial till
Soil type	Inceptisol (lithic cryochrept, coarse loamy)	Alfisol (typic cryoboralf, loamy skeletal)	Inceptisol (lithic cryochrept, loamy skeletal)	Alfisol (typic cryoboralf, fine loamy)	Alfisol (typic cryoboralf, loamy skeletal)	Inceptisol (typic cryochrept, fine loamy)

* Measured as a 1:1 soil water suspension (Jackson 1958).
† Dry ashing at 600°C (Jackson 1958).
‡ The mean of five pits, using the excavation method (Blake 1965).

TABLE 3. Elevation and hydrologic characteristics of the eight study areas in the Medicine Bow Mountains, Wyoming.

	Two adjacent stands at Chimney Park		Two adjacent stands at Dry Park					
Stand feature	I	II	I	II	Albany	Nash Fork	French Creek	Rock Creek
Elevation (m)	2730	2730	2750	2750	2750	2900	2970	3050
Snow melt coefficient (cm/°C)	0.0100	–	0.0100	0.0070	0.0110	0.0054	0.0110	0.0096
Maximum rate of water flux from zone A to zone B (cm/h)	–*	–	0.100	0.100	0.100	0.100	0.100	0.010
Maximum rate of water flux from zone B to outflow (cm/h)	–	–	0.017	0.021	0.100	0.100	0.200	0.010
Maximum available storage (cm)								
Forest floor	0.2	0.4	0.3	0.4	0.2	0.5	0.5	0.3
Root zone A	–	–	7.5	7.8	4.0	5.3	5.0	3.7
Root zone B	–	–	14.0	12.0	1.6	11.0	16.0	7.9
Sapwood	0.03	0.9	0.9	0.7	0.4	1.1	0.6	0.7
Foliage	0.002	0.06	0.07	0.05	0.03	0.08	0.04	0.05
Maximum snow water equivalent (cm), with total annual precipitation (cm) in parentheses†								
1977	–	–	18 (–)	20 (–)	–	–	–	33 (–)
1978	–	–	23 (–)	24 (–)	–	42 (–)	89 (–)	–
1979	25 (41)	27 (43)	35 (63)	42 (70)	47 (72)	47 (71)	49 (79)	72 (90)
1980	32 (58)	30 (56)	34 (60)	37 (63)	40 (63)	39 (66)	49 (80)	55 (75)
1981	10 (–)	10 (–)	14 (43)	14 (43)	19 (45)	28 (56)	31 (61)	–

* – indicates no data.

† Total precipitation estimates do not include snowfall intercepted or sublimated in the forest canopy.

Soil temperature at 0.25 m was measured periodically with a bimetallic probe to determine seasonal trends.

Biomass distribution and LAI

The biomass values in Table 1 were estimated using standard dimension analysis techniques on a total of 80 trees harvested from the various stands (Pearson et al. 1984). Foliage, branch, bole, and root masses were estimated separately. Sapwood volume was calculated from measurements of stem height, basal area, sapwood width (from inside bark) and heartwood diameter. Leaf area for a stand was calculated by multiplying total leaf mass by the fresh leaf surface area per gram of dry mass, which in turn was determined separately for each stand as follows. Ten samples, each of 50 fresh needles, were collected randomly from each stand and measured for length of the green portion (to nearest millimetre) and mid-length diameter (to nearest 0.1 mm with a vernier caliper). The fascicles were then dried for 48 h at 100°, cooled in a desiccating cabinet, and weighed to the nearest 0.1 mg. Leaf area per needle was calculated using the formula, Area = $(\pi dl + 2\,dl) \times 0.94$, where d is the needle diameter and l is the length. The formula is that for a split cylinder, with a correction factor of 0.94 to account for needle taper (Waggoner and Turner 1971). The values ranged from 64.5 to 89.1 cm^2/g (Table 1).

For root biomass, two to five trenches each 4–5 m long were dug by backhoe as deeply as possible (usually down to 2 m) in each stand. The distribution and mass of lateral root biomass was then estimated using a planar intersect technique (Pearson et al. 1984); root crown and fine root mass were determined by excavation. The trenches were also used for determining soil characteristics. Forest floor biomass was estimated as the combined mass of the 01 and 02 layers (Fahey 1983).

Snow water equivalent and water storage capacity

Water equivalent of the snowpack (in centimetres) was monitored in each stand at 5–10 d intervals, using a calibrated Montrose snow sampler. Data collection began in March or April, prior to the initiation of snow melt, and continued until the snow disappeared. At least 20 snow cores were weighed on each sampling date, a sample size which usually provided a standard error of <10% of the mean. The data were used to estimate maximum water equivalent in the snowpack and the rate of snow melt for each stand during the 3-yr study period. Snowfall that occurred during the snow melt period but after the maximum snowpack measurement was treated as a rainfall event (vernal precipitation, VP). No attempt was made to measure snow interception or sublimation in the forest canopy, so our values for total annual precipitation are minimum estimates. We assumed no water input by lateral flow or by capillarity from below the rooting zone, but this was subsequently found not to be true for three stands. Because we did not measure this input, hydrologic budgets for these stands could not be calculated.

Water storage capacity was measured in six compartments: leaves, sapwood, forest floor, canopy, surface soil (0–0.4 m), and subsurface soil (>0.4 m, down to 2.0 m wherever possible). Leaf, sapwood, and forest floor storage were estimated as the difference between the amount of water in each when maximally hydrated, shortly after snow melt, and the amount after an extended period with no rain. Throughfall was estimated using 25 randomly located collectors in four of the stands; canopy storage was calculated as the difference between throughfall and total rainfall, expressed for modelling purposes as centimetres of water per square centimetre of leaf area. Stemflow in our stands was observed very infrequently and therefore was not measured.

Aluminum tubes were installed in the soil (8–12 tubes per stand) to allow water measurement by neutron thermalization (Gardner 1965) with a Campbell-Pacific neutron probe. Holes were drilled with a pneumatic rock drill using a 6.4-cm bit, after which the tubes were tamped firmly into place using soil from a nearby trench. Probe readings were taken at 20-cm depth intervals. Using the manufacturer's calibration curve, volumetric soil water content was estimated for the surface soil and subsoil at the time of saturation (within 48 h after the snow-free date) and then biweekly until late September or early October, when the soil profile was driest. Storage capacity was calculated as the difference between the maximum amount estimated in the spring and the lowest value observed in the fall. No field calibration of the neutron probe was attempted, partly because no other field method is as precise as neutron thermalization (van Bavel 1958), but also because our primary interest was in the change in water volume through time rather than in the actual amount of water in the soil at any particular time. We assumed that soil organic matter remained constant, so that the change in hydrogen content was due solely to a change in soil water. Soil water values (e.g., Fig. 4) were calculated as the product of maximum storage capacity, estimated as described above, and the percent of the maximum probe reading at the time of interest.

Collection and chemical analysis of precipitation and soil leachate

Samples of the accumulated snowpack were collected from large forest openings adjacent to four of the stands prior to the onset of snow melt in March of 1979 and 1980. Snow samples were collected directly into 0.5-L polyethylene bottles from three depths at 10 randomly selected points at each site. Bulk precipitation in the spring, summer, and fall was collected after most measurable rainfall events (97 collections in 2 yr), using polyethylene funnels attached to 0.5-L plastic bottles and placed above the canopy or in unobstructed openings at five sites. A glass fiber plug was inserted in the funnel to intercept large particulate matter, but dry atmospheric deposition contributed to the element concentrations measured in the samples. Volume-weighted mean element concentrations were calculated by dividing element fluxes in bulk rain by the total rainfall volume.

Samples of outflow water were obtained using 6–8 porous-cup soil water collectors (Parizek and Lane 1970) located near the bottom of the rooting zone (near bedrock or at 1.5–2.0 m depth). As with the neutron probe access tubes, holes were made with a pneumatic rock drill. The ceramic cups were embedded in fine silica powder at the bottom of each hole, and sifted soil from approximately the same depth was tamped firmly around the tube up to the surface. The collectors were evacuated to a tension of 0.012 MPa shortly after the initiation of snow melt, and samples were collected at 2–5 d intervals until ≈2 wk after snow disappearance. Although the water samples often remained in the collectors for several days, the water and soil temperatures during this period were only 1°–2°. Concentrations of certain elements in the soil water could have been altered by collector installation, but we assumed that the collectors equilibrated with the surrounding soil after 1 yr because in most cases the 2nd-yr data were not significantly different from the 3rd-yr data. In this paper we use only data obtained during the 3rd yr (1982).

Collecting soil water samples through porous cups, or any other device, is problematical because it cannot be known with certainty whether the sample represents capillary water or macropore water (Shaffer et al. 1979). This problem may be negligible in stands such as ours, where soil saturation may allow micropore and macropore water to reach chemical equilibrium. In any case, additional investigation on the occurrence and chemistry of macropore (unsaturated) flow is needed.

All liquid water samples were returned to the laboratory on the day of collection and filtered through glass fiber filters. Samples were stored at ≈2° for a maximum of 72 h (usually <36 h) before being analyzed for ortho-P, $NO_2 + NO_3$, and NH_4 using standard methods for a continuous flow autoanalyzer (Scientific Instruments, Pleasantville, New York). To avoid hydrolysis of organic N (White and Gosz 1981), color development in the NH_4 analysis was carried out at 37°, buffered at pH between 11 and 12. Samples were stored for up to 2 wk at 2° before being analyzed for Ca, Mg, K, and Na by atomic absorption spectrophotometry (Perkin-Elmer 560); 1% lanthanum was added in the Ca and Mg analyses to limit interference. Following no more than 6 wk storage at 2°, total P and total Kjeldahl nitrogen (TKN) were determined by colorimetric methods on the autoanalyzer after standard digestions (Golterman et al. 1978). Total N values reported in this study represent the sum of TKN and $NO_2 + NO_3$. Following thawing and filtering, snow water samples were analyzed by the same methods.

Estimating outflow by computer simulation

Soil water collectors can be used to obtain samples of outflow water, but they do not provide an estimate of outflow quantity. Because there are no reliable methods for measuring this parameter, most studies of out-

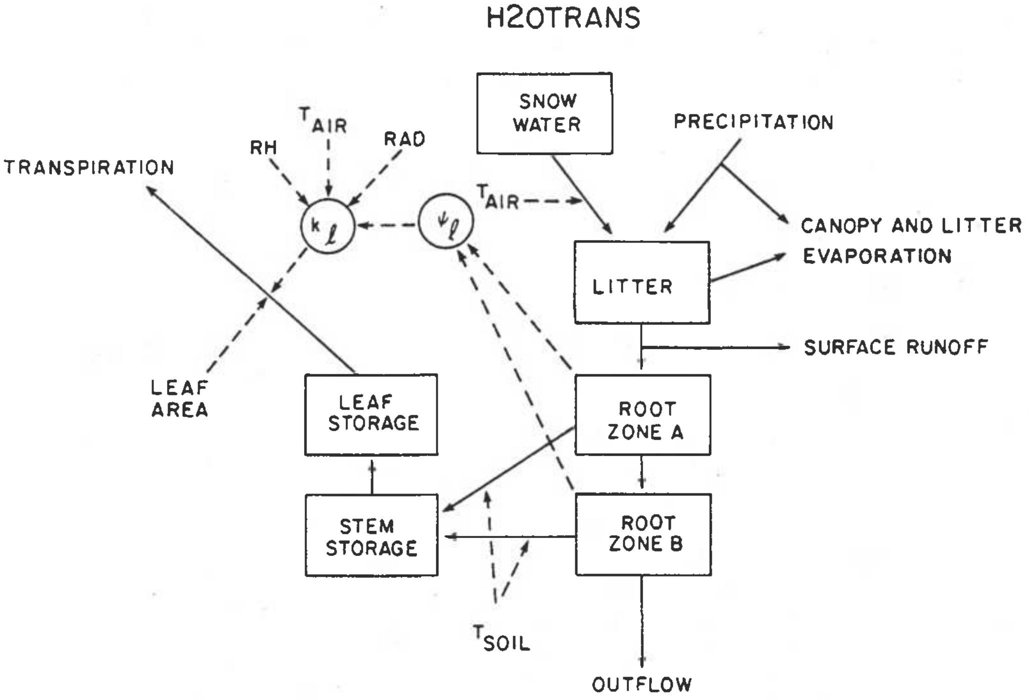

FIG. 1. H2OTRANS, a mass-balance simulation model used to estimate outflow. Solid lines indicate water flows, and dashed lines indicate influences on water flows of relative humidity (RH), air temperature (T_{AIR}), soil temperature at 25 cm (T_{SOIL}), solar radiation (RAD), leaf area, leaf conductance (k_ℓ), and predawn leaf water potential (ψ_ℓ). Six compartments are treated as state variables (boxes), and there are four summation compartments (outflow, transpiration, canopy and litter evaporation, and surface runoff). For other details see Study Area and Methods: Estimating Outflow.

flow from ecosystems have been done on watersheds with impervious bedrock, using weirs. During the last 10 yr, however, considerable progress has been made in modelling water flow through forest stands (Tan et al. 1978, Halldin 1979, Persson 1980, Black and Spittlehouse 1981, Sollins et al. 1981, Waring et al. 1981). These computer simulation models calculate outflow after integrating the factors or processes affecting water movement.

Transpiration is a major pathway for water loss from forests but is difficult to model, especially in situations where the actual evapotranspiration is considerably less than potential evapotranspiration, due to stomatal resistance. The success of forest outflow models often is determined by the extent to which the stomatal control of transpiration can be modelled. Considerable data have been accumulated on the transpiration and stomatal responses of lodgepole pine in our study area (Swanson 1967, Fetcher 1976, Fahey 1979, Running 1980*a*, *b*, *c*, Knight et al. 1981, Kaufmann 1982). This physiological information provided the basis for the development of a stand-level model (H2OTRANS; Running et al. 1983, Running 1984) from a single-tree model constructed originally for Douglas-fir (Waring and Running 1976).

H2OTRANS is a mass-balance model with 10 state variables (Fig. 1) and 5 driving variables: precipitation (excluding water in the snowpack), air temperature, relative humidity, soil temperature (at 0.25 m depth), and incoming shortwave radiation. The status of each state variable is calculated hourly, including the summation variables: transpiration, outflow, surface runoff, and evaporation. Subsurface outflow is calculated when water influx as rainfall or snow melt occurs at a time when the litter and root zone compartments are full. The model allows for slow drainage from a saturated soil profile (determined empirically by observing the rate of water table decline in soil pits). Data on soil hydraulic conductivity are not used by the model in its present form.

Our general approach was to (1) make careful measurements of snowpack water equivalent (S), subsequent precipitation during the snow melt period (P), and soil water change (ΔQ); (2) model transpiration and evaporation of water intercepted by the canopy (ET) during the drainage period; and (3) calculate drainage (D) below the rooting zone using the relationship

$$D = S + P - \Delta Q - ET. \qquad (1)$$

For the present analysis we set model parameters so that no surface runoff occurs, an assumption that is realistic for most sites in the lodgepole pine ecosystem and for all but one of our study areas. Transpiration is calculated by modelling the effects of soil water, air temperature, relative humidity, and solar radiation on leaf conductance (k_ℓ), with the model calculating one k_ℓ value for the forest canopy. Computation of a single canopy k value fits the resolution of our modelling objectives and has been used with success by others (Sinclair et al. 1976, Luxmoore et al. 1978, Tan et al. 1978, Federer 1979, Halldin 1979, Lohammar et al. 1980). Transpiration rate (T) is calculated as

$$T = k_\ell \times HD \times LA \times 3600, \qquad (2)$$

where HD is the absolute humidity deficit (in grams per cubic centimetre) and LA is leaf area per hectare. The units for T are cubic centimetres per hectare per hour.

The simulation of water flow begins with the date snow melt is initiated as the snowpack becomes isothermal, which is determined by field measurements. Snow melt rate is calculated using an empirically derived degree-day function; constructing an energy budget model for snow melt was beyond the scope of our study. In the model, water passes into root zone A after the litter is saturated, and similarly into the other storage compartments as the storage volume of the previous compartment is exceeded. Evaporation and transpiration occur continuously as conditions permit, with evaporation from the canopy and forest floor calculated as a simple function of HD. Sublimation and evaporation from the snowpack and soil are not calculated by the model, nor is transpiration from understory vegetation; all are difficult to measure and are believed to constitute a small proportion of the hydrologic budget in our stands.

Tables 1 and 3 include values for the initial conditions and parameters that were used for simulating water movement through each of the eight stands. Certain parameters were constant for all stands: maximum mean canopy leaf conductance (0.15 cm/s), maximum predawn leaf water potential (−0.6 MPa), leaf osmotic potential (−2.0 MPa), and the canopy interception coefficient (.05 cm/LAI). Running (1984) provides more details on the structure of H2OTRANS.

Model validation

Model validation was an integral part of our research program, and separate data sets were collected for that purpose throughout our study. While most of the physiological data used to develop H2OTRANS were collected at a site in northern Colorado (Running 1980*a*, *b*, *c*), the validation data were collected from our stands in nearby southern Wyoming. Predictions of outflow could not be validated, but several values calculated by H2OTRANS could be measured, namely predawn leaf water potential (ψ_ℓ), leaf conductance (k_ℓ), and soil water depletion. Simulated values for these parameters were compared to measured values. In addition, model estimates of hourly and daily transpiration were compared to values obtained using whole-tree potometers (Knight et al. 1981).

Soil water depletion (or recharge) was calculated by subtracting soil water volume measured at t_{0+1} from that measured at t_0. Soil water depletion can be used for estimating summer ET, but not vernal transpiration (VT) in the spring. Actual ψ_ℓ was obtained between 0200 and 0500 on 5–6 mid-canopy twigs using a Scholander pressure chamber, and canopy k_ℓ was estimated from an average of 5–10 values obtained at mid-canopy level using a null-balance, diffusion porometer (Beardsell et al. 1972). The k_ℓ data for validation were gathered from one of our study areas (Albany) in 1979, with a set of data being collected at 2-h intervals on a clear day during the 1st and 2nd wk of each summer month.

RESULTS

Our analysis of factors affecting water and nutrient outflow is dependent on the characteristics of the stands we chose to study and on the validity of H2OTRANS. Here we will first describe the features of our stands and then our evaluation of model adequacy. We will then proceed to an analysis of (1) water and nutrient outflow patterns on a seasonal and annual basis, and (2) simulation experiments that demonstrate the importance of certain stand features.

As noted previously, the eight study areas differed greatly in both vegetative and hydrologic features (Tables 1 and 3). The climatic characteristics of the eight stands were similar, however, with daytime temperatures in the warmest stand (Albany) averaging 3°–5° above those in the coolest (French Creek), and with maximum radiation, maximum air temperature, and minimum relative humidity occurring in late June or during July (Fig. 2). Rainfall patterns in the stands also were similar during the 3-yr period (Fig. 4). Total annual rainfall accounted for 34–67% of annual precipitation, ranging from 23–31 cm (for all stands during 3 yr), with 20–40% of the rainfall occurring during the snow melt period.

Snow water equivalent ranged from a low of 10 cm in 1981 (Chimney Park) to a high of 89 cm at French Creek in 1980, and varied annually during the 4-yr study period by as much as 300% (Dry Park II, Table 3). Snow melt usually began in April or early May but, depending on snowpack size, air temperature, and insolation, the duration of the snowpack varied among stands and among years (Fig. 3). The snow-free period at Dry Park II began ≈30 d earlier in 1977 than in 1979 (Fig. 3A). As discussed below, the duration of snow melt can affect outflow.

The soil is by far the largest ecosystem compartment for the storage of snow water. The maximum available soil storage in each stand ranged from 6 to 22 cm (Table 3). Soil water depletion continued through the summer, with small amounts of summer rain percolating to the soil on one or two occasions (Fig. 4). Soil drawdown occurred to a minimum observed water potential of −1.0 MPa at 15 cm depth and −0.4 MPa at 100 cm (Fahey and Young 1984).

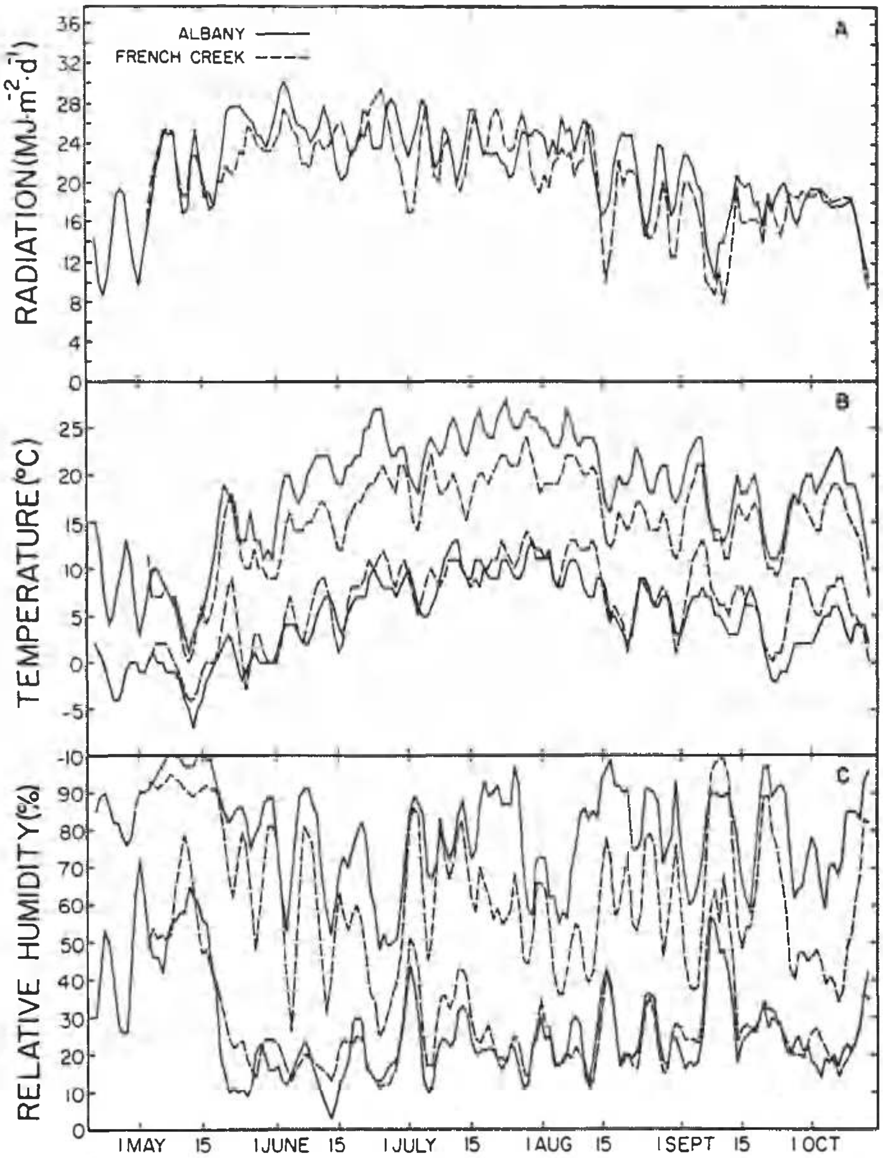

FIG. 2. Variation in solar radiation above the canopy and in air temperature and relative humidity in the canopy during the growing season of 1980 in the coolest (French Creek) and warmest (Albany) of the study areas. The data have been smoothed by 3-d averaging. Mean minimum and maximum values are shown for temperature and humidity.

The trenches in each stand provided an opportunity to observe soil drainage patterns. Little or no water accumulated in the trenches at Albany and Nash Fork, suggesting rapid drainage of gravitational water; however, water accumulated in the trenches at the other six stands. As will be shown, slow drainage amplified the effect of vernal transpiration on outflow.

Special hydrologic conditions also were observed at Rock Creek and the two stands at Chimney Park. Rock Creek has more clay in the soil (mass at 0–15 cm depth = 39% of <2-mm fraction) than the other stands, which led to slower infiltration and considerable surface runoff in both 1979 and 1980. Our attempts to measure surface runoff at Rock Creek were unsuccessful and, consequently, we have not been able to calculate a water budget for that stand.

The two Chimney Park stands occur at the lower part of a catchment and, although no surface runoff occurred, lateral subterranean flow probably occurred over the shallow (1 m) bedrock. We could not measure the quantity of subterranean inflow, and consequently we could not calculate hydrologic budgets for these two stands.

Model validation

H2OTRANS was run for 1979, 1980, and 1981, using stand-specific and year-specific input data for five of the eight stands. In this section we compare certain model predictions with field measurements to evaluate the adequacy of the model for estimating subsurface water outflow.

Predawn leaf water potential (ψ_ℓ) *and leaf conductance* (k_ℓ).—The observed and predicted values of ψ_ℓ diverged considerably at Nash Fork, but a close correspondence between the values was noted at Albany and Dry Park (Fig. 5). At Nash Fork the model predicted much greater predawn water stress than was actually observed, but this divergence proved to be inconsequential to predictions of transpiration because of the fact that k_ℓ was reduced to near zero by the model well before the low ψ_ℓ values were reached. The correspondence between predicted and observed midday k_ℓ was good (Fig. 6).

Soil water depletion and evapotranspiration.—Comparing model predictions to measured soil water values was viewed as a critical validation test, and the results were encouraging (Fig. 4). In most cases the model predicted soil water content to within 2 cm during June and July. A notable discrepancy did occur in late summer, with the model predicting more water left in the soil than was actually observed. However, error at this time of year was not critical to our present analysis, because outflow does not occur in late summer and we did not depend on the model for an estimate of storage capacity for the following spring snow melt. The discrepancy between observed and predicted soil water values for French Creek may be attributable to our lack of transpiration estimates for the understory vegetation, which is relatively more abundant there (Table 1).

In general, the model did not predict accurately the quantity of soil water recharge after summer rains. This problem resulted from an inadequate data base on canopy interception, a process that depends on rainfall duration and intensity and on intermittent evaporation (Rutter et al. 1972). Our data were inadequate to suggest how the canopy interception coefficient should vary from one stand to another, but our value of 0.05 cm/LAI obviously led to an overestimation of interception in some stands and underestimation in others (Fig. 4). This deficiency is not critical to our present analysis, but the problem would be amplified if H2OTRANS were used to simulate conditions over >1 yr.

As with the ψ_ℓ and k_ℓ data, the qualitative behavior of the model in predicting soil water depletion was logical. Soil recharge was indicated only after sufficient rainfall had occurred, due to complete interception of other rainfall, and a surge in transpiration occurred following these recharge events (Fig. 4). Also, outflow was predicted only during and just after the snow melt period, and early spring transpiration was retarded (Fig. 4) as would be expected due to the nighttime frost effect (represented in the model by retarding stomatal opening as a linear function of below-freezing temperatures; Fahey 1979). On clear days in June the predicted 24-h transpiration rate was 0.38 cm at Nash Fork and 0.31 cm at Dry Park, values which are close to the 0.34 cm estimated with whole-tree potometers (Knight et al. 1981). The onset of water stress was predicted sooner than observed in the field, resulting in underestimation of summer transpiration, but this discrepancy did not affect the estimation of outflow that we desired.

Based on the analysis above, we conclude that H2OTRANS is adequate for predicting transpiration during the snow melt period and capable of giving reasonable estimates of outflow below the rooting zone for stands with no subterranean inflow. Further improvements are required before the model can be run for several years in sequence or applied to stands with (1) more than one dominant tree species, (2) abundant understory vegetation, (3) outflow events following summer rains, or (4) lateral flows of soil water. The required improvements would include better treatments of snow melt, canopy interception, and soil water flux.

Water outflow, interception, and transpiration.—Water outflow beyond the rooting zone was indicated by the model only during the snow melt period and was highest at Albany, with an estimated total outflow of 43 cm in 1979 and 18 cm in the low snowfall year of 1981 (Fig. 4). Albany had the lowest LAI and soil storage capacity. The least outflow occurred from the two Dry Park stands, where high soil storage capacity

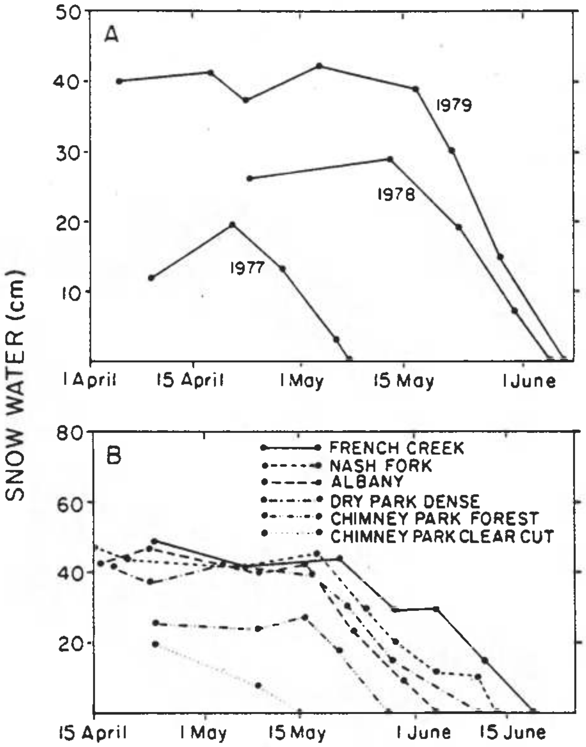

FIG. 3. Variation in snow ablation from the study areas. (A) Annual variation at Dry Park II. (B) Interstand variation in 1979. Coefficients of variation were usually <10%.

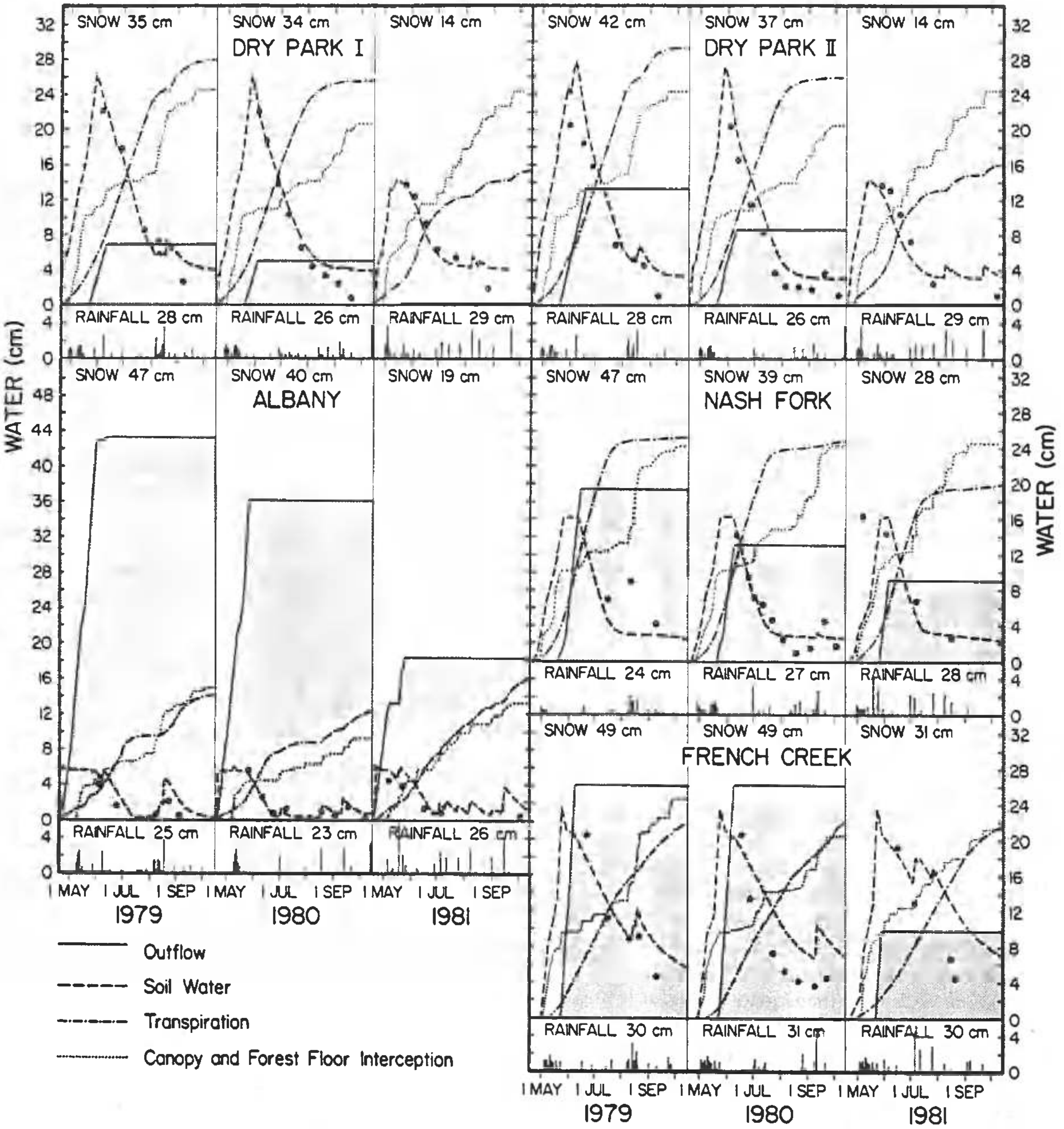

FIG. 4. Outflow, transpiration, interception, and soil water recharge and depletion from five contrasting stands as calculated by H2OTRANS for 1979, 1980, and 1981. Shaded areas indicate outflow volumes. Data points (○) indicate soil water content as measured by neutron thermalization (coefficients of variation usually were <10% at Albany, <15% at Dry Park, and <20% at Nash Fork and French Creek). Annual total water inputs in the form of snow and rainfall are given for each stand and year. Individual rainfall events are also shown. Note the response of transpiration to summer rainfall, and the reduced transpiration rates in midsummer, except at French Creek, which is more mesic.

and a prolonged VT period (due to slow drainage and snow melt) combined to reduce predicted outflow to only 7 cm in 1979 and to zero in 1981.

Canopy and forest floor interception prevented complete soil moisture recharge in the summer. The model calculated rainfall interception values ranging from 13 cm at Albany, where the LAI and forest floor mass were low, to a maximum of 25 cm at Nash Fork, where surface area and forest floor mass were high. At French Creek, Nash Fork, and Albany the model estimates for total water intercepted often were similar to the estimates for total amount transpired (Fig. 4).

Estimates of total annual transpiration and *ET* ranged from lows of 12 and 21 cm, respectively, at Albany (1980, Fig. 4) to highs of 29 and 53 cm at Dry Park II (1979, Fig. 4). For all stands and years, transpiration accounted for 50–61% ($\bar{x}$ = 55%, n = 15) of *ET* as estimated by H2OTRANS, which does not consider winter evaporation or sublimation. Estimated water loss by VT was 2–11 cm, or 9–44% ($\bar{x}$ = 25%, n = 13) of total transpiration and 5–22% ($\bar{x}$ = 13%, n = 13) of *ET*. Estimated *ET* during the spring, summer, and fall accounted for 33–95% of total annual precipitation ($\bar{x}$ = 73%) during the 3-yr study period; the percentage was lowest at Albany, where leaf area, VT, and soil storage capacity were low. Stomatal control appears to reduct *ET* later in the summer, though summer rains can lead to the resumption of rapid transpiration (Fig. 4).

Estimated VT and outflow varied considerably among the five stands for which a water budget could be calculated, with VT accounting for 4–20% of the snow water in 1980 (Fig. 7). Outflow accounted for 11–75% of the 1980 snow water. Comparing the Albany, Nash Fork, and Dry Park stands illustrates that the quantity of outflow can be quite different even though water input is nearly the same, whereas comparing Nash Fork to Dry Park I shows that outflow can be different even though forest structure, soil storage capacity, and water input are similar (Fig. 7). Interestingly, the two Dry Park stands were very similar in both VT and outflow despite their great difference in structure (Table 1), as noted by Knight et al. (1981).

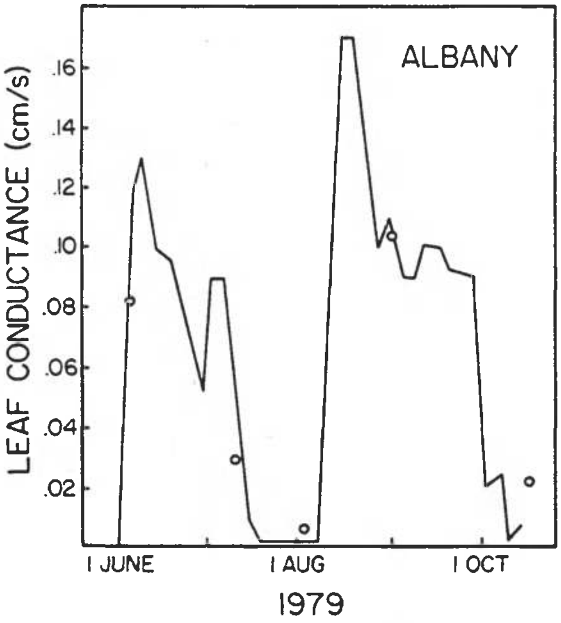

FIG. 6. Observed (O) and simulated (——) midday leaf conductance at Albany in 1979.

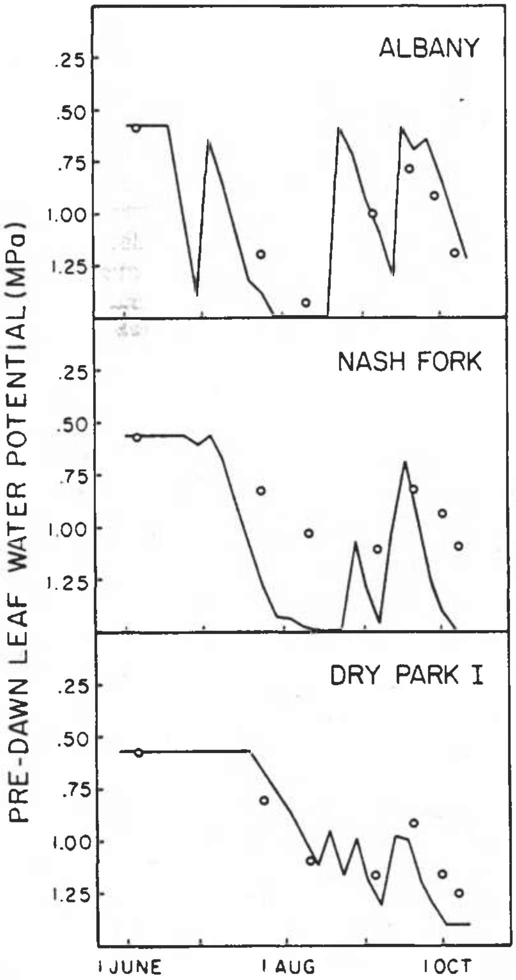

FIG. 5. Observed (O) and simulated (——) variation in predawn leaf water potential (−MPa) at Albany, Nash Fork, and Dry Park I in 1980.

To estimate nutrient outflow we needed a stand hydrograph showing daily water outflow rate during the entire outflow period. Fig. 8 represents our attempt to produce such hydrographs for 1980, but a major deficiency must be acknowledged, namely that percolation through the soil profile is treated simplistically by H2OTRANS and thus the dips, peaks, or plateaus in daily outflow rate may not be accurate. However, because of close correspondence between measured and predicted soil water depletion rates, we think that total outflow for a period of a week or more is estimated reasonably well.

Though predicting daily outflow rates is beyond the scope of H2OTRANS, it is useful to compare the stand hydrographs in Fig. 8. The initiation of outflow probably begins earliest at Albany because of (1) its lower elevation and LAI, which contribute to early snow melt, and (2) the fact that less snow water is required to exceed the storage capacity of this stand. Outflow occurs over a longer period because snow melt may be slow initially, except on occasional warm days (which coincide with the outflow peaks) and because more water moves as outflow due to lower storage capacity and less vernal transpiration. The low dip in the Albany hydrograph during 10–15 May coincides with a cold period when little snow melt occurred. Outflow from both the Nash Fork and Dry Park stands began ≈1

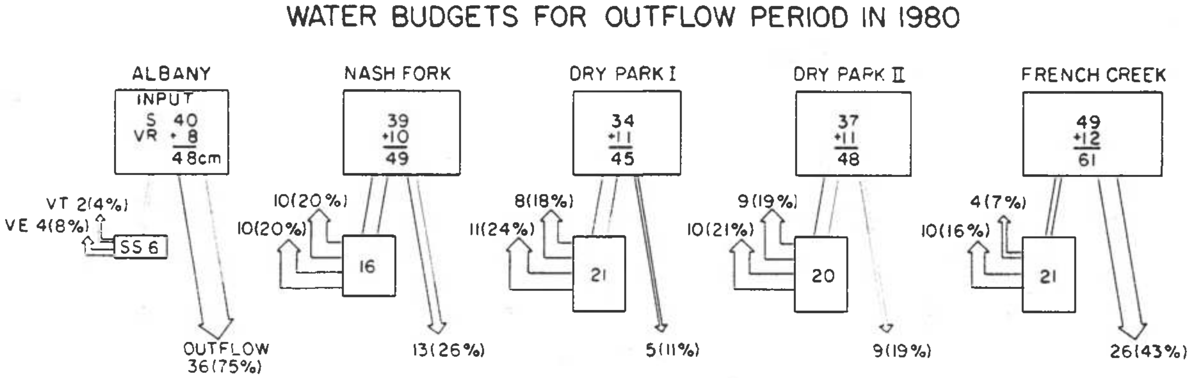

FIG. 7. Diagrams depicting the water budgets (in cm H_2O) of five contrasting stands during the 1980 outflow period (from the initiation of snow melt until the end of drainage). For annual budgets see Fig. 4. The amount added to the value for maximum snow water equivalent (S) is vernal rainfall (VR), i.e., rainfall that occurred during the snow melt period. The smaller boxes, for soil storage (SS), are full at the end of the outflow period, and the 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 by H2OTRANS).

mo later than Albany, due to later initiation of snow melt, more soil storage, and more VT. The retarded drainage at Dry Park is obvious.

Element input and outflow.—Element concentrations in bulk precipitation were comparable to other values in the literature for the region (Stottlemeyer and Ralston 1970, Lewis and Grant 1979). Weighted mean annual concentrations (in milligrams per litre) for total N, K, P, and Ca in snow water and in rain were, respectively: total N (mostly NO_3^- and NH_4^+), 0.17 mg/L in snow water, 0.56 mg/L in rain; K, 0.08 mg/L, 0.23 mg/L; total P, 0.004 mg/L, 0.010 mg/L; and Ca, 0.26 mg/L, 0.83 mg/L. These values were multiplied by the corresponding volumes of snow water and rain to provide an estimate of total annual input via bulk precipitation (Table 4). We do not have values for aerosol impaction on plant surfaces, which can be another source of nutrients (White et al. 1971, Schlesinger and Reiners 1974, Gorham et al. 1979), and therefore our estimates of atmospheric input are probably low.

Concentrations of N, P, K, Na, and Ca in the soil solution changed significantly ($P < .05$) in most of the stands as the 1982 snow melt season progressed (Fig. 9). TKN concentration declined for ≈30 d before increasing slightly. Other elements had different patterns of change in different stands. For example, Ca, Mg, and Na were present at relatively high levels and tended to increase during the snow melt period at Nash Fork and Dry Park, while a decline was observed in the concentrations of the same elements at French Creek and Albany. In all cases, however, the mean concentrations of Ca, Mg, K, and Na in soil solution were significantly higher than in snow water. Snow and subsoil solution did not differ significantly in total N and P concentrations, but, as observed also by Sollins et al. (1980), most of the N in soil solution was in organic forms (not the NH_4^+ and NO_3^- that predominated in bulk precipitation). Fahey (1977) observed similar patterns in a nearby study area.

To calculate nutrient outflow, the element concentrations in deep soil water (Fig. 9) were multiplied by the quantity of outflow predicted (Fig. 8) during the 4–7 d intervals between collections. Nutrient outflow was then summed over all periods to provide an estimate of total nutrient outflow, expressed both as kilograms per hectare per year and as a ratio of nutrient outflow to atmospheric input (bulk precipitation). As can be seen in Table 5, considerable variation in element outflow was predicted; N outflow varied among stands by a factor of 12 (0.09–1.12 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$), P by a factor of 6 (0.01–0.06 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$), K by a factor of 17 (0.17–2.9 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$), Ca by a factor of 1.3 (8.7–10.9 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$), Na by a factor of 1.9 (2.8–5.2 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$), and Mg by a factor of 1.6 (2.7–4.5 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$). Compared to outflow estimates from several International Biological Program (IBP) sites (Cole and Rapp 1981), our estimates are on the low ends of the ranges for N and K (IBP values: 0.6–14.9 and 1.0–8.9 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$, respectively) but closer to the middle of the ranges for P, Ca, and Mg (IBP values: 0.02–0.20, 2.3–59.8, and 0.45–6.0 $\mathrm{kg\cdot ha^{-1}\cdot yr^{-1}}$, respectively).

Nutrient outflow was replenished to varying degrees by atmospheric input; there was a calculated net accumulation in N for each of the stands and calculated net accumulations in K and P at Nash Fork and both Dry Park stands (Table 5). We did not measure denitrification, but this pathway for N loss is believed to be low in our stands because conditions (NO_3^- in solution, flooding accompanied by high microbial activity) favoring that process are uncommon in lodgepole pine forest ecosystems. Nutrient outflow/atmospheric input ratios were consistently >1.0 for Ca, Na, and Mg, but, due to a lack of data on weathering, such ratios cannot be interpreted as suggesting net losses. The stands may or may not be in steady state for soil-derived elements, but they appear to be accumulating N and perhaps P and K.

Simulation studies

The results presented thus far are for conditions observed during the 1979–1982 study period. Questions now arise about outflow under different conditions. Here we describe the effects predicted using H2OTRANS of (1) varying snowpack water equivalent, holding constant LAI, soil storage capacity, temperature, rainfall, and all other characteristics; and (2) reducing LAI to nearly zero, thereby increasing snow melt rate and reducing the potential for canopy interception and VT.

The first simulation was done using three contrasting stands and realistically high (60 cm), low (10 cm), and intermediate values for maximum snow water equivalent. The model suggests a linear or nearly linear increase in outflow with increasing snow water in all three stands (Fig. 10). At Albany predicted outflow was highest and increased most rapidly with additional snow, whereas outflow was lower and less responsive to snowpack size at Nash Fork and Dry Park, stands with greater capacity for water storage and VT. The results suggest that a snowpack water equivalent of 10 cm would cause outflow of 0, 0, and 7 cm at Dry Park, Nash Fork, and Albany, respectively, given the conditions of those stands in 1980 (Fig. 10).

To calculate the effect of varying snowpack on nutrient outflow, stand-specific element concentrations for specific times were multiplied, as before, by the quantity of outflow predicted by H2OTRANS for the period since the last soil water sample. With very little snow (and outflow), the chemical composition of the outflow is largely that of the early soil water samples, whereas with a larger snowpack the amount of element loss is affected by concentrations observed later in the outflow period. The predicted losses of N, K, P, and Ca generally varied in a nonlinear manner with the quantity of outflow, with the shape and average slope of the curve differing with different stand characteristics (Fig. 11). If water outflow were to triple (from 12 to 36 cm) at both Albany and Nash Fork, our calculations suggest that N outflow would be multiplied by 2.5 (from 0.4 to 1.0 $kg \cdot ha^{-1} \cdot yr^{-1}$) at Albany, and would double (from 0.1 to 0.2 $kg \cdot ha^{-1} \cdot yr^{-1}$) at Nash Fork. Comparable values for K are three times (1.0–3.0 $kg \cdot ha^{-1} \cdot yr^{-1}$) at Albany and a factor of 2.2 (1.7–3.8 $kg \cdot ha^{-1} \cdot yr^{-1}$) at Nash Fork. N and P outflow increased much less rapidly with increasing water outflow than did K and Ca.

Increasing the snow-water equivalent causes more nutrient outflow, but there is a corresponding increase in nutrient input from the additional snow. In order to place the simulated outflow values into perspective, the ratio of outflow to atmospheric input was calculated for varying amounts of snow water. Rainfall remained the same for all simulations. Element outflow was calculated as described above, whereas input was calculated as the sum of inputs from the snowpack and summer rains. Although ratios <1.0 indicate nutrient accumulation, ratios >1.0 cannot be interpreted as a net loss without additional data on aerosol impaction and weathering.

The simulation results suggest that even the highest levels of snow water are inadequate to cause a net loss

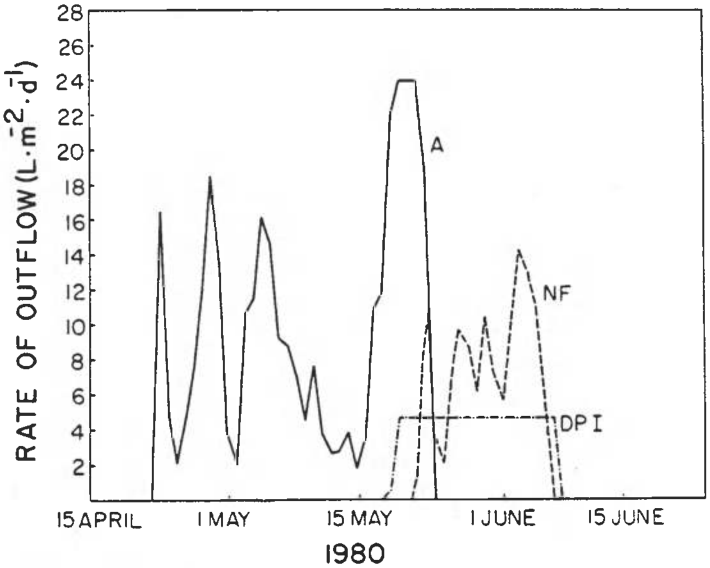

FIG. 8. Simulated stand hydrographs for three contrasting stands in 1980. A = Albany. NF = Nash Fork, DP I = Dry Park I. Due to limitations of H2OTRANS. only the general pattern of outflow is meaningful (see Results: Water Outflow, Interception, and Transpiration).

of N in our study areas (Fig. 12). The outflow/input ratios for P and K are more variable and may exceed 1.0 with increasing snow water in some stands (Fig. 12).

A second simulation was performed to study the effect on water outflow of reducing LAI (to 0.1), as might occur after a timber harvest. For the model to be realistic, variables other than LAI had to be changed also (Luxmoore et al. 1981). First, the microclimatic conditions in an area with low LAI are considerably different than in dense forest. At Chimney Park we monitored air temperature and humidity both in a clearcut and in the adjacent forest; these climatic data were used in conjunction with the stand data for Nash Fork and Albany. We chose these two stands because we felt most confident about the predicted water budgets there and because they represented quite different stand conditions, Nash Fork having much higher LAI and soil storage capacity than Albany (Table 1).

Soil storage capacity was also changed because we decided to simulate 2nd-yr outflow, i.e., outflow from a stand where LAI reduction had greatly restricted soil water drawdown during the first growing season, thereby causing a much reduced storage capacity for the following spring. For our simulation we assumed a storage capacity of 3 cm rather than 14 cm at Nash Fork and 2 cm rather than 6 cm at Albany. Increasing storage capacity by 3 cm made little difference in simulated outflow. Snowpack water equivalent and rainfall were assumed to be equal for the two stands.

The most striking result of the harvest simulation was a much greater increase in water outflow at Nash Fork than at Albany (Fig. 13), a pattern which can be attributed to the removal of a larger amount of biomass and leaf area at Nash Fork. Outflow increased by only 36% at Albany (from 36 to 49 cm), whereas outflow at Nash Fork increased by 277% (from 13 to 49 cm). Outflow at Nash Fork was 20% (13 cm) of the total annual precipitation (66 cm) before the simulated harvest and 74% (49 cm) the second year after harvest, whereas outflow at Albany was 55% (36 cm) of annual precipitation prior to harvest and 74% (49 cm) after. A decrease in total *ET* was indicated for both stands,

TABLE 4. Nutrient inputs ($kg \cdot ha^{-1} \cdot yr^{-1}$) in the bulk precipitation of three stands in the Medicine Bow Mountains, Wyoming (1979–1980).

	Stand		
Element	Albany	Nash Fork	Dry Park
N*	1.60	1.72	1.55
P†	0.03	0.04	0.03
K	0.90	0.95	0.86
Ca	2.48	2.69	2.41
Na	0.96	1.04	0.93
Mg	0.41	0.44	0.40

* Total Kjeldahl nitrogen plus nitrate.
† Total organic and inorganic phosphorus.

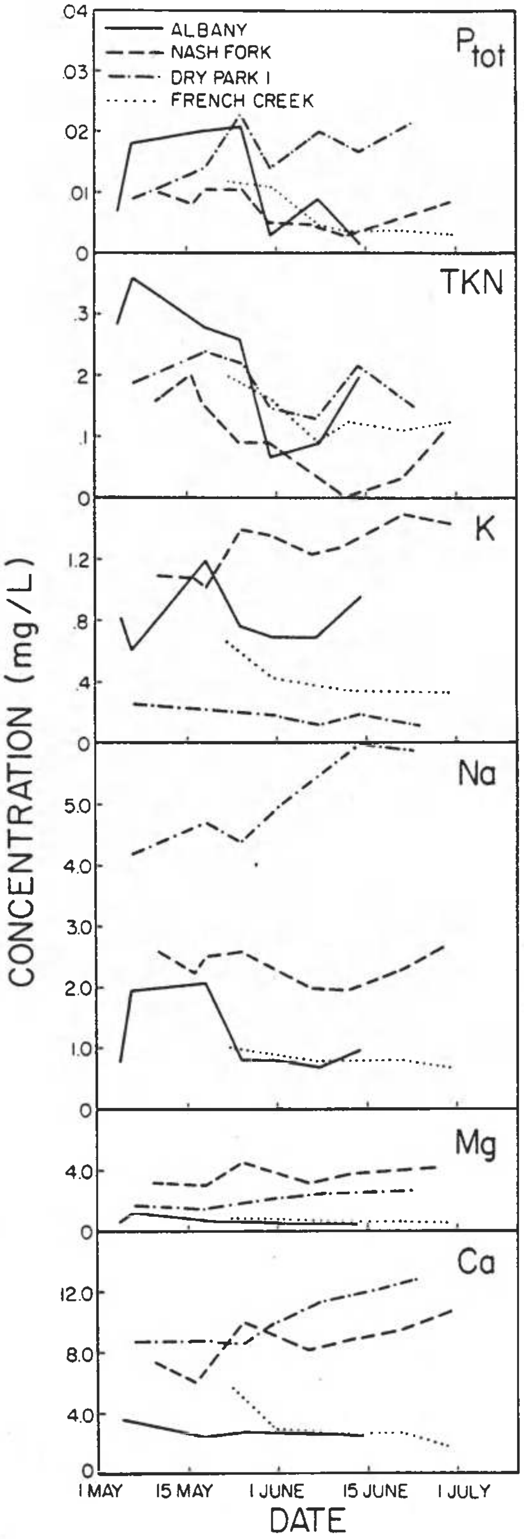

FIG. 9. The concentration of various elements in 1982 soil water samples collected at the bottom of the rooting zone in five stands. The data from Dry Park I and Dry Park II were averaged, as they were not significantly different. For most elements, concentrations changed significantly with time ($P < .05$). TKN = total Kjeldahl nitrogen plus nitrate.

from 80% of annual precipitation to 26% at Nash Fork and from 45 to 26% at Albany (Fig. 13).

We had hoped to estimate nutrient outflow after the simulated harvest, but our data are still insufficient to show how outflow water chemistry changes following timber harvest. Stark (1979), Hart et al. (1981), and C. P. P. Reid et al. (*personal communication*) provide data on element concentrations in soil solutions before and after timber harvest in our region, but no outflow estimates.

General Discussion

Water and nutrient outflow during the annual spring flush clearly varies substantially among sites in the lodgepole pine ecosystem. Stands differing in site or habitat type (Pfister 1981) experience different rates of water and element losses at different times during the snow melt period, and contribute differentially to streamwater quality and hydrograph shape. Furthermore, as illustrated by our simulation experiments, outflow from different parts of a catchment may change considerably or only slightly following perturbations and/or fluctuations in annual snow-water equivalent. Much of the observed variability can be attributed to the degree of biotic control, with nutrient outflow being affected by a different combination of factors than water outflow.

Initially we hypothesized that subsurface outflow of water from some stands during certain years could be reduced to zero. Such a situation was indicated by H2OTRANS at Dry Park in 1981. The frequency of such an occurrence may be high or low, depending on stand characteristics, and can be caused by various combinations of factors. In the simplest case, the maximum snow water is inadequate to saturate the soil profile, as was the case in 1981 at Dry Park, but outflow can also be reduced under conditions maximizing the amount of VT. Factors that tend to produce a high rate of VT include high evergreen LAI, climatic conditions favorable to VT, and a reduced rate of snow melt and percolation. LAI at the time of snow melt is a key factor, not only because VT occurs through the leaves but also because the leaf area shades the snowpack, thereby prolonging snow melt and, consequently, the VT period. Topography is another factor, as north slopes with less intense radiation may have a longer VT period than south slopes (Alexander and Watkins 1977). Up to 20% or more of the snowpack water may flow by VT in some stands (Fig. 7).

TABLE 5. Estimated total outflow ($kg \cdot ha^{-1} \cdot yr^{-1}$) and the ratios of outflow to atmospheric input (in parentheses) for three contrasting stands in the Medicine Bow Mountains, Wyoming, and six elements during 1980. Input values are in Table 4.

	Stand		
Element	Albany	Nash Fork	Dry Park
N*	1.12 (0.7)	0.09 (0.1)	0.16 (0.1)
P†	0.06 (2.0)	0.01 (0.3)	0.01 (0.3)
K	2.94 (3.3)	0.93 (0.9)	0.17 (0.2)
Ca	9.60 (3.8)	10.91 (4.1)	8.74 (3.6)
Na	5.22 (5.4)	2.82 (2.7)	4.37 (4.7)
Mg	2.73 (6.7)	4.48 (10.2)	3.02 (7.5)

* Total Kjeldahl nitrogen plus nitrate; nitrate concentration was consistently <.01 mg/L in soil solutions.

† Total organic and inorganic phosphorus.

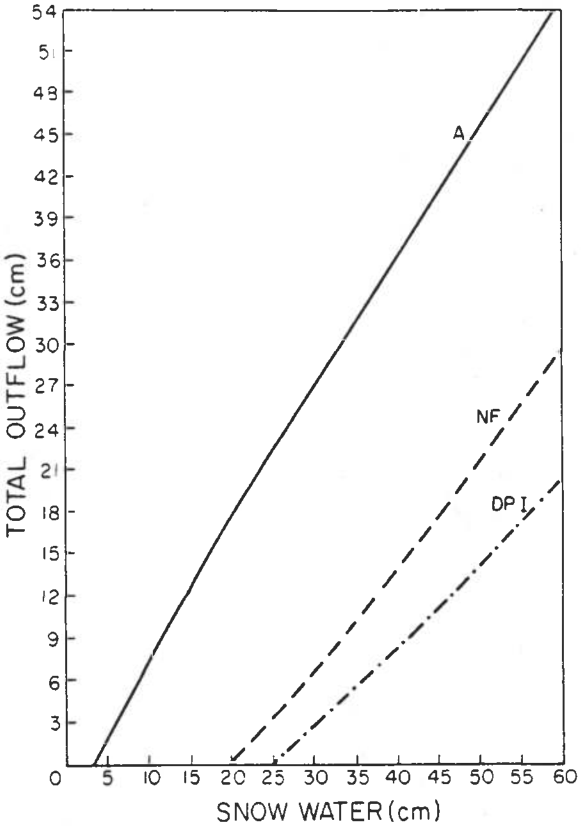

FIG. 10. Simulated water outflow from Albany (A), Nash Fork (NF), and Dry Park I (DP I) under varying conditions of snow water.

Summer *ET* is also important in providing storage capacity in the soil for the following spring, with soil water depletion occurring to a depth of >2 m (Dahms 1971, Dietrich and Meiman 1974, Johnston 1975). Both VT and *ET* are dependent on LAI (and root area), which can be reduced by natural perturbations or land management practices. Watershed managers know that streamflow often increases following LAI reduction, whether by insects (Love 1955, Bethlahmy 1974), timber harvest (Douglass 1967, Leaf 1975), or fire. Our results suggest that the increase in water outflow following harvesting is dependent in part on the amount of leaf area removed, a stand feature that is dependent on site quality (Grier and Running 1977, Waring et al. 1978) and, in unmanaged stands, relatively independent of natural stand denisty or basal area (Knight et al. 1981). Characterizing habitat types in terms of leaf area could be helpful in refining watershed management practices (Pfister 1981, Kaufmann et al. 1982). Changes in root distribution (Douglass 1967) or snow distribution (Gary 1974, Leaf and Alexander 1975) following timber harvest are other factors affecting water outflow.

If the outflow of water is reduced to zero in an intact forest, then nutrient outflow is reduced as well. Nutrient inputs continue, however, leading to a period (at least 1 yr) of improved nutrient availability for the biota. The importance of such nutrient enrichment episodes for decomposition, productivity, or pest resistance is unknown.

Even if water outflow does occur, there may not be a net loss of certain elements. Nitrogen, for example, is in short supply in western coniferous forests and appears to be assimilated whenever available (Fahey 1977, Gosz 1980, Sollins et al. 1980, Johnson et al. 1982). The same may occur for K and P. Fahey (1977, 1983) found levels of inorganic N and K to be lower in surface runoff than in snow, which suggests that biotic immobilization occurs in the forest floor. Nutrient outflow is affected both by immobilization processes and by the quantity of water outflow, as well as by other factors that determine element concentrations in outflow water, such as anion availability (Johnson et al. 1982), the occurrence of soil frost (Lewis and Grant 1980), or organic N adsorption in the mineral soil (J. B. Yavitt and T. J. Fahey, *personal observation*). Further research may show how the major factors affecting element outflow will vary depending on whether the outflow/input ratio is <1 or >1 (sensu Fig. 12).

Successional trends influence water and nutrient outflow from forests such as those we studied. For example, a common successional pattern is for aspen (*Populus tremuloides* Michx.) to give way to subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and sometimes to lodgepole pine, i.e., a change from deciduous forest with less capacity for interception and VT to evergreen forest where VT and interception are greater. A reduction in outflow is predictable (Jaynes 1978), as has been observed by a number of investigators working in other areas (Urie 1967, Ayer 1968, Rutter 1968, Swank and Douglass 1974). Another successional pattern is for Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir to replace lodgepole pine. Although this change could lead to increased leaf area (Kaufmann et al. 1982), the effects on outflow, if any, are not known.

The major perturbations to lodgepole pine forests in our area are fire, timber harvest, and outbreaks of the mountain pine beetle. Any one of these may cause a reduction in leaf area, thereby increasing water outflow,

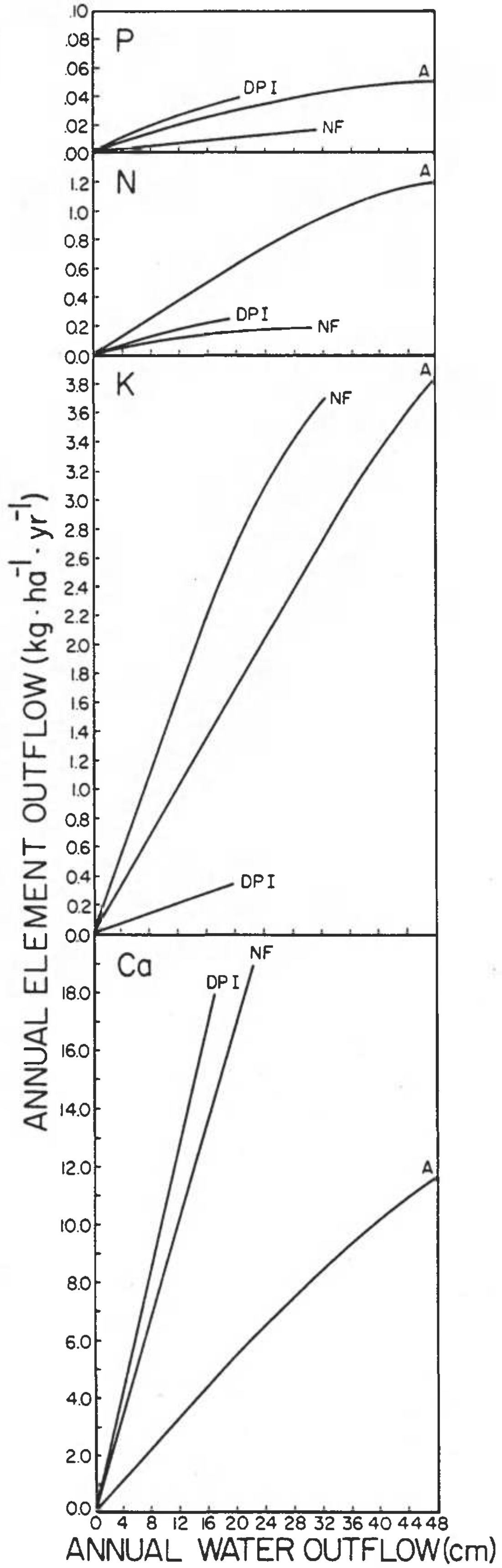

FIG. 11. Simulated annual outflow of N, P, K, and Ca in relation to total water outflow from three contrasting stands (Albany, Nash Fork, and Dry Park).

but the loss of limiting nutrients should be much greater following fire because of volatilization, reduction in forest floor carbon, and the greater erodability of ash. Woodmansee and Innis (1973) studied the effects of fire and clearcutting on long-term K availability and tree growth in lodgepole pine forests, and concluded that additional data are required before an accurate comparison is possible.

Our results are relevant to several hypotheses offered to explain the observed variation in nutrient conservation by ecosystems. Odum (1969) postulated that nutrient conservation increases as more species occupy an ecosystem through time, but species diversity is so low throughout the successional sere in Rocky Mountain coniferous forests that this factor probably is minor. Another hypothesis suggests that spring ephemerals serve to conserve nutrients in ecosystems at times when outflow is potentially high (Muller and Bormann 1976, Muller 1978, Blank et al. 1980). However, biotic immobilization and the VT of evergreen conifers dwarf the role of small herbaceous plants, which are, in fact, almost entirely absent from upper montane coniferous forests in our region, being restricted to meadows and other openings.

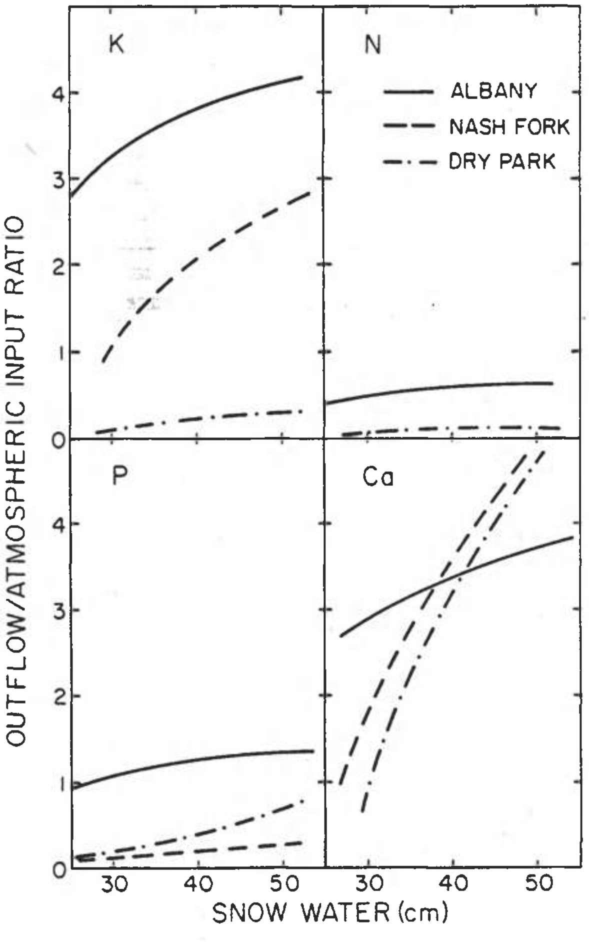

FIG. 12. Simulated outflow/atmospheric input ratios for N, P, K, and Ca in relation to total snow water equivalent at three stands during 1980. Ratios <1 indicate nutrient accumulation. See Results: Element Input and Outflow.

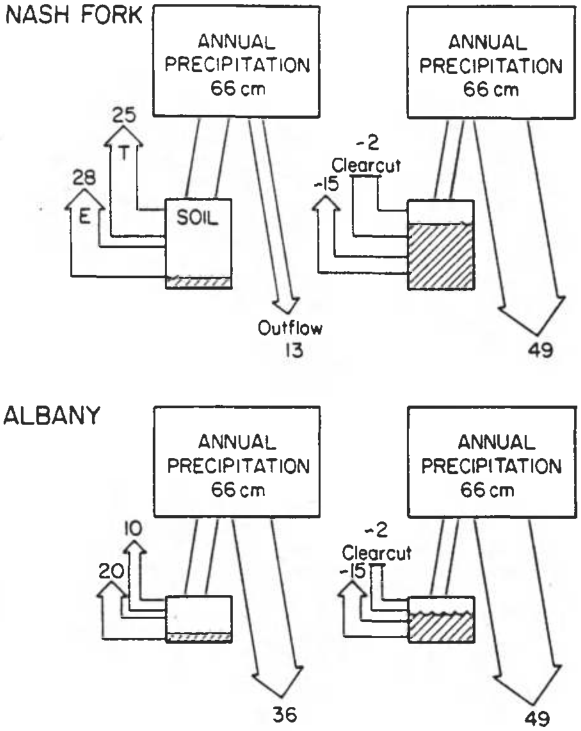
NASH FORK
ANNUAL PRECIPITATION 66 cm
ANNUAL PRECIPITATION 66 cm
25
T
28
E
SOIL
-2
Clearcut
-15
Outflow 13
49
ALBANY
ANNUAL PRECIPITATION 66 cm
ANNUAL PRECIPITATION 66 cm
10
20
-2
Clearcut
-15
36
49

FIG. 13. Estimated water outflow from two contrasting stands before and after a simulated clear-cutting experiment. The annual hydrologic budget is depicted, with returns to the atmosphere being transpiration (T) and evaporation (E). The hatching in the soil compartment suggests differences in soil water storage capacity, with greater storage capacity before the clearcut (left) than in the 2nd yr after harvest (see Results: Simulation Studies).

Vitousek and Reiners (1975) suggested that the loss of limiting nutrients is reduced as long as biomass accumulation is occurring, but the ratios between carbon and various limiting nutrients such as N and P are so high in western coniferous forests (Gosz 1980) that microbial immobilization and formation of resistant humus may reduce nutrient outflow even in the absence of biomass accumulation (Fahey 1983). It seems doubtful that losses of limiting elements increase as succession progresses toward climax, especially considering that a catastrophic fire would probably occur before attainment of maximum biomass or climax (Romme and Knight 1981, Pearson 1982). For soil-derived, nonlimiting elements, outflow depends more on soil water flux; stand features that minimize water outflow will also limit element outflow.

Our research leads us to conclude that, given a certain amount of snow water in mature lodgepole pine forests, variation in nutrient retention (or outflow) is more dependent on the development of maximum LAI (and root area) than on biomass accumulation, higher species diversity, or the presence of spring ephemerals. With the increase in LAI there is the potential for more VT, as discussed previously, in addition to more summer transpiration which dries the soil and thereby raises the storage capacity for water. Biomass may continue to accumulate long after maximum LAI is reached, but with little effect on the quantity of water and nutrient outflow. Similarly, a gradual decline in biomass (as in a degrading ecosystem) may not lead to increased outflow unless evergreen LAI is reduced also. Miller et al. (1979), Gosz (1980), and Johnson et al. (1982) discuss the various mechanisms for nutrient retention in coniferous forests. As suggested by Woodmansee (1978) for grasslands, net losses of limiting nutrients probably occur primarily in pulses after abiotic perturbations. Fire could be the most significant abiotic perturbation in lodgepole pine forest, though Lewis and Grant (1980) present data which suggest that frozen soils during low snowfall years could interfere with biotic immobilization and cause increased outflow of limiting elements.

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