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Trajectory analysis of forest canopy effects on chemical flux in throughfall

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Abstract. Short interval sampling of precipitation inputs and stemflow-throughfall (SF-TF) outputs was conducted in a subalpine balsam fir forest to analyze the controls on canopy ion flux. A canopy hydrology model was used to separate the effects of abiotic and biotic processes. The time lag between precipitation inputs and SF-TF outputs caused by the storage of water in the canopy required that time-course patterns of SF-TF flux be examined graphically. The resulting trajectory analyses disclosed patterns from which we generalized about canopy processing of precipitation inputs. Changes in the ion concentration gradient across canopy tissue surfaces appeared to be an important factor in regulating the rate of flux of ions between canopy tissues and SF-TF. These changes were in turn determined by changes in such factors as apoplast ion concentrations and the residence time of water in the canopy. These generalizations permit qualitative predictions of SF-TF flux in other canopies over time based on only rudimentary knowledge of canopy structure and function.

Introduction

Forest canopies play an important role in biogeochemical cycling in terrestrial ecosystems. They serve as the receptive stratum for dry deposition and alter the flux of waterborne materials in stemflow and throughfall (SF-TF). A voluminous literature exists describing how canopy systems alter SF-TF (Parker 1983) on an empirical, system-specific basis. Studies of the actual mechanisms underlying such behavior are unusual and there is no conceptual model from which general predictions for whole canopy systems can be made. This is particularly true for situations involving short time intervals or varying chemical inputs. Such a model is developed in this paper.

The research system

We studied a subalpine balsam fir forest which is characteristic of elevations between 1220 and 1450 m in mountains of northeastern U.S.A. (Reiners and Lang 1979). Research was conducted at 1220 m elevation on Mt. Moosilauke (71° 50′ W, 49° 1′ N) in the White Mountains of New Hampshire. The research stand was essentially monospecific balsam fir (*Abies balsamea* (L.) Mill.) bearing an extensive growth of epiphytic lichens (Lang et al. 1976, 1980).

Initial SF-TF measurements indicated that, relative to precipitation inputs, the canopy increased the flux of some ions (Ca^{2+}, K^+ and SO_4^{2-}) whereas it decreased the flux of others (NH_4^+ and NO_3^-) (Cronan 1980, Olson et al. 1981). SF-TF water flux exceeded incoming rain flux by as much as 29%, indicating substantial water and ion input from the capture of cloud droplets (Olson et al. 1981).

These long-term studies were followed by short interval, sequential SF-TF sampling within individual storms. Our results indicated that the flux of ions in SF-TF was not directly correlated with the SF-TF water flux rate. Ion concentrations in SF-TF were generally lower in the second half of a storm than in the first half, even at similar rates of water flux.

Our continuing study of the forest canopy had two goals. The first was to use a canopy hydrology model developed at the research site (Lovett 1981) to generate a detailed description of water and chemical fluxes during individual storms. This model provides estimates of cloud water and chemical inputs (Lovett et al. 1982), evaporation, and storage of water in the canopy. These are parameters that cannot be directly measured. The second was to determine if general and repeatable patterns of chemical flux from this canopy do occur, and if so, to describe the processes underlying such patterns.

Methods

Throughfall and stemflow were collected in a 10 m by 10 m plot via ten throughfall troughs, each measuring 10 cm by 100 cm, and 15 stemflow collars. The collars were distributed by a stratified random design ensuring representation of all bole size classes. Rain rates were measured with a baffled Alter gage in an adjacent clearing. Rain samples for chemical analysis were collected by funnels located 2 m above the canopy on a 15-m micrometeorological tower. Cloud water was collected by vertical strands of monofilament nylon line strung on a plexiglass frame mounted above the canopy (Lovett 1984).

Five storms were sampled in the summer of 1981. Water samples were collected at intervals as short as 15 min. Meteorological variables needed for the hydrologic model were measured continuously. Parameters included wind speed, net radiation, temperature, relative humidity and cloud liquid water content (Lovett 1984).

Concentrations of six ions (SO_4^{2-}, K^+, Na^+, H^+, NH_4^+, and NO_3^-) were measured in cloud water, rainfall, stemflow and throughfall. These ions were selected to represent a range of sources (atmospheric vs canopy tissues) and behaviors (net efflux from the canopy vs net uptake). Hydrogen ion was measured as pH and concentrations of the other ions were determined by standard Technicon colorimetric and flame photometry methods (Reiners and Olson 1984).

The basis of the predictive model of SF-TF chemistry was Lovett's (1981)

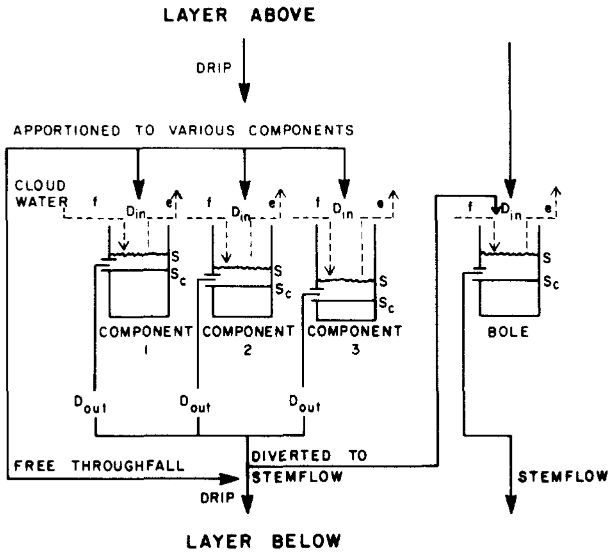

Figure 1. Diagrammatic representation of the canopy hydrology model developed by Lovett (1981). This diagram shows only three canopy branch components plus the bole. S = storage, S_c = retention capacity, f = cloud water deposition, e = evaporation, and D = drip. See text for further explanation.

hydrology model (Figure 1). This model computed the water balance of seven tissue types in 1 m height strata within the canopy. Inputs to each layer were vertical drip and cloud water deposition, outputs were drip and evaporation, and the difference between inputs and outputs was the change in water storage on the tissues. Measured rainfall amounts were added to the top stratum, and cloud water deposition and evaporation were calculated from transfer resistances and water concentrations (liquid and vapor) in the atmosphere using the equations described by Lovett (1984). Drip from layer to layer was calculated as a function of the current water storage and the water retention capacity of each tissue type, such that drip rate increased with increasing water storage (Rutter et al. 1971). Part of the drip from each stratum was apportioned to stemflow. The model calculated the water balance and drip from each tissue type in each stratum at 15 min intervals.

Predictions of SF-TF chemistry were made by a simple mixing model superimposed on the hydrology model. At the beginning of each interval, all water stored in the canopy was considered as a single pool. Rain and cloud inputs (both hydrologic and chemical) to the various canopy layers were treated as inputs (or outputs in the case of evaporation) to the storage pool. New chemical concentrations were calculated for the stored water and this concentration was assigned to the SF-TF generated by the model.

These predictions ignored the effects of interactions between precipitation and the canopy: the differences between predicted and observed SF-TF ion concentrations represent the canopy effects. The measured field concentrations were assumed to represent the concentrations in the canopy water at the start of each sample interval. Differences for each time interval represented canopy effects for that interval only. In this way, we tracked changes in the canopy-precipitation interaction through time.

This approach assumed that the washoff of dry-deposited material from canopy surfaces was negligible. Several factors led us to believe that dry deposition inputs were a minor component of total atmospheric deposition at this site. First, the site was in a remote, forested area far downwind of any significant pollutant sources, agricultural activity, or salt water that might contribute H^+, SO_4^{2-}, NO_3^- or Na^+ to the atmosphere. Atmospheric deposition of K^+ is generally considered much less important than foliar leaching in controlling SF-TF fluxes. Second, chemical inputs via precipitation and cloud water were extremely high in this system (Lovett et al. 1982), which diminished the relative importance of dry deposition. Third, the amount of time the canopy was dry was limited by the high frequency of cloud and rain events.

In any case, Lindberg and Lovett (in press) and Olson and Reiners (unpub. data) have demonstrated that dissolution of most surface-deposited material occurs within 3–4 minutes after leaves are wetted. Thus, we expected any dry deposition effects to be manifested only in the first time interval of the storms we sampled.

Results

Hydrology

Due to equipment failures, complete meteorological records were obtained for only two storms. The storms followed very different hydrologic patterns. The July storm (Figure 2) was over 14 hours long during which time the canopy was continuously immersed in clouds. Once rain commenced, rain rates increased steadily over five hours to a peak and then declined. Total net precipitation (cloud + rain − evaporation) for the storm was 4.65 cm, approximately 10% of which entered as cloud water. In-storm evaporation amounted to 0.16 cm.

In contrast, the August storm (Figure 3) was a brief thundershower that struck an initially dry canopy. Heavy initial rain rates declined rapidly over 1.25 hours, resulting in cumulative net precipitation of 1.75 cm. There was no cloud input, and owing to the brevity of the storm, in-storm evaporation equalled only 0.03 cm.

Changes in canopy water storage followed changes in the net precipitation rate. Because cloud inputs began prior to measurements of the July storm, the initial canopy water storage shown in Figure 2 represents the equilibrium level for the meteorological conditions existing at that time.

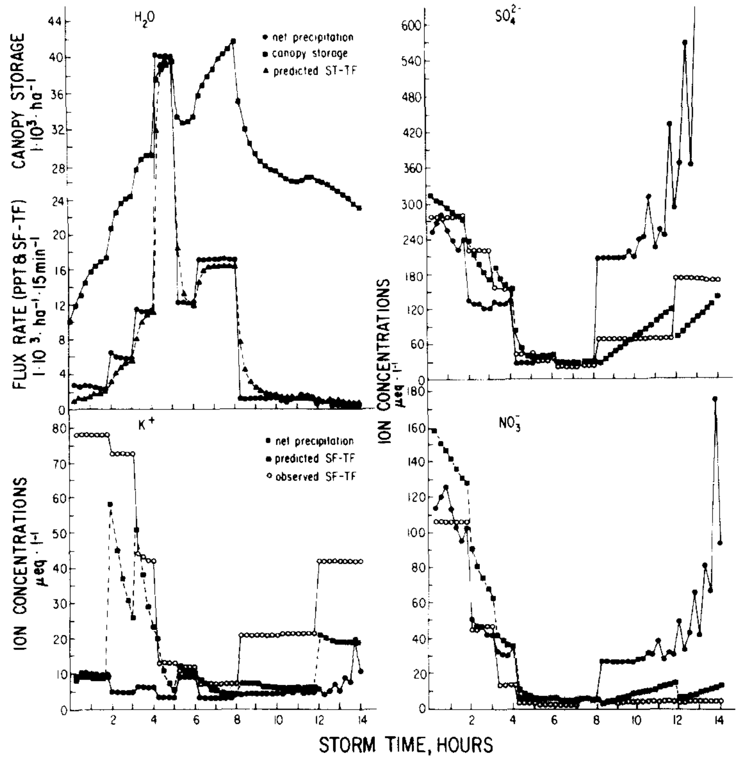

Figure 2. A record of hydrological and chemical behavior during the storm of 26 July 1981. The panel upper left shows the time course of combined rain and cloud droplet input minus evaporation (net precipitation), the estimated storage of water, and predicted SF and TF. Other panels show changes in concentrations of three ions in net precipitation and observed combined SF-TF compared with predicted SF-TF. Predicted SF-TF is based on precipitation chemistry, evaporation rates, and the concentrations of SF-TF in the previously recorded time interval. Differences between predicted and observed represent canopy effects in enriching or diluting the canopy storage pool.

Measured throughfall volume was often less than predicted, and often less than net precipitation even after correction for interception loss. Subsequent open field testing of throughfall troughs against a standard baffled rain gage showed that troughs gave an underestimate of water flux at high rain rates due to splash loss. Because of this, the throughfall volumes predicted by the hydrology model were used to determine SF-TF for these storms.

SF-TF flux followed precipitation rates but with a slight lag. This was very pronounced for the August storm (Figure 3) as most of the rain of the initial 15 min was held by the canopy. For the remaining hour, SF-TF volume exceeded net precipitation as the canopy drained.

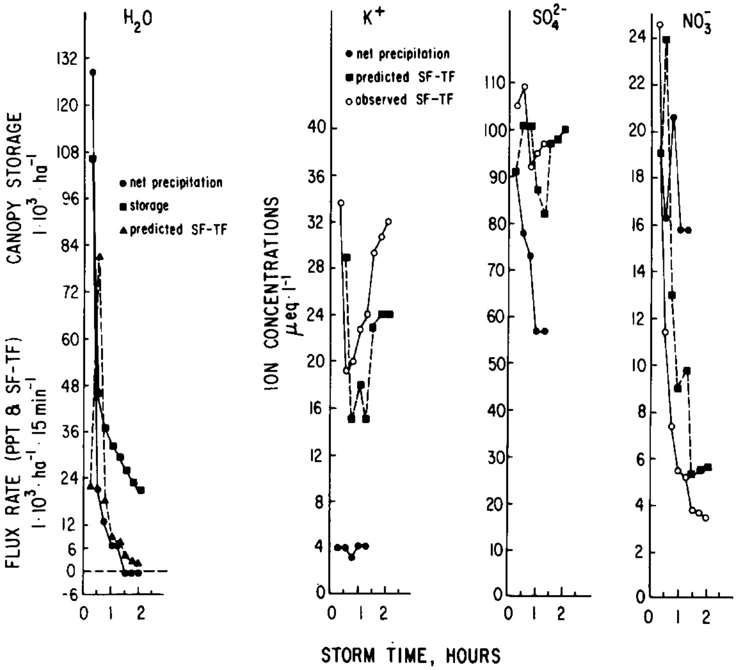

Figure 3. A record of hydrological and chemical behavior during the storm of 11 Aug. 1981. See Figure 2 for details.

Chemistry

The concentration patterns of K^+, SO_4^{2-}, and NO_3^- were closely matched by those of Na^+, H^+, and NH_4^+, respectively. Therefore, only the former set will be discussed. Predicted and observed SF-TF concentrations of the ions are shown for both storms in Figures 2 and 3. If observed SF-TF concentrations exceeded predicted, ions were added to through fall from the canopy. Observed SF-TF concentrations below predicted showed removal of ions from SF-TF. For both storms, SF-TF was greatly enriched in K^+, slightly enriched in SO_4^{2-}, and depleted in NO_3^-.

The July storm illustrated the importance of cloud interception as a source of chemical inputs to this forest and the necessity of separating this input from the effects of canopy components on rain chemistry. The mean concentration of ions studied was six times greater in clouds than in rain. Although clouds represented only 10% of the hydrologic input, they provided 38% of the total chemical input as measured in equivalents. Similarly high cloud concentrations have been measured elsewhere in this region (Falconer and Falconer 1980, Castillo et al. 1983). The only chemical not showing a high input via clouds was K^+, whose mean rain and cloud concentrations were equal.

One determinant of the pattern of change in the concentration of ions through a storm was storage of water by the canopy. For hours 8–13 of the July storm, a simple comparison of net precipitation and SF-TF concentrations would show SO_4^{2-} uptake by the canopy (Figure 2). In reality, most of the SF-TF generated during this period came from the drainage of water stored in the canopy during earlier hours, especially that accumulated during hours 4–8 which had the highest net precipitation rates and the lowest precipitation SO_4^{2-} concentrations. When SF-TF concentrations for hours 8–13 were predicted based on the addition of rain and cloud water to the pool of water stored in the canopy, the predicted concentrations were equal to or less than observed, indicating a net efflux of SO_4^{2-} from the canopy during this period. A steady increase in SF-TF sulfate concentrations was predicted as rain and cloud water with high SO_4^{2-} concentrations continued to be added to the storage pool. The observed SF-TF concentrations also increased with time, but faster than predicted due to the flux of SO_4^{2-} from canopy tissues to throughfall. In general, canopy water storage created a time lag between precipitation inputs and SF-TF outputs. This lag was especially evident in the August storm where drainage of stored water elevated SF-TF volumes above net precipitation volumes for all but the first interval (Figure 3).

Discussion

Mechanisms of canopy interactions with precipitation

The movement of ions (influx or efflux) across the surface of canopy tissues results from the physical process of diffusion (Mecklenburg et al. 1966, Hamilton et al. 1982). The major variables determining the rate of diffusion are temperature, viscosity of solvent, solute radius, area and thickness of cuticle, and the concentration gradient across the tissue surface (Price 1982). Of these variables, only the concentration gradient is likely to change appreciably during a single storm.

For any ion, the steepness and direction of the concentration gradient depends on the relative concentrations of the dissolved ion in the pools located on opposite sides of the tissue surface. The initial concentration of ions in the canopy water pool is determined by the ions added with rain and clouds and washed from tissue surfaces. The internal pool consists of dissolved ions in the apoplast. Differences in concentrations between these pools drive diffusion across the surface.

We did not directly measure the chemistry of the canopy water and apoplast, but we did make qualitative predictions of canopy chemical flux based on considerations of chemical gradients. If the concentration gradient between the apoplast and the canopy water remains constant throughout a storm, the flux rate of ions to or from the canopy remains constant (Figure 4A, curve a). If diffusion occurs across the cuticle, interior and exterior

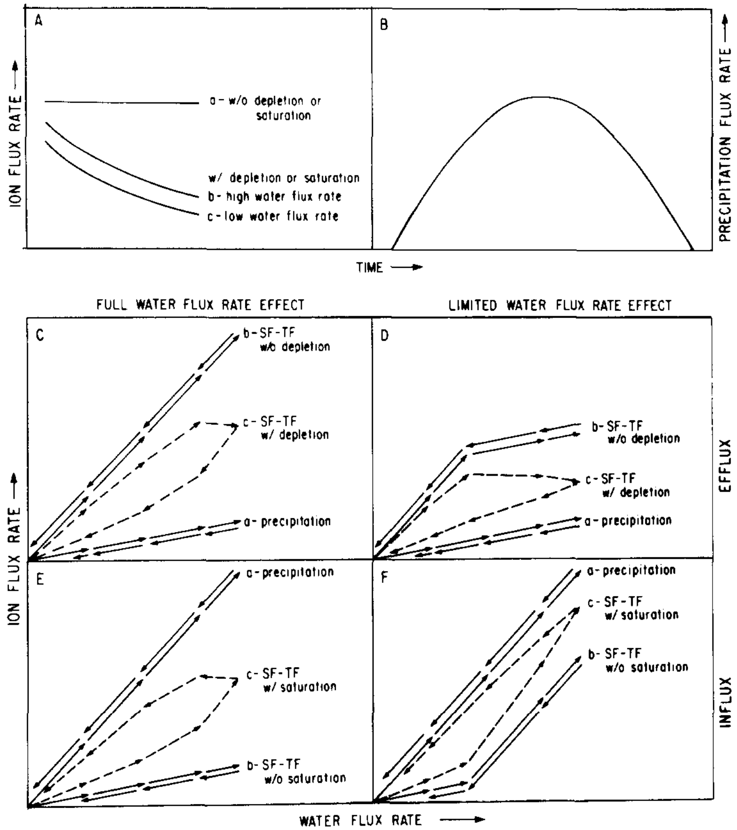

Figure 4. Assumptions and predictions for canopy influences on SF-TF chemical flux over the course of a storm. A – Two possible patterns of ion flux between canopy components and the canopy water pool: a – no change in flux rate over time, b and c – decreasing efflux rate (depletion) or influx rate (saturation) over time. Differences between b and c demonstrate effects of rates of water application rate (or storage pool residence time) on the positions of the depletion or saturation curves. B – an assumed pattern of precipitation input over time for examples C–F. C through F – Predicted time course trajectories for ion flux in precipitation and SF-TF for eight conditions: with or without depletion/saturation behavior, efflux vs influx, and contrasting responses to water flux rate (full effect over entire range of precipitation rates and limited effect only over the low range of precipitation rates).

concentrations will tend to equalize, and the rate of diffusion will decline over time (Figure 4A, curve b). In a series of simulated rain storms involving isolated canopy components, Reiners and Olson (1984) produced efflux curves like Figure 4A, curve b for SO_4^{2-}, K^+, and Na^+. A similar curve represented the rate of removal of NH_4^+ from the simulated rain.

Given the simplifying assumption of constant rain chemistry, two factors control the rate and extent of the decline in ion flux rate. First, if the residence time of water in the canopy is long, the water will approach chemical equilibrium with the tissues, and flux across the surfaces will slow. Low rain rates and high canopy surface area both increase the residence time of water in the canopy. In Figure 4A, curves b and c contrast the expected ion flux rates corresponding to low and high water flux rates. Unfortunately, real storms rarely have constant rain rates. Figure 4B shows a more realistic pattern of rain rate vs time, in which the rate of rainfall peaks in the middle of the storm. We will use this hypothetical pattern in our discussion of time course trajectories below.

The second factor that controls the ion flux rate is the rate at which ions are transferred between the apoplast and symplast (Uribe and Luttge 1984). If ions diffusing from the apoplast to the surface (K^+, SO_4^{2-}) are not replaced, the resulting depletion slows the flux rate. If ions diffusing into the apoplast (NO_3^-) are not removed, the resulting saturation reduces the rate of influx.

Hypothetical time course trajectories

To interpret patterns of SF-TF flux from the canopy, we found it instructive to consider chemical flux vs water flux as a time-course trajectory for each storm. Frequently used to describe population cycles (Wilson and Bossert 1971), time course trajectories have also been used to interpret watershed hydrology and resultant water quality (Toler 1965, Miller and Drever 1977, Bond 1979, Drever 1982). The three variables described above – water flux rate, depletion/saturation effects, direction of chemical flux (influx or efflux) – provide a framework within which to discuss patterns of canopy chemical flux. Given the simplifying assumption that these effects either do or do not occur, there are eight possible combinations of the three variables. For a hypothetical storm with constant precipitation chemistry, each of the eight combinations results in a different predicted trajectory of SF-TF chemical flux (Figure 4C–F). For all cases, the flux of ions in precipitation establishes a basic track that is then modified by interaction with the canopy. Because a symmetrical shape was assumed for the flux of rainwater during the hypothetical storm (Figure 4B), precipitation ion flux increases linearly with water flux to the midpoint of the storm and then decreases along the same track.

Figures 4C and D show hypothetical flux patterns for an ion with net efflux. SF-TF flux always exceeds precipitation flux because of additions from the canopy. In Figure 4C, curve b, flux from canopy tissues is proportional to water flux over all water flux rates. This increases the slope of the SF-TF flux track relative to the precipitation track, but leaves the linear pattern intact. Figure 4D, curve b shows the same initial SF-TF track until a maximum tissue efflux rate is reached. Further increases in water flux rate have no effect on tissue ion efflux and subsequent increases in SF-TF ion flux are due solely to increases in precipitation ion flux.

Figures 4C and D, track b assume that the apoplastic ion pool is not depleted. If the tissue ion pool is depleted, the efflux rate is reduced. Because depletion is a continuous process, the difference between the depletion (Figures 4C and D, track c) and precipitation (track a) trajectories decreases with time. This gives the depletion tracks their characteristic oval shape. Because SF-TF flux rates are higher in the first half of the storm, progression around the depletion ovals is clockwise.

When ions diffuse into canopy tissues, flux curves are always lower than the precipitation curves (Figures 4E,F). Accumulation of ions in the apoplast reduces influx rates which in turn gives the SF-TF flux track an oval shape (track c). Because the rate of removal of ions from precipitation decreases with time, progression around the SF-TF track is in a counter-clockwise direction.

Interpretation of observed trajectories

Precipitation during the July and August storms established ion flux trajectories that were then modified through interaction with the canopy (Figure 5). In both cases, the K^+ SF-TF track was displaced entirely above its precipitation track, SO_4^{2-} showed little displacement, and NO_3^- showed obvious downward displacement. The displacement of the trajectories of these ions should have lessened with time if depletion or saturation of the apoplastic ion pool occurred (Figure 4). Changes in canopy water chemistry that reduced the ionic gradient would also have lessened the displacement. Changes in the displacement of the SF-TF flux trajectory can be examined by comparing the net SF-TF chemical flux of two widely separated sample periods that had similar SF-TF water flux rates (to avoid flow rate effects). In the July storm, sample periods 2 and 3 had a SF-TF water flux of 6900 $l*ha^{-1} * 15\,min^{-1}$ while the rate for periods 6 and 7 combined was 7500 $l*ha^{-1} * 15\,min^{-1}$. The periods were separated by 2 hours and 45% of the total net precipitation.

The net efflux (observed minus predicted) of K^+ from the canopy in periods 2 and 3 equaled 0.12 $eq*ha^{-1} * 15\,min^{-1}$ while the corresponding K^+ flux rate for periods 6 and 7 was 0.03 $eq*ha^{-1} * 15\,min^{-1}$. Sulfate showed little difference between the periods. Nitrate was taken up by the canopy at 0.19 $eq*ha^{-1} * 15\,min^{-1}$ in periods 2 and 3, but at only 0.02 $eq*ha^{-1} * 15\,min^{-1}$ in periods 6 and 7.

According to this interpretation, the reduction in the flux rates of K^+ and NO_3^- was due to a reduction in the steepness of the ion gradients driving these fluxes. The estimated mean canopy water concentrations of K^+ were 38 $\mu eq*l^{-1}$ for periods 2 and 3, and 5 $\mu eq*l^{-1}$ for periods 6 and 7. This reduction would steepen the K^+ gradient from the apoplast to the canopy water. Thus, the lower K^+ flux rate in periods 6 and 7 implies that the apoplast K^+ pool was depleted relatively more than the canopy water K^+ pool. Nitrate had a mean storage water concentration of 59 $\mu eq*l^{-1}$ during periods 2 and 3, but only 7 $\mu eq*l^{-1}$ during periods 6 and 7. This reduced

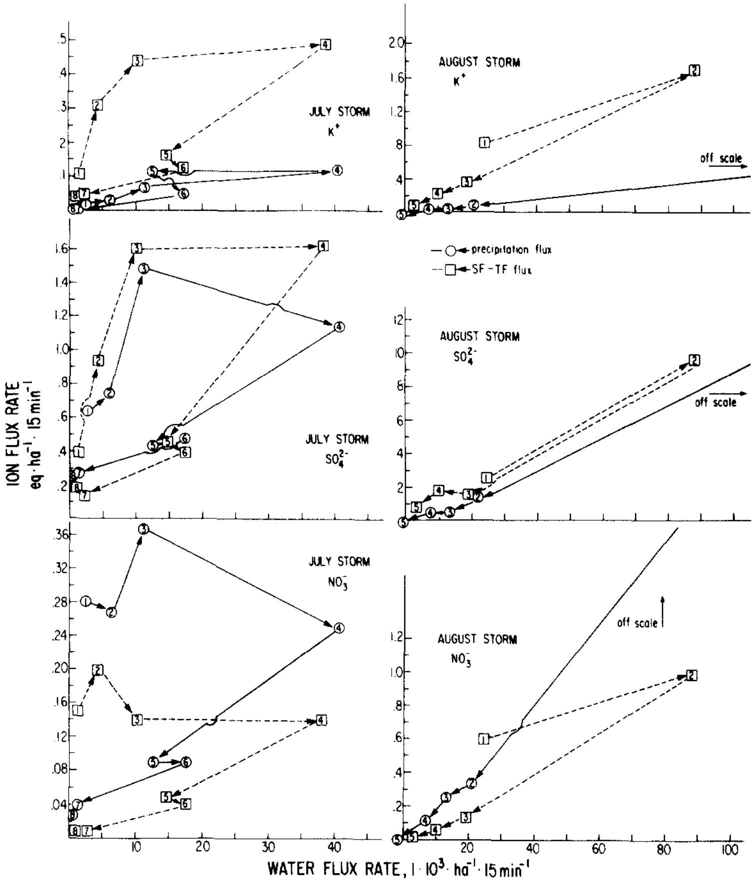

Figure 5. Time course trajectories for ion flux in precipitation and SF-TF for the storms of 26 July and 11 August 1981. Numbers correspond with sequential collection intervals.

concentration gradient explains the reduced uptake of NO_3^- by the canopy.

Water flux rate effects were evident only for K^+. A positive correlation between water flux rate and net efflux of K^+ from the canopy is evident for periods 1–3 of the July storm and all periods of the August storm (Figure 5).

We hypothesized that ions taken up by the canopy would have counter-clockwise SF-TF trajectories (Figure 4E,F). However, the actual NO_3^- SF-TF trajectories had a clockwise progression (Figure 5). This apparent discrepancy results from the fact that declining NO_3^- concentrations in precipitation during the storms (Figures 2,3) caused the precipitation NO_3^- flux in the later part of the storms to fall below the initial SF-TF NO_3^- flux (Figure 5). The SF-TF trajectories still, as hypothesized, turned toward the precipitation trajectories, but in a clockwise direction because of the pattern set by the precipitation.

Conclusions

Short-time interval sampling over the course of a rain storm provides more information on canopy chemical cycling than does bulk sampling of entire storms. While each storm is unique, certain basic patterns of behavior do exist. Atmospheric inputs establish patterns of Hydrologic and chemical fluxes that are modified through interaction with the canopy. The degree of modification is influenced greatly by the physical structure of the canopy. The more complex the structure, the longer precipitation water resides in the canopy. This lag causes mixing of precipitation of different chemical concentrations, increases the time available for exchange of ions with canopy components, and affects the timing of SF-TF fluxes out of the canopy. The rate at which the canopy alters SF-TF chemistry is not constant throughout a storm, but changes as the physiological state of the canopy changes.

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