THROUGHFALL VOLUME AND CHEMISTRY AS AFFECTED BY PRECIPITATION VOLUME, SAPLING SIZE, AND DEFOLIATION INTENSITY

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ABSTRACT.—Throughfall and stemflow are important components of hydrologic processes in forests, but relative contributions of multiple factors, including precipitation volume, plant size, and folivory (leaf removal by defoliators), on throughfall/stemflow have not been reported. This paper reports the relative influences of precipitation volume (0–230 L m⁻²), sapling size (1.4–6.7 cm diameter at root collar; 0.07–0.45 kg calculated dry foliage mass), and manipulated folivory (0–20% foliage removal) on throughfall volume and N, K, and Ca fluxes as evaluated with stepwise multiple regression in a young Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) ecosystem.

Precipitation volume explained most variation in throughfall volume ($R^2 = 0.81$). Folivory and sapling size each had significant but minor effects on throughfall volume and nutrient fluxes. These data indicate that folivore effects, while significant, are masked by precipitation in this wet ecosystem. Wider ranges in sapling size and folivory and/or drier conditions likely would improve interpretation of their influence on throughfall volume and chemistry.

Key words: throughfall, nutrient cycling, defoliation, nitrogen, potassium, calcium, conifer, ecosystem, forest, plantation.

Forest canopies are the major interface between the biosphere and atmosphere, filtering water, nutrients, and aerosols and determining the rate of ecosystem acquisition of these resources. The canopy also modifies the chemistry of precipitation percolating through it and reaching the forest floor as throughfall and stemflow (hereafter, throughfall). Water intercepted by the canopy affects canopy processes (such as evapotranspiration) and soil/ litter processes (such as erosion, leaching, and decomposition). Hence, factors influencing volume and chemistry of throughfall are key regulators of hydrologic and biogeochemical cycling processes.

Several factors contribute to throughfall volume and chemistry, especially precipitation volume and chemistry, canopy surface area, and folivory, or leaf area removed by defoliators (Parker 1983, 1995, Lovett et al. 1996). Precipitation volume clearly affects the amount of water that penetrates the canopy and contributes to leaching from foliage surfaces. Low precipitation volumes may be entirely intercepted by the canopy, whereas volumes exceeding canopy storage capacity contribute to throughfall (Rothacker 1963, Rutter et al. 1975, Gash 1979). Interception by the canopy depends on canopy surface area, which increases as trees grow (Parker 1983). Hence, throughfall volume is inversely proportional to canopy surface area. Folivory (consumption of foliage) reduces foliage surface area and increases the rate at which water and nutrients (via leaching from damaged leaves and litterfall components) reach the forest floor (Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991).

Previously, the effects of factors influencing throughfall have been studied separately, so their relative contributions in a single study are unknown. Few studies have evaluated folivore effects experimentally. Schowalter et al. (1991) reported that throughfall volume and nutrient turnover were significantly correlated with manipulated folivore abundance on young Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) in western Oregon, but only during the relatively dry spring and summer. Regression coefficients for effects of folivore abundance were low, further indicating important effects of other varying factors in that study, such as precipitation and sapling size. Measurements of precipitation volume and sapling size, as well as folivore abundance, in that study provide a unique opportunity to evaluate the degree to which precipitation volume and sapling size influenced folivore effects on throughfall.

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MATERIALS AND METHODS

This study was conducted on watershed 10 at the H.J. Andrews Experimental Forest Long Term Ecological Research (LTER) site from April 1984 to April 1986. The Andrews Forest is a 6100-ha facility in the central western Cascades of Oregon (latitude 44°N, longitude 122°W) operated jointly by the USDA Forest Service Willamette National Forest and Pacific Northwest Research Station and Oregon State University. Elevation ranges from 500 to 1500 m. The maritime climate is characterized by wet, relatively mild winters and dry, warm summers. Average annual temperature is 7.9°C; average annual precipitation is 2400 mm, with >75% occurring as rain from October through April. Snow is frequent, but accumulations are rare and of short (<2 wk) duration at the study site (Grier and Logan 1977, Gholtz et al. 1985).

Watershed 10 covers 10 ha at the western boundary of the Andrews Forest. Elevation is 430–670 m with slopes of 25–50%. This site was harvested and replanted with Douglas-fir during 1975 (Gholtz et al. 1985). At the initiation of this study, 1- to 1.5-m-tall Douglas-fir saplings were widely spaced (2–4 m apart) and intermixed with young maple (Acer spp.) and dogwood (Cornus) sprouts, as well as various shrubs and herbs. Foliage loss to herbivores in young Douglas-fir on this and other sites at the Andrews Forest typically is <1% of standing crop, but has ranged up to 10% (Schowalter 1989, 1995, and unpublished data).

Thirty Douglas-fir within a 1-ha area on the north-facing slope were involved in this study. These saplings were selected on the basis of similarity in crown geometry, foliage color, and density; absence of prior deer browsing; and relative isolation from surrounding vegetation. Selections attempted to minimize variation that could confound isolation of factors affecting throughfall chemistry (Schowalter et al. 1991). All naturally occurring herbivores were manually removed every 2 wk. Ten trees served as an herbivore-free treatment. The remaining trees were treated to an experimental range of intensities (5-60 caterpillars kg foliage-1) of the silver-spotted tiger moth, Lophocampa argentata (Packard) (Lepidoptera: Arctiidae), a common, naturally occurring folivore found at elevated population levels in the Cascades during the experimental period. This range of intensities caused 0–20% foliage removal, compared to typical rates of 0–10% in this forest (e.g., Schowalter 1995). Caterpillar density was manipulated by counting and replacing missing caterpillars every 2 wk to maintain target densities (Schowalter et al. 1991). Foliage mass was calculated from measured stem diameter, as described below.

Experimental saplings could not be killed for direct measurement of mass. Stem diameters were measured at the root collar in April (before new foliage production and new stem growth) each year. Because foliage mass should be a better predictor than sapling diameter of sapling capacity to intercept precipitation (thereby affecting throughfall), dry foliage mass was estimated for each tree as

$\ln Y_F = 3.8 + 1.3 \ln X (P < 0.0001, R^2 = 0.91),$

where X is stem diameter in centimeters (range 0.3–6.1 cm), and Y is dry foliage mass in grams (M. Klopsch unpublished LTER data, 1989).

The regular conical crown oriented along the bole axis for young conifers simplified collection of throughfall and stemflow for each sapling. Triangular, galvanized steel pans, 8 cm deep with a 36° angle fitted to the bole (to collect stemflow with throughfall) and covered beyond the crown perimeter (to avoid nonintercepted precipitation), were used to collect throughfall, stemflow, and litterfall from 10% of the area covered by the crown. Covers were reduced as crown diameters increased. Hence, sampled area ranged from 0.04 m^2 to 0.08 m^2 . Collectors were connected by plastic tubing to a 20-L plastic bottle that stored throughfall. An aluminum mesh $(1 \times 1 \text{ mm})$ was inserted into each collector to retain particulate material and prevent blockage of the drain. Although litterfall was removed from the collectors every 2 wk, throughfall likely was augmented to some extent by nutrients leached from litterfall intercepted by the mesh. An additional 3 collectors (identical construction) were placed in open areas to sample incident precipitation.

Precipitation and throughfall were measured in L m⁻² interception area. A 1-L subsample was collected every 2 wk during the wet season (November–April) and after individual rainfall events during the remainder of the year. Forty-five collections were made over the 3-yr period. Subsamples were filtered and frozen until they could be thawed and analyzed for

elemental concentrations, using autoanalyzer techniques for Kjeldahl N and standard atomic absorption spectrophotometry for K and Ca. These elements were selected for analysis because of their biological importance (N in protein and nucleic acids, K and Ca for muscle and nerve activity), their relevance to previous studies of folivore effects (e.g., Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991), and the range of ecological mobilities represented (K highly mobile, Ca relatively immobile; e.g., Gholtz et al. 1985). Biweekly sampling was appropriate because precipitation is nearly continuous between November and April, low temperatures during this period limit microbial activity, microbicides could confound elemental analyses, and earlier studies indicated satisfactory results of this timing for N (Klingaman and Nelson 1976). The collection bottles were washed in 1 N H₂SO₄ and rinsed with deionized water every 6 mon.

Sapling diameter and calculated foliage mass were divided by 10 to represent the 10% area sampled. Nutrient concentrations in throughfall were multiplied by throughfall volumes for each sample to calculate g m⁻² in throughfall. Nutrient concentrations in precipitation were multiplied by precipitation volume to calculate g m⁻² which were then subtracted from throughfall to indicate net nutrient fluxes.

Data were transformed, as necessary, using natural logarithms to improve normality and homoscedasticity. Stepwise multiple regression was used to evaluate relative contributions of precipitation volume, sapling size (diameter or foliage biomass), and folivore intensity on throughfall volume and net N, K, and Ca fluxes. Because diameter and foliage biomass were correlated variables, separate analyses were used for these variables. Variables were required to meet a P < 0.15 significance level to be added to the regression equation, but were considered significant only if P <0.05. Each regression had 1000-1345 (30 saplings × 45 collections) error degrees of freedom, depending on numbers of missing values. SAS software (SAS Institute 1982) was used for statistical analyses.

RESULTS

Precipitation volumes for individual collections ranged from 0 to 230 L m⁻² (0–230 mm of precipitation). Sapling sizes ranged from 1.4–4.8 cm diameters the 1st yr to 2.3–6.7 cm diameters the 3rd yr. Calculated foliage mass ranged from 0.07–0.35 kg the 1st yr to 0.15–0.45 kg the 3rd yr. Manipulated folivore intensity (number kg foliage⁻¹) ranged from 0 to 0.06 g⁻¹ foliage, resulting in 0–20% foliage reduction, estimated visually.

Results for regressions incorporating these variables are shown in Table 1. Several results are noteworthy. First, precipitation clearly had a dominant effect on throughfall. Plant size and folivory had significant, but relatively unimportant, effects ($R^2 < 0.2$). Second, although foliage mass was calculated as a function of stem diameter, the regression equations resulting from the 2 measures of plant size differ, especially in the sign of the plant size effect (+ for diameter, - for foliage mass) on flux of all 3 elements. Third, the folivore effect was significant only for K flux when stem diameter was included, but the slope was negative using either measure of plant size.

DISCUSSION

Although Schowalter et al. (1991) reported that folivory significantly affected seasonal throughfall and net nutrient fluxes when standardized for sapling size, this study (using the same dataset) indicated that precipitation and sapling size had greater effects on throughfall volume and chemistry than did manipulated folivore abundance. The long, narrow structure of conifer needles and the typical truncation of needles by conifer defoliators probably minimize the surface area available for leaching following wounding, perhaps minimizing the folivore effect on leaching losses, especially of K, which is highly leachable from foliage. However, needle loss should reduce canopy interception capacity and hence increase throughfall volume.

Precipitation volume was the most important predictor of throughfall volume, and the wide range of precipitation volumes likely masked the influence of the other 2 factors, which had relatively narrow ranges. Sapling size and folivory each had significant (but minor) effects on throughfall volume, with volume showing the expected decrease with sapling size and increase with folivore intensity.

Effects of sapling size and folivory on fluxes of N, K, and Ca were less clear. Sapling diameter was a better predictor of throughfall volume and chemistry (higher P and R^2),

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TABLE 1. Parameter estimates (\pm standard errors), F statistics, and partial correlation coefficients for regression equations to predict throughfall volume and N, K, and Ca fluxes from precipitation volume, sapling size (stem diameter in cm or foliage mass in kg), and herbivore intensity in regenerating Douglas-fir in western Oregon.

Ya	X _i b	Parameter estimate	Standard error	F	Р	Partial R ²
Volume	Intercept	16	3.6	21	0.0001	
	Precipitation	1.0	0.01	5600	0.0000	0.81
	Diameter	-7.9	0.95	70	0.0001	0.010
	Folivore intensity	13	4.7	7	0.008	0.001
Volume	Intercept	-5.1	3.1	3	0.1	
	Precipitation	1.0	0.0	5600	0.0000	0.81
	Folivore intensity	13	4.8	7	0.007	0.001
	Foliage mass	-0.01	-0.01	4	0.059	0.0005
N	Intercept	95	35	8	0.006	
	Diameter	89	8.6	100	0.0001	0.09
	Precipitation	0.3	0.1	6	0.02	0.005
Ν	Intercept	510	28	330	0.0001	
	Foliage mass	-0.3	0.1	14	0.0002	0.01
K	Intercept	550	180	9	0.002	
	Diameter	650	44	210	0.0001	0.17
	Folivore intensity	-450	220	5	0.03	0.004
	Precipitation	1.3	0.67	4	0.05	0.003
K	Intercept	2000	160	160	0.0001	
	Foliage mass	-0.8	0.4	5	0.03	0.004
	Folivore intensity	-387	247	3	0.117	0.003
Ca	Intercept	-85	90	1	0.34	
	Precipitation	3.7	0.3	120	0.0001	0.09
	Diameter	160	22	49	0.0001	0.04
Ca	Intercept	730	76	93	0.0001	
	Precipitation	3.5	0.3	110	0.0001	0.09
	Foliage mass	-0.8	0.2	19	0.0001	0.02

^aVolume in L m⁻² 2-wk period-1; N, K, and Ca in g m⁻² 2-wk period-1

^bPrecipitation in L m-², tree diameter in cm, foliage mass in kg, and herbivore intensity in number kg foliage-1

compared to calculated foliage mass (which should better represent the surface area for interception and nutrient flux). Fluxes of K and Ca should be proportional to foliage mass or area because of net leaching from foliage, especially for K, whereas N flux should reflect canopy uptake (Lovett et al. 1996). Fluxes of all 3 elements were positively correlated to sapling diameter, but negatively correlated to foliage mass. Because these 2 measures of plant size were highly correlated, their different effects on regression analysis suggest that the range of values was too small, compared to other factors, or that interaction with other factors influenced their effects.

Nutrient fluxes, especially of K, have been positively related to folivore intensity in earlier studies (Kimmins 1972, Seastedt et al. 1983, Schowalter et al. 1991). When effects of folivory were standardized by foliage mass, N, K, and Ca fluxes were significantly positively related to folivore intensity (Schowalter et al. 1991). However, when effects of folivory were standardized by ground area in this study, K flux was negatively related to folivore intensity and fluxes of other nutrients were not significant (Table 1). These results suggest that different methods used to standardize data influenced the apparent effect of folivores, perhaps because standardized area exacerbated deviation of calculated foliage mass from actual foliage mass as reduced by folivory. These differences should be noted by ecologists who measure and standardize throughfall based on ground area or plant size.

The range of sapling sizes (1.4-6.0 cm diameter) and folivory $(0-0.06 \text{ caterpillars kg} \text{foliage}^{-1}$, causing 0-20% foliage reduction) was relatively narrow compared to the range of precipitation volumes in this study. The wide range of precipitation volumes dominated regression analyses and probably masked the effects of narrower ranges in other factors and may even have influenced their apparent

relationships to throughfall chemistry. Studies relating throughfall volume and chemistry to a wider range of plant size and/or folivory should improve the predictive power of models reported here. Alternatively, better separation of litter and throughfall nutrients under drier conditions could improve resolution of nutrient fluxes.

Regression equations can be used to calculate the effect of each factor on throughfall volume. A 2-cm-diameter sapling would intercept virtually no precipitation, regardless of volume, whereas a 6-cm-diameter sapling could intercept about 32 L m⁻² before throughfall appeared. At the maximum precipitation volume observed in this study (230 L m⁻²), a 6cm-diameter sapling would intercept about 14%, within the range of 10-30% for various older forests, as reviewed by Parker (1983). Rothacker (1963) reported interception ranging from 100% for storms less than 10 L m⁻² (0.05 inch) to 18% for storms over 75 L m⁻² (3 inches) and estimated interception at only 4% for storms over 180 L m⁻² (7 inches) in old-growth Douglas-fir stands at the Andrews Forest.

The larger calculated proportion of precipitation intercepted in this study, compared to Rothacker's, likely reflects my integration of several precipitation events, generally over 2wk periods (compared to individual storm volumes in Rothacker's study), and my selective placement of throughfall collectors under crowns (compared to random placement in Rothacker's study). Selective placement of throughfall collectors under crowns limits comparison between these data and those from collectors placed randomly. However, more controlled conditions for throughfall collection in this study better represent the linkage between canopy processes and throughfall. Nonetheless, potential influences of these 2 collection methods on evaluation of folivore, or other, effects should be noted. Data for individual trees and open areas can be integrated to model throughfall under a heterogeneous canopy, but data collected without reference to canopy structure cannot be extrapolated.

In conclusion, this study is the first to evaluate relative effects of precipitation volume, sapling size, and folivory on throughfall volume and chemistry. These data indicate that precipitation volume in this temperate rainforest had the greatest effect on throughfall volume. Although sapling size and folivore abundance significantly affected throughfall volume and N, K, and Ca fluxes, their effects were largely masked (and perhaps modified) by precipitation volume when analyzed by multiple regression in this study. Folivore effects should be more important under drier conditions that typically promote folivore outbreaks.

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