Chapter 13
Assessing the Ecological Significance of Throughfall in Forest Ecosystems

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13.1 Introduction

13.1.1 Throughfall: The Hydrologic Context

Throughfall is defined as precipitation that reaches the ground surface following passage through a vegetative canopy, or "the portion of incoming gross precipitation that penetrates or drips through the canopy" (Hewlett 1982; Fig. 13.1). Throughfall is an important hydrologic flow path in many ecosystems. Although shrublands and grasslands produce throughfall, relatively few papers assess this topic (e.g., Vega et al. 2005; Levia and Germer 2015). In this chapter, we will thus focus on the better-studied forest environment, while also recognizing that throughfall may play an equally important role in other ecosystems. The quantity of throughfall (TF) in a forested ecosystem is determined by the balance between precipitation inputs, the production of stemflow (SF), and return of precipitation to the atmosphere due to evaporation following canopy interception (I) (Fig. 13.1; Crockford and Richardson 2000). Stemflow is produced when precipitation is delivered to the forest floor by flow down boles or stems. It is a considerably smaller hydrologic flux than throughfall. For a given precipitation regime, interactions among the quantity and timing of atmospheric inputs, micrometeorology of the site, and architecture of the forest canopy all play a role in determining the quantity of SF, I, and TF that occur during an individual storm or an entire year at a forested site (Crockford and Richardson 2000; Levia et al. 2011).

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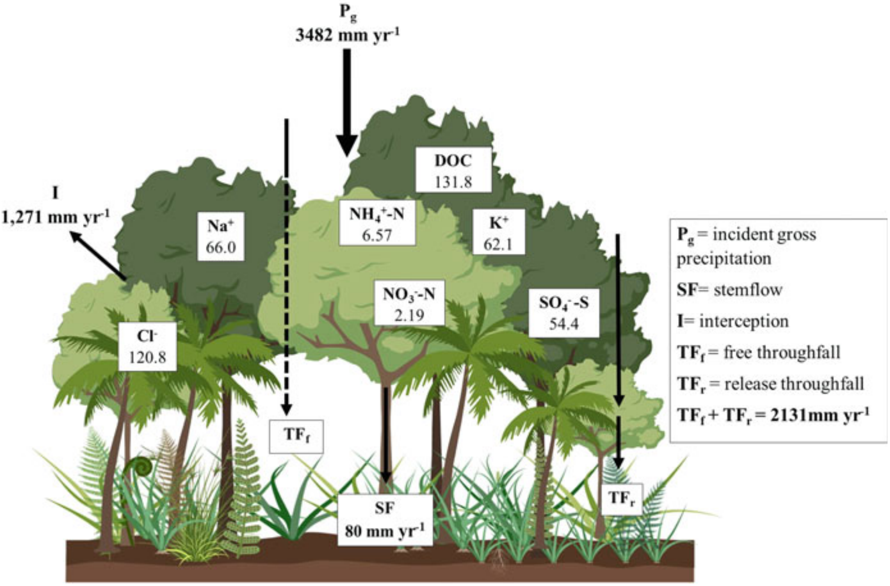

Fig. 13.1 Mean throughfall fluxes for solutes and chemical species (kg ha^{-1} y^{-1}) based on weekly samples in a tropical rainforest during a 15-year period (1988–2002). Data taken from Heartsill-Scalley et al. (2007). Values for incident gross precipitation (P_g), throughfall (TF_f + TF_r), and interception (I) were taken from Heartsill-Scalley et al. (2007) after estimating stemflow (SF) from precipitation (Scatena 1990). This figure was created with BioRender software (BioRender.com)

13.1.2 Mechanisms Generating Throughfall

The processes that result in throughfall generation have been studied in considerable detail. Throughfall can be classified into two types: free and release. Free throughfall refers to precipitation that passes through the canopy without interacting with any vegetation; release throughfall refers to incoming precipitation that is first intercepted and then drips from the plant (Levia and Frost 2006; Fig. 13.1).

In forested ecosystems, most of the incoming precipitation that is transferred from the canopy to the soil is deposited as throughfall (Lawson 1967; Henderson et al. 1977; Cape et al. 1991; Crockford and Khanna 1997; Huber and Iroumé 2001; Levia and Frost 2003; Carlyle-Moses et al. 2004; Lilienfein and Wilcke 2004; Levia and Frost 2006). The amount of precipitation that reaches the forest floor is determined by the canopy coverage, total leaf area, the number of layers of vegetation, tree species, and the intensity as well as the duration of rainfall events (Brooks et al. 2012). The total amount of throughfall produced in an individual storm varies considerably as a function of precipitation received (Fig. 13.2), because once the canopy is wetted and throughfall begins to be produced little additional canopy storage and subsequent evaporation can be expected (Carlyle-Moses and Gash 2011). This principle has been invoked to explain the high interception loss at

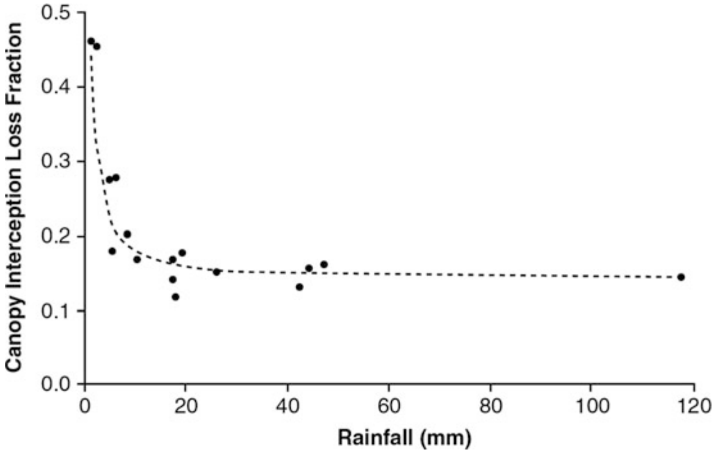

Fig. 13.2 Canopy interception (proportion) as a function of rainfall during a storm (mm). (From Carlyle-Moses and Gash (2011). Reproduced with permission of Springer)

tropical forest sites in Puerto Rico, where steady winds, consistently warm temperatures, and small average size of an individual rainstorm lead to ideal conditions for canopy interception, resulting in a watershed-scale estimate of throughfall that is only 59% of precipitation (Scatena 1990). Because the size and shape of the canopy also directly affect the amount, intensity and distribution of throughfall, it shows high temporal and spatial variability.

13.1.3 Field Collection Methods

Many localized factors within the forest canopy influence the amount of throughfall that is generated within a given forested stand, making quantification of throughfall at the watershed scale challenging. A wide variety of methods have been developed to quantify throughfall and collect it for additional analyses. Usually, throughfall is collected in forests using individual funnels or troughs that are installed suspended above the forest floor in order to limit any overestimation due to splash from the forest floor (Levia and Frost 2006). Both of these collection techniques consist of the same principle, with throughfall collected from a known surface area in order to estimate overall inputs for an entire plot (Levia and Frost 2006). However, the sampling strategy applied and the number of collectors installed are important elements that affect the accuracy of throughfall measurements in forested ecosystems (Helvey and Patric 1965; Lloyd and Marques 1988; Thimonier 1998; Price and Carlyle-Moses 2003; Levia and Frost 2006).

Lloyd and Marques (1988) showed that switching the position of throughfall collectors randomly can increase the accuracy of throughfall estimates compared to those made with collectors at fixed position. Holwerda et al. (2006) compared these two approaches for sampling throughfall (fixed and roving collectors) in a tropical rainforest. They found that both fixed and roving deployments can give similar values, but at least 100 fixed gauges are required to obtain values within the 95% confidence interval of those obtained from 30 roving gauges (Holwerda et al. 2006). Therefore, fewer throughfall collectors are needed when using the roving method. Rotating collectors are not always desirable, however, as they preclude comparisons over time under a given set of canopy conditions, and might limit ability to understand throughfall dynamics and drivers of biogeochemical fluxes when canopy conditions change at a given location (Levia and Frost 2006).

Another aspect of the hydrologic regime that influences the quantity of collectors needed is the magnitude of rainfall during individual precipitation events. During a given storm, as precipitation input increases, variability in the volume of throughfall among individual collectors decreases, meaning that throughfall is more spatially consistent (and a larger proportion of incoming precipitation; Fig. 13.2) when greater inputs of precipitation are entering the canopy (Price and Carlyle-Moses 2003). In fact, Price and Carlyle-Moses (2003) determined that more gauges are needed to adequately sample a precipitation event of less than 2 mm than for one that has an input of >4 mm. Zimmermann et al. (2010) developed a model to evaluate the performance of various sampling schemes. They found that a greater sample size is required to be able to quantify small events, due mainly to increases in the coefficient of variation for throughfall during small events. In general, a longer period of record and as many collectors as is practical are recommended to characterize throughfall quantity adequately (Zimmermann et al. 2010).

13.1.4 Global Variation in Quantity of Forest Throughfall

The structure of the canopy, specifically the arrangement, size and angle of the leaves plays an important role in determining the amount of throughfall that is generated because a greater individual leaf size and canopy surface area results in more interception and less throughfall reaching the forest floor (Brooks et al. 2012). Due to differences in canopy architecture, leaf area index (LAI) as well as physical positioning of leaf area are likely to be important in determining throughfall quantity. The relationship between throughfall and precipitation has been established for a variety of forest types in different parts of the world. These relationships are based on the dependence throughfall has on the canopy surface, area, and cover (Brooks et al. 2012; Table 13.1) and may be best addressed in future studies through the use of LIDAR to quantify canopy structure (e.g., Roth et al. 2007). In regressions that describe the relationship between throughfall and precipitation, the slope typically is near 90%, and depending on the size of canopy storage, the intercept (related to canopy storage) is several mm (Table 13.1). Alteration of the forest canopy by hurricane defoliation (Heartsill-Scalley et al. 2007) or spatial variability in forest canopy structure from other, more subtle causes (Konishi et al. 2006) can lead to increased throughfall and decreased interception. In the case of Puerto Rico,

Table 13.1 Relationship between throughfall and precipitation for different vegetative canopies[a]

Vegetative canopy	Throughfall relationship	Notes
Eastern Hardwood Forest, USA (Helvey and Patric 1965)	Growing Season	T_h is throughfall (in); P is total precipitation (in); and n is number of storms
	$T_h = 0.901\ (P) - 0.031\ (n)$	
	Dormant Season	
	$T_h = 0.914\ (P) - 0.015\ (n)$	
Southern Pine Forests, USA (Roth and Chang 1981)	Longleaf Pine	T_h is throughfall (mm) and P is total rainfall (mm)
	$T_h = 1.002(P) - 0.0008\ (P)^2 - 1.397$	
	Loblolly Pine	
	$T_h = 0.930\ (P) - 0.0011(P)^2 - 0.610$	
New Zealand Vegetation Communities (Blake 1975)	Kauri Forest	T_h is throughfall (mm) and P is total rainfall (mm)
	$T_h = 0.60\ (P) - 3.71$	
	Manuka Shrub	
	$T_h = 0.44\ (P) - 0.10$	
	Mountain Beech Forest	
	$T_h = 0.69\ (P) - 1.90$	

[a]Modified from Brooks et al. (2012)

revegetation returned relationships between P and I to near pre-hurricane levels within a year following Hurricane Hugo in 1989 (Heartsill-Scalley et al. 2007).

13.2 Throughfall as a Biogeochemical Flux

Throughfall chemistry integrates the effects of multiple biogeochemical drivers. These include the chemistry of incoming precipitation, the transfer of materials deposited on leaf surfaces by dry deposition, insect activity, the leaching of intracellular materials from canopy leaves or needles, and the net uptake or release of solutes by epiphytic organisms such as lichens, mosses, bromeliads, and algae. Because throughfall represents the largest internal transfer of water within many forest ecosystems, the solutes that it contains can represent significant biogeochemical fluxes from forest canopy to forest floor (e.g., McDowell 1998).

Fluxes of throughfall are often remarkably enriched in K^+, at levels 10–40 times higher than precipitation (e.g., Table 13.2), and often enriched in dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and NH_4^+ but much more variable in terms of NO_3^- concentrations and fluxes (e.g., Filoso et al. 1999; Hervé-Fernández et al. 2016). The literature contains many examples of specific studies of individual elements or groups of ions in throughfall, such as extensive work on DOC in throughfall (summarized in Table 13.3), but it is relatively sparse in

Table 13.2 Solute fluxes in throughfall (kg ha^{-1} yr^{-1}) at several sites with relatively complete major ion, nutrient, and organic matter fluxes

Solute	Beddgelert (Stevens 1987)	Site		
		Luquillo (Heartsill-Scalley et al. 2007)	Brazil São Paulo (Forti et al. 2005)	Brazil Negro River (Filoso et al. 1999)
NO_3^--N	6.51	2.19	9.09	0.62
NH_4^+-N	4.47	6.57	6.56	0.51
DOC	–	131.8	–	158.5
Na^+	75.8	66.1	12.4	3.83
K^+	15.1	62.1	110	27.7
Ca^{2+}	9.14	20.8	10.6	5.54
Mg^{2+}	9.72	13.1	5.86	2.70
H^+	1.02	0.015	0.01	0.05
SO_4^{2-}-S	26.5	54.4	30.1	1.71
Cl^-	136.1	120.8	61.3	5.38

complete descriptions of major anions, cations, nutrients, and organic matter for individual sites that, taken together, would provide a global understanding of throughfall across biomes. This is a major shortcoming in understanding the biogeochemistry of throughfall at the global scale and leads us to recommend that more comprehensive studies on the full range of throughfall biogeochemistry be undertaken in the future.

13.2.1 Net Uptake and Release of Solutes

Determination of net uptake and release of solutes from the forest canopy as throughfall is generated requires measurement of solute fluxes, which are the product of volume and solute concentrations. Because the quantity of liquid water returned to the atmosphere through evaporation can be substantial (Fig. 13.1), evaporative concentration of solutes can result in an increase in solute concentrations even when canopy interactions result in no net uptake or generation of solutes (Hansen et al. 1994).

Many sources within the forest canopy can contribute to the increases in solute concentrations and fluxes that are frequently observed when comparing precipitation and throughfall. Comparison of deposition (incoming precipitation) and throughfall yields a measurement sometimes referred to as “net throughfall” (Lovett and Lindberg 1984). The concept of net throughfall is particularly useful in addressing the sources of solutes entering a forest ecosystem. In one of the simpler applications of the concept, net throughfall can be used to estimate dry deposition of sea salt aerosols onto the forest canopy by comparing Na^+ and Cl^- fluxes in throughfall and

Table 13.3 Ranges of dissolved organic carbon (DOC) concentrations in throughfall (TF) for different forest types[1]

Forest Type	Range of [DOC] (mg C L^{-1}) in TF	Reference
Tropical rain	6–17	McDowell (1998)
		Tobón et al. (2004)
		Goller et al. (2006)
		Wanek et al. (2007)
		Heartsill-Scalley et al. (2007)
Tropical moist	5–9	Möller et al. (2005)
		Fujii et al. (2009)
		Hofhansl et al.(2012)
Tropical dry and seasonally dry	7–12	Laclau et al.(2003)
		Schrumpf et al.(2006)
		Germer et al. (2007)
Subtropical humid	5–11	Liu and Sheu (2003)
		Wang et al. (2004)
		Jian-fen et al. (2005)
Subtropical steppe	5–11	Ciglasch et al.(2004)
Temperate oceanic	14–17	Moore (1987)
		Solinger et al.(2001)
		Levia et al. (2012)
Temperate continental	9–29	Moore (1987)
		McDowell and Likens (1988)
		Qualls et al. (1991)
		Currie et al. (1996)
		Chang and Matzner (2000)
		Hagedorn et al. (2000)
		Guggenberger and Zech (1994)
Temperate steppe	18–20	Kolka et al. (1999)
Boreal	9–20	Dalva and Moore (1991)
		Moore (2003)
		Turgeon and Courchesne (2008)
Boreal tundra	49–57	Koprivnjak and Moore (1992)

[1] Modified from Van Stan and Stubbins (2018)

precipitation. Using this principle, for example, McDowell (1998) showed that dry deposition of marine aerosols provides a measurable but relatively small increase (15%) in total atmospheric deposition to a tropical forest with considerable rainfall (3.5 m). Because Na^+ and Cl^- are relatively inert under most circumstances (little biotic uptake or release), their quantification in net throughfall provides an effective measure of inputs of marine aerosols and other sources of dry deposition. In a more complex application of the same principle, use of net precipitation was pioneered by Lovett and Lindberg (1984) to estimate dry deposition of atmospheric pollutants with somewhat limited potential for biotic uptake. By measuring SO_4^{2-} fluxes in net throughfall, they inferred that dry deposition of SO_4^{2-} aerosols provided a significant input to forest ecosystems in much of the eastern USA and provided very important early estimates of the magnitude of dry deposition as a component of acidic atmospheric deposition (Ollinger et al. 1993). This use of net throughfall to estimate dry deposition is problematic, however, for more biologically active elements such as nitrogen. Lovett and Lindberg (1984) concluded that canopy interactions precluded use of net throughfall N concentrations to estimate dry deposition of nitric acid. Net throughfall below surrogate surfaces (artificial trees; Davidson et al. 1985) provides another way to estimate dry deposition, although little research on artificial collector surfaces has been conducted recently.

13.2.2 Spatial and Temporal Variation in Throughfall Chemistry

The chemical composition of throughfall varies considerably among biomes (Lovett and Lindberg 1984; Stevens 1987; Ollinger et al. 1993; Lovett et al. 1996; Li et al. 1997; Filoso et al. 1999; Liu et al. 2002; Tobón et al. 2004). A variety of factors influence throughfall chemistry, including dry deposition of various solutes to the forest canopy, intracellular foliar uptake or release, uptake or release by epiphytic canopy communities, and insect infestations. Dry deposition affects throughfall chemistry primarily when aerosol particles settle on canopy leaves and are subsequently solubilized in throughfall (Lovett and Lindberg 1984; McDowell 1998). Canopy exchange processes include both active exchange across the cell walls of the leaves or needles that make up the forest canopy and the uptake or release of solutes by associated epiphytic communities. Foliar uptake of nutrients (Wittwer and Teubner 1959) and nutrient loss from leaf tissue (Tukey Jr 1970) were both recognized over 50 years ago as important processes that can affect throughfall chemistry, but the importance of epiphytic processes has only been widely documented more recently (e.g., Clark et al. 1998; Filoso et al. 1999). Because of the large effects of epiphytes on soluble organic matter, Van Stan and Pypker (2015) hypothesized that canopy epiphytes may play a particularly important role in the organic matter cycles of forest ecosystems. Insect infestations have also been recognized as contributing to variation in throughfall chemistry, with particularly large effects on DOC and DON fluxes. Insect infestations can damage leaves or result in the deposition of waste materials on leaf surfaces that can contribute to throughfall solute fluxes. Le Mellec et al. (2011), in a study of throughfall in oak stands, found that fluxes of DOC increased by a factor of 2.5 with insect infestation, resulting in a flux of 166 kg/ha during the growing season. This flux is similar to or higher than those observed on an annual basis in wet tropical forests (Table 13.2).

Spatial variation in the two primary regulatory processes (dry deposition and canopy exchange) varies by geographic location, extent of pollution sources, and biome. Indeed, even variations within a forest can have an influence on the chemical composition of throughfall. In forests with a wide range of canopy species such as tropical rainforests, the chemical composition of throughfall can differ between neighboring transects in an otherwise similar environment. In the Rio Negro basin of Brazil, for example, phosphate flux was more than double in the stand with the highest flux, compared to the stand with the lowest, apparently due to differences in canopy composition among the stands (Filoso et al. 1999). For base cations the range among stands was lower, with differences of 10–25% depending on the cation. Other small-scale spatial variation in throughfall has been attributed to differential exposure to pollution sources. In Japan, Chiwa et al. (2003) found that pine forest sites with exposure to urban atmospheric inputs had higher solute fluxes, while nearby sites facing away from the urban area had lower NO_3^-, NH_4^+, and SO_4^{2-} net throughfall deposition.

Throughfall solute concentrations can vary during an individual storm as well as by season, providing potential insights into the drivers of temporal variation in throughfall chemistry and elemental fluxes. One of the most thorough examinations of variation in throughfall concentrations during storms found that the concentrations of most ions peaked early in a storm, as sources (dry deposition, internal pools of readily leachable solutes) tended to become depleted following the initial flushing associated with the start of a rainstorm (Hansen et al. 1994). Seasonal variation in throughfall chemistry has been described in the Rio Negro basin, Brazil by Filoso et al. (1999). They found that dissolved NO_3^- in throughfall was lower than incoming precipitation during the wet season but not during the dry season, suggesting enhanced foliar or epiphytic uptake of nitrate during the wet season. In contrast, the concentration of NH_4^+ in throughfall was higher than the concentration in precipitation during the dry season, suggesting the possibility of higher rates of dry deposition of ammonium aerosols during the wet season (Filoso et al. 1999). In Puerto Rico, seasonality in solute concentrations has been reported for rain (McDowell et al. 1990; Gioda et al. 2011, 2013), with highest NO_3 concentrations in April and May, but throughfall at the site shows few seasonal patterns (Heartsill-Scalley et al. 2007). More long-term studies are needed to assess the seasonality of throughfall chemistry in multi-year studies across the globe.

Sampling interval can affect throughfall chemistry, as solute concentrations can change while samples are held in collection vessels prior to removal and processing for chemical analysis (Thimonier 1998). Biologically active solutes such as nutrients or organic matter, and the solutes that can be leached from particulate matter (dust, pollen) are susceptible to potential changes due to collection frequency. The influence of collection frequency on the chemical composition of throughfall samples is variable, with reports of both increases and decreases in the concentrations of various solutes (reviewed by Thimonier 1998). Early assessments of the stability of bulk and wet-only deposition chemistry reported little influence of collection interval on chemical concentrations (Galloway and Likens 1976; Madsen 1982; Thimonier 1998) but the influence of collection interval on throughfall chemistry is much less well documented. Van der Mass and Valent (1989) found an increase in the concentration of ammonium when throughfall samples were collected at longer intervals, which they attributed to mineralization of organic matter in the collector prior to sample retrieval. Decreases in the concentration of throughfall ammonium as a function of collection interval have also been observed, and pH has been observed to both increase and decrease with collection interval (Liechty and Mroz 1991; Ferm 1993; Thimonier 1998). Routine sampling programs for throughfall are often weekly (Heartsill-Scalley et al. 2007), although biweekly (e.g., US National Ecological Observatory Network) and monthly (e.g., Oulehle et al. 2017) collection intervals have been employed. Interpretation of throughfall chemistry should include assessment of the possible impacts of collection interval on solute concentrations, particularly in regions where acid deposition is not driving throughfall chemistry to low pH values.

13.2.3 Dissolved Organic Matter in Throughfall

Dissolved organic matter (DOM) is a particularly important and enigmatic solute flux in forest throughfall. On a mass basis, it represents one of the dominant solutes in throughfall. Even when measured by its carbon content alone (as DOC), which explicitly underestimates the overall solute load found in DOM by excluding the nitrogen, hydrogen, and oxygen content of organic compounds, DOC is typically dominant (e.g., Table 13.2). Little of the DOC in throughfall, which can range up to an average of 57 mg L^{-1} at individual sites (Table 13.3), is from precipitation, which globally averages only about 1–2 mg L^{-1} (Willey et al. 2000). The recent compilation of throughfall DOC concentrations by Van Stan and Stubbins (2018) shows a strong latitudinal trend in DOC concentrations, suggesting that there are fundamental differences in the production of throughfall from the tropics to the boreal zone. This broad global generalization includes many different forest types, as well as latitudinal patterns in the length of the growing season, precipitation, and temperature. All of these co-varying factors should be investigated in order to understand what is driving spatial variability in this important carbon flux among forest ecosystems. Biome-scale patterns may also be obscured by regional factors. In a study of similar Canadian northern hardwoods forest communities, DOC concentration was 30% higher at a northern than a southern site (in keeping with the global pattern) but was attributed to higher rainfall in the southern site, rather than any difference in DOC flux as a function of latitude (Liechty et al. 1995).

Compared to the other dominant solutes in throughfall (Na^+, Cl^-, or SO_4^{2-}), DOC is the only major solute contributed almost entirely by biotic processes, as high SO_4^{2-} is usually from dry deposition of anthropogenic pollutants (e.g., Lovett and Lindberg 1984) and Na^+ and Cl^- are largely from marine aerosols when found in high concentrations in precipitation (e.g., McDowell et al. 1990). Whether from leaf leaching, aphid excretion, insect feces, or epiphytic sources rich in DOC such as tank bromeliads (Richardson et al. 2000), DOC in throughfall is derived almost exclusively from sources that originate in the forest canopy, rather than materials deposited on the canopy by atmospheric processes. Potassium is the only other solute in throughfall that is almost exclusively from vegetative sources (rather than deposition) and is thought to be derived largely from leaching of intracellular sources within the canopy (Tukey Jr 1970; Hansen et al. 1994). Examination of possible mechanistic links between production of K^+ and organic solutes in throughfall has not yet been undertaken.

13.3 Ecological Impacts of Throughfall

13.3.1 Effects on Forest Floor Respiration, Greenhouse Gas Production, and Microbial Activity

It is difficult to disentangle the effects of throughfall (water and solutes) from the effects of water alone on the biogeochemistry of the forest floor. Observational studies can only be used to make inferences about the possible roles of water, nutrients, or organic matter that are all delivered to the forest floor by throughfall. Multiple experiments have been conducted to examine the effects of both solute additions (e.g., NITREX and other nitrogen saturation experiments; Lamersdorf et al. 1998; Aber et al. 1998) and water additions or removals (e.g., Lamersdorf et al. 1998; Nepstad et al. 2007) on plant growth and forest floor processes. The design of most experimental additions or removals of throughfall rarely considers the role of water alone, and thus it is difficult to untangle the effects of added water and solutes on any forest floor response. Typical responses to manipulations of incoming throughfall or water input in tropical forests include modest changes in soil greenhouse gas fluxes in a wet tropical forest subjected to additional water input (Hall et al. 2013), reduced tree growth in Amazonian forest subjected to decreased water inputs (Nepstad et al. 2007), and increased greenhouse gas production when additional water input was provided in a seasonally dry Amazonian forest (Vasconcelos et al. 2004). These manipulative experiments suggest that the spatial and temporal heterogeneity of throughfall might drive hot spots and hot moments of biogeochemical fluxes in the forest floor (McClain et al. 2003; Siegert et al. 2017; Van Stan and Stubbins 2018).

In temperate forests, Kalbitz et al. (2007) found that doubling the amount of throughfall that reaches the forest floor of a Bavarian forest affects the microbial transformation of mineral nitrogen and production of DON. They found that when the amount of throughfall increased long-term, there was a significant decline in the concentrations of DOC and DON in the forest floor (Kalbitz et al. 2007). This experiment did not separate the importance of water fluxes and other biogeochemical inputs on the production of dissolved organic matter (DOM). Another long-term throughfall manipulation shows that significant changes in deep rooting can occur during a 12-year manipulation (Johnson et al. 2008). Johnson et al. (2002)

studied the effects of manipulating throughfall fluxes on soil leaching by decreasing (−33%) or increasing (+33%) total throughfall. By contrasting these treatments to the unmanipulated control, they found that nitrogen fluxes in soil solution increased in the wet treatment and decreased in the dry treatment (Johnson et al. 2002). Ion concentrations increased in the dry treatment but were unchanged in the wet treatment. These differences were attributed primarily to the differences in soil water flux with increasing depth (Johnson et al. 2002). After 12 years of throughfall manipulation, however, relatively few long-term biogeochemical changes resulted from either of the experimental treatments (Johnson et al. 2008).

13.4 Evolutionary Implications of Throughfall Biogeochemistry

The loss of nutrients and organic matter from canopy foliage and other components of the canopy ecosystem such as epiphytic bromeliads has uncertain implications for the evolution of forest vegetation and forest canopies. The measurement of throughfall biogeochemistry at the stand level has been driven largely by consideration of the impacts of atmospheric pollution and the extent to which vegetation takes up, responds to, or transforms atmospheric pollutants such as acidic deposition (e.g., Lovett and Lindberg 1984). This focus emphasizes the important role of throughfall as a responsive component of the forest ecosystem that can buffer the underlying forest floor from various inputs.

Early work on throughfall in the flux of DOC through forest ecosystems (e.g., McDowell and Likens 1988) did emphasize the importance of throughfall as a distinctive flux of organic matter with characteristic functional groups (more carbohydrates, less phenolics) than those fluxes deeper in the solum, but the implications of this distinctive chemical signature have not been fully explored. Throughfall can be metabolized as an energy source by microbes, as was established decades ago by seminal papers such as Qualls and Haines (1992). Nevertheless, there has been a surprising lack of investigation into the specific physiological role that throughfall may play in fueling or inhibiting microbial communities and seedling success on the forest floor (Levia et al. 2017), although some research groups have addressed this topic recently (Bischoff et al. 2015).

When compared to the role that other organic compounds are known to play in the ecology of forest communities and ecosystems, the lack of information on the function and evolutionary significance of organic matter in throughfall is striking. Decades of research have focused on the role of volatile compounds that are released by forest canopies under attack by herbivores (Baldwin and Schultz 1983; Dicke and Baldwin 2010) and that appear to serve as a form of communication among plants. To what extent does dissolved organic matter production in throughfall represent simply an unfortunate waste of energy, or purposeful release of organic compounds that drive a specific response in the forest floor? The example of juglone provides some evidence that throughfall release of DOC may be more than an accident. The throughfall and foliage of black walnut trees, *Juglans nigra* L., are known to release the compound juglone in throughfall, which is phytotoxic to all but black walnut seedlings (Gabriel 1975; Von Kiparski et al. 2007). These early observations of what is termed "allelopathy" have led to dozens of studies of plant interactions, which typically provide experimental evidence of the phytotoxic or insecticidal properties of various foliage. Although originally published as a contribution to the field of chemical ecology, interest in the topic has now contributed to explosive growth in the field of alternative agriculture and organic farming using natural plant defense mechanisms (Macías et al. 2019). In a similar vein, allelopathy is now being used in attempts to control harmful algal blooms through the use of allelochemicals (Tan et al. 2019). Despite this successful translation from forest ecology to organic agriculture and aquatic ecology, understanding of potential allelopathy and the ecological role of organic matter in throughfall has lagged behind. The strong latitudinal variation in throughfall DOC concentrations (Table 13.3) suggests that there may be different drivers controlling DOC leaching from plant canopies among biomes, with uncertain implications for ecosystem function and evolution of forest plants.

13.5 Future Directions

Future research on the role of throughfall in forested ecosystems should focus in three primary areas: temporal dynamics, elemental interactions, and functional significance. These focal areas are not meant to be mutually exclusive, and in fact a robust research portfolio on throughfall should include all three. Our review shows that there is remarkably little long-term data on throughfall chemistry. Throughfall biogeochemistry is likely to change as a function of changing climate, changing rates and nature of atmospheric deposition, and changing stand age or composition. Despite these well-recognized changes in the forest environment, throughfall response to long-term drivers has typically been limited to sites documenting dramatic changes in atmospheric deposition (e.g., Oulehle et al. 2017) and forest dynamics in response to major canopy disturbance by hurricanes (e.g., Heartsill-Scalley et al. 2007). Other more subtle or gradual changes that might be occurring as a result of drivers such as increased atmospheric CO_2 concentrations or warming remain unexplored. Three of the best-studied forest ecosystems in the USA, for example, the Hubbard Brook, Coweeta, and HJ Andrews Experimental Forests, have ongoing hydrological and biogeochemical measurements of forest function, but no long-term sampling of throughfall chemistry.

Understanding the elemental interactions that drive biogeochemical fluxes from the forest canopy is another area that has received relatively little study in the past few decades. After a flurry of intensive work on the effects of acidic atmospheric deposition including some studies that spanned several decades (e.g., Matzner and Meiwes 1994), interest in the biogeochemistry of throughfall has waned at most sites in Europe and North America. In regions where acidic deposition has declined, significant opportunities now exist for assessing the fundamental controls on production and alteration of the most important solutes generated by canopy processes (DOC, DON, and K^+). With declines in acidic deposition, before-after studies might provide useful insights into the interactions among these solutes as well as their response to changes in acidity. Similarly, in regions now undergoing extensive acidification of deposition due to increased industrial output, an emphasis on understanding how fundamental changes in canopy biogeochemistry occur during acidification is warranted. To what extent are production of DOC, DON, and K^+ responding to similar or different drivers across a range of acidic deposition? Is there any evidence that production of these solutes is linked physiologically? Another impetus for focusing on the organic matter in throughfall is the widespread increase in DOC in some surface waters in northeastern USA and western Europe (e.g., Gavin et al. 2018, Monteith et al. 2007). Understanding the importance of throughfall as a potential source of DOC to surface waters should take on new importance with the ongoing increases in DOC now observed at a wide range of sites.

Generating new insights into the ecological and evolutionary significance of throughfall, especially the role of specific organic compounds in throughfall, is now possible with recent advances in analytical instrumentation and growing interest in DOC over the last thirty years. Recent work in Germany shows that additional analytical chemistry might help to provide insights into the role of DOC in throughfall. Bischoff et al. (2015) studied beech and spruce throughfall with solid-state ^{13}C nuclear magnetic resonance spectroscopy with cross-polarization and magic-angle spinning (CPMAS-NMR). They found large differences by species, with much greater proportions of phenolic and presumably recalcitrant molecules in beech throughfall and suggested that this production of aromatic materials might have implications for allelopathic interactions with other tree species. They also make the case that fine particulate organic matter (0.45 to 500 μm) should be studied, as very little is known about its origin or ecological significance in throughfall. Given the extensive body of literature related to allelopathy in crops, ecosystem ecologists should be examining insights from this literature to better understand controls on forest community structure, soil respiration, microbial greenhouse gas production from the forest floor, and carbon accumulation in forest soils.

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