
Throughfall
(Water+Solutes)
Litter
Decomposition

11

Role of Precipitation Partitioning in Litter Biogeochemistry

Robert G. Qualls

Abstract

Passage of precipitation though the plant canopy can conceivably affect litter decomposition in two ways; reduction in *quantity* of precipitation and alteration of throughfall *chemistry*. In many ecosystems, interception ratios are of the magnitude to possibly reduce decomposition rates due to moisture limitations. Simulations indicate that these are especially likely to limit decomposition at higher temperatures, lower monthly precipitation rates, and in the presence of evergreen canopies. However, this review has not located any experiments that directly test the hypothesis that canopy interception can reduce litter decomposition. There have been many observational surveys and experiments with different objectives, such as evaluation effects of climatic change and at least three have noted decreased decomposition rates with partial exclusion of throughfall. Canopy removal by clearcutting or thinning generally reduce decomposition rates because of temperature and moisture effects. The most definite effect of throughfall chemistry on litter decomposition is its effects on immobilization of N and P in litter during the early stages. The two studies that directly address the effects of throughfall on litter decomposition showed that simulated throughfall containing inorganic nutrients increased the uptake of N and P and speeds up the rates of net mineralization but only one showed a difference in mass loss. Studies using fertilization of litter have shown mixed results in its effect on decomposition rate. There is an extremely diverse array of organic substances in throughfall that could hypothetically cause priming effects or even inhibitory effects (e.g. polyphenols). However, these substances are also present in freshly senesced litter and maybe in higher concentration in litter. However, experiments using realistic concentrations characteristic of throughfall appear to be lacking.

Keywords

Litter decomposition • Throughfall • Stemflow • Mineralization • Carbon • Nitrogen • Phosphorous • Moisture • Water

11.1 Introduction

Since precipitation that falls on plant litter lying on the soil surface has generally passed through the plant canopy, it can conceivably affect litter decomposition in two ways; reduction in *quantity* of precipitation and alteration of throughfall *chemistry*. Factors that are generally known to affect decomposition can be divided into external and intrinsic factors (Berg and McClaugherty 2014) that result from intersecting biotic and abiotic influences (Fig. 11.1). Examples of external factors include moisture content, temperature, exogenous nutrient supply (N, P, and others), oxygen supply, pH of the external solution, salinity, UV radiation, decomposer community, and dissolved organic matter. Factors intrinsic to the litter substrate include initial contents of carbohydrates, lignin, N, P, polyphenols, soluble organic matter, and the N/lignin ratio. Of these factors which have been known to affect litter decomposition, canopy interception and chemical modification of throughfall would most likely affect the external factors. The most likely of these to be modified would be moisture content (by reducing

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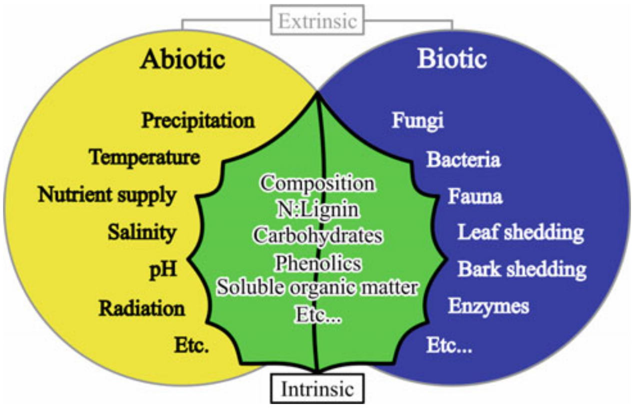
Fig. 11.1 Illustration showing common biotic and abiotic influences and their relationship with intrinsic and extrinsic factors affecting litter decomposition



net precipitation), nutrient supply (via inputs of N, P, Ca, etc.), pH of the external solution, and certain components of dissolved organic matter (DOM) leached from the canopy or stems. We should recognize that the presence of the canopy itself exerts a strong influence on temperature of the litter, evaporation rates from litter, and UV radiation. However, this discussion will not include those effects directly, except that in field experiments it is often difficult to separate the effects of shading from effects of its alteration of throughfall quantity and composition.

11.1.1 The Composition and Boundaries of Litter

Litter includes shed leaves, woody debris, shed bark, and reproductive parts. It may also include roots that have grown into the plant debris, fungi, bacteria, and fauna. In USDA terminology, the O horizon is the organic horizon that overlies the mineral soil boundary. The upper portion is the Oi horizon (i.e., the L horizon), which consists of plant litter that is only slightly decayed, retains some light brown color, and is not highly fragmented. Below that is the Oe horizon, which is more highly fragmented, dark brown or gray, but the origin of the materials is still apparent visually. The lowest horizon is the Oa, (i.e., “humus”, or H layer) which is very dark or black, the origin of the material is not obvious, except for woody debris, and roots and the material can be smeared, leaving a black stain that reflects the humic substances that comprise a large portion of the organic matter.

11.1.2 Scope of This Review

There have been very few experiments that have been directly aimed at distinguishing the effects of canopy interception or alteration of throughfall (or stemflow) chemistry on litter decomposition. In this review, only two studies were located that explicitly aimed to determine the effect of throughfall on litter decomposition in a way that specifically compared it with the absence of a canopy (Beare et al. 1989; Seastedt and Crossley 1983). Both of these studies noted a significant effect on nutrient cycling in the enclosed litter, but only one found an effect on mass loss (Beare et al. 1989). These will be discussed in subsequent sections. Because of the scarcity of studies that directly address the effect of throughfall on litter biogeochemistry, this review will discuss the known effects of the canopy and canopy interception on the forest floor environment and the *possible* effects that have been shown to be in some way, to control litter decomposition and biogeochemistry.

As a set of examples of a studies of throughfall and stemflow in an ecosystem biogeochemistry perspective, this review will periodically refer to studies from the Coweeta Hydrologic Laboratory because it has been an early center for studies of interception effects on the watershed scale, detailed hydrologic budgets, studies of litter biogeochemistry, and studies of throughfall chemistry and fluxes on a watershed scale (Swank and Crossley 1988; Swank and Webster 2014). While the term “forest floor” may be used in this review, any environment under a vegetative canopy (e.g., under shrubs, grass canopies, crop canopies, tundra vegetation) is included. This review will conclude by suggesting experimental approaches to address the gaps in knowledge.

We will summarize the hypothetical effects of canopy interception including (a) interception reduction of precipitation *quantity* on litter moisture, and (b) throughfall chemistry nutrient deposition, pH alteration, and organic substances. As a caveat, we will also review the many other indirect effects (e.g., litter temperature, evaporation) that may be confounding factors in interpreting studies.

11.1.3 Scale of Experiments

Experiments that may evaluate the effect of the canopy on the forest floor could be classified as (a) observational (e.g., canopy gaps compared to areas with canopy), (b) field manipulations (e.g., canopy removal, throughfall diversion, artificial canopy replacement or irrigation), or (c) laboratory incubations or mesocosm experiments. There are advantages to each. With observational studies or field manipulations there could be other associated effects on the forest floor, such as temperature, UV radiation, litterfall reduction that are *not* due to the effects on throughfall alteration. Laboratory incubations are capable of isolating the effect on quantity and chemistry, and typically include controls, but may not include other factors present in the actual environment (such as wetting and drying cycles).

11.2 Effects of Canopy Interception on Moisture Supply for Litter

The first question we should ask is whether the quantities of interception are large enough to significantly affect the litter moisture regime. We might also ask whether litter decomposition would be affected in ecosystems in very moist environments such as rain forests. A widely cited early review by Parker (1983) gave a general range of values for interception found in studies of 2–30%. For stemflow the values given were 0–30%. Other more extensive ranges for interception are given in previous chapters in this volume. Since the distribution of small versus. large precipitation events affect I/P (interception as a percentage of precipitation) and potential evaporation are important, a study by Radtke et al. (2001) is useful because they simulated I/P from hourly precipitation records of a large number of stations for deciduous forests spanning the latitudes of the eastern U.S. The majority all values of I/P ranged from 2 to 22%. Generally, sites with less precipitation and sites at more southerly latitudes had greater I/P ratios. For effects on litter decomposition, values of 2% may be difficult to distinguish, but values over the median, about 12% might hypothetically be significant where moisture limits litter decomposition. Where snow dominates precipitation, effects may be very different and these are dealt with in a separate section. Leaf area index and its seasonality, as well as the extent to which the canopy was “evergreen” was important in interception (Radtke et al. 2001). For example, Gerrits (2010) cited a number of studies of conifer forests in which the I/P varied from 10 to 42% (median 32%) for 17 studies. Total forest interception capacities ranged from 15 to 42 mm. Thus, we might expect an evergreen canopy with a high leaf area index to be more likely to affect the moisture status of the litter beneath. In fact the impact of changing a deciduous canopy to an evergreen canopy was demonstrated on a watershed scale at the Coweeta Hydrologic Laboratory, in which a young pine plantation decreased streamflow compared to an adjacent control deciduous watershed (Swank 1968). The interception was more important than transpiration in causing the difference. The difference in interception was significant in the growing season but was much greater during the season in which the deciduous canopy had undergone leaf fall. Litter decomposition rates were slower in the pine plantation compared to the adjacent deciduous forest the first two years but then were similar over the entire 13 years of the decomposition study (Qualls 2016). However, the high lignin content of the pine litter made it impossible to separately evaluate the effects of lower net precipitation on the forest floor.

The distribution of small precipitation events is important because an event with insufficient precipitation to “saturate” the canopy is likely to have little ability to influence litter moisture as a result of being nearly completely intercepted. Two thresholds may be important in considering the effect of interception on litter moisture during an individual precipitation event (1) canopy interception capacity, and (b) litter interception capacity. This may be simplified as a two “bucket” system where the canopy capacity must be filled before the litter begins to become moistened and the litter water storage capacity must be filled before the maximum moisture capacity of the litter is attained (e.g. Fig. 11.2). In a review of literature values, Gerrits (2010) listed values ranging from 0.2 to 3.8 mm precipitation per event for canopy water storage capacity and values of 0.6–2.8 mm per event for litter water storage capacity (although few studies were available). For the studies with conifer canopies, the water storage capacities ranged from 0.75 to 3.8 mm (excluding one outlier of 0.2) and a more recent study on *Pinus elliottii* litter where the water storage capacity equaled 3.2 mm (Van Stan et al. 2017). In a situation where the litter is initially dry, then it might be presumed that litter respiration would increase until the water storage capacity is reached.

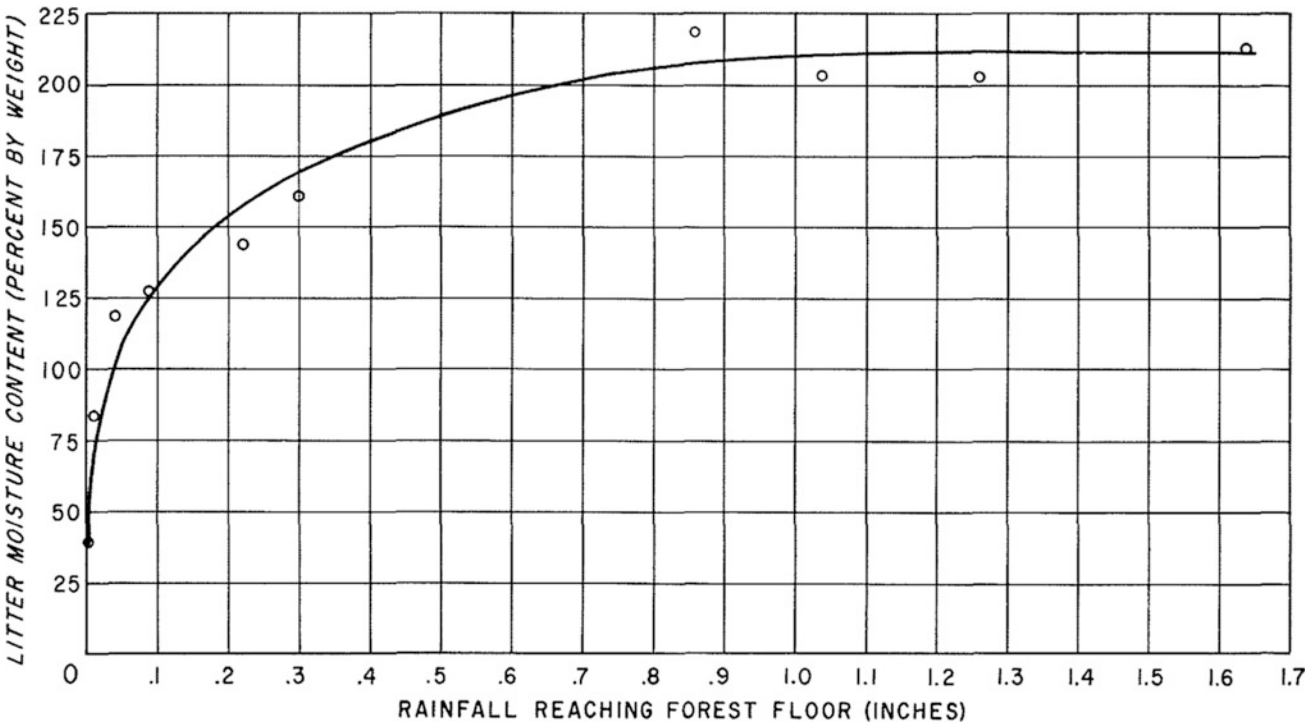


Fig. 11.2 The amount of throughfall necessary to wet the forest floor to its maximum water holding capacity after allowing it to drain for 24 h. While protected from evaporation (Reproduced from Helvey 1964, U.S. Forest Service). Measured in a mixed deciduous forest at the Coweeta Hydrologic Laboratory. Litter interception (evaporation) was 5.6 cm for the year, canopy interception was 25.9 cm, or 15% of precipitation during the year of measurement. Each point represents a particular storm, so note that 60% of the storms did not fully wet the litter to its moisture holding capacity

This simple view is complicated by the fact that the antecedent litter moisture content can affect the actual capacity and that evaporation from the litter creates varying moisture contents between wetting events. However, models that incorporate water storage capacity, rainfall intensity, and evaporation rates have been used to simulate litter moisture content over time (Bulcock and Jewitt 2012).

11.2.1 Simulations of the Hypothetical Effect of Interception on Litter Decomposition

Are the observed reductions in net precipitation large enough to affect decomposition? First, we should consider the general relationship between decomposition (or respiration) and litter moisture content. The effect of temperature and moisture must be considered simultaneously. For example, dry litter at high temperature is unlikely to respire as much as under average conditions. Wet, but frozen, litter is also likely to respire less than under average conditions (however, see the later discussion on decomposition under snowpacks). Most data on litter moisture during decomposition is measured in units of g water per g dry weight of litter or gravimetric % water. A more direct measure of water availability to decomposer microorganisms is water potential, but it has not been measured in most studies. Paul (2001) summarized a number of models for the response of soil mineralization (N mineralization) and assembled a general model for the temperature *at optimum moisture content* that is exponential up to about 40 °C:

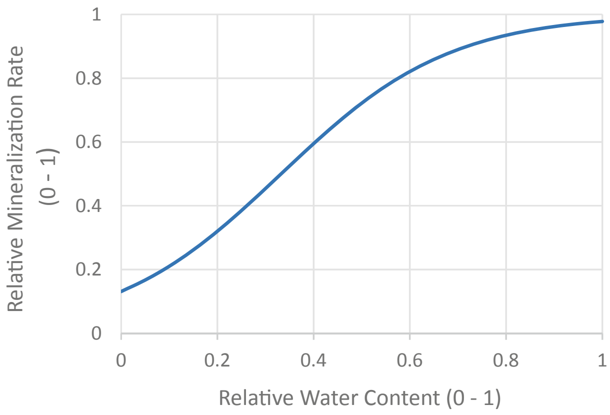
$$\text{N mineralization rate} = \exp\left[3.36\,(\mathrm{T} - 40)/(\mathrm{T} + 31.79)\right] \qquad (11.1)$$

where T is temperature.

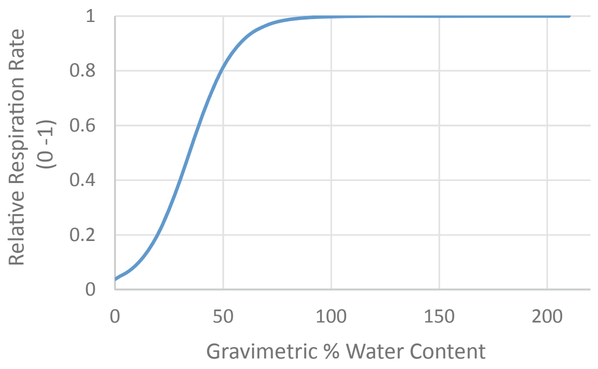
Curves of mineralization as a function of relative water content are generally hyperbolic or logistic, that is, they rise with water content with decreasing slope until a maximum is reached. The equation presented by Paul et al. (2003) relates the relative mineralization rate or respiration rate at a given temperature ($R_{\mathrm{max\ at\ T}^\circ}$) as a logistic equation:

Fig. 11.3 Relationship of relative mineralization of N (**A**) or litter respiration (**B**) plotted from an equation derived from Paul et al. (2003). Relative mineralization or respiration is scaled from 0 to 1 representing the minimum and maximum observed at a given temperature. The relative water content in panel **A** is scaled to represent the minimum and maximum water content observed in the field (or incubation). The difference in the approach to the asymptote between panels **A** and **B** probably reflects the different relationship of water content to matric water potential between litter and soil

(A) Relative N Mineralization Rate (0-1)



(B) Litter Respiration as a function of % Water Content (water / dry mass)



$$R_{\text{max at T°}} = 1/[1 + a * \{\exp\ (b * M)\}] \tag{11.2}$$

where M is the gravimetric % water content, and a and b are coefficients derived from a set of data. Figure 11.3a, b illustrate this logistic relationship of N mineralization (Fig. 11.3a) and respiration rate of incubated litter (Fig. 11.3b) that may decline at values near saturation (Paul 2001). A decline at values near saturation might be attributed to restriction of oxygen supply when the pore spaces become filled. In the case of litter that is not submerged in a depression or with otherwise restricted drainage (e.g., the frozen tundra), oxygen restriction may be less common and less applicable to the question of the effects of net precipitation reduction. The application of Eq. 11.2 to the effect of interception is that net precipitation that would result in reduction of water content in the "steep" portion of the curve would result in the greatest impact on litter and soil microbial content.

A model presented by Raich et al. (2002), was based on global soil respiration data and expressed soil respiration as an integrated function of monthly average temperature and precipitation (as an approximation of water availability). It is:

$$R_{\text{monthly}} = R_0 * e^{(Q * Ta)} * [P/(K + P)] \tag{11.3}$$

where equation R_{monthly} is the mean monthly soil respiration (g-C m^{-2} d^{-1}), R_0 (g-C m^{-2} d^{-1}) is the soil respiration at 0 °C without moisture limitation, Q defines the exponential relationship between soil respiration and temperature, and K (cm) is the half-saturation constant of the hyperbolic relationship of soil respiration with monthly precipitation. Raich et al. (2002)

Table 11.1 Effect of increasing I/P (0–30%) on soil respiration, for average temperature (T) of 20 °C, precipitation = 10 cm month^{-1}. Precipitation refers to that above the canopy and net precipitation to that below the canopy

Ave. T (°C)	Precipitation (cm month^{-1})	Net precipitation (cm month^{-1})	Respiration with 0–30% interception (mg-C m^{-2} d^{-1})	% reduction in respiration due to interception
25	10	10.0	3.43	0
25	10	9.5	3.37	1.5
25	10	9.0	3.32	3.2
25	10	8.5	3.25	5.0
25	10	8.0	3.19	6.9
25	10	7.5	3.12	9.1
25	10	7.0	3.04	11.3

found values for the parameters $R_0 = 1.25$ g C m^{-2} d^{-1}, Q = 0.05452 $°C^{-1}$; and the half-saturation constant for monthly precipitation, K, was = 4.259 cm. The effect of the precipitation term, P/(K + P), is such that at very high rates typical of rain forests, the term approaches 1.0. The advantage of this particular model for predicting the effects of interception is that precipitation is incorporated instead of the less frequently measured effects on soil moisture. Consequently, we can estimate the predicted effect of precipitation reduction by a given percentage. There are several reservations that should be noted about applying this model to the reduction in net precipitation and its effect on litter decomposition. First, the time step is monthly and does not consider antecedent moisture conditions explicitly as might be desired for a model that considers individual precipitation events. Secondly, the model is based on soil respiration measured as surface efflux from all soil horizons including some amount of root respiration, and the R_0 factor may reflect different soil temperatures that are present in surface air mean temperatures (and may lead to an overestimate). Thirdly, litterfall also affects soil respiration and is correlated with precipitation and temperature.

By making some simulations with this model we can illustrate the hypothetical impact of interception on soil respiration as a function of (1) the percentage I/P, (2) precipitation using a given I/P, and (3) average monthly temperature, using a given I/P. Table 11.1 presents predictions for a mean temperature of 25 °C, and a mean precipitation of 10 cm month^{-1} for a range of I/P ratios from 0 to 30% Column 3 shows the net precipitation (out of 10 cm precipitation) and column 5 summarizes the percent reduction in respiration compared to the base case (0% interception). This column indicates that there would be significant reductions in soil respiration for I/P ratios typical for many forests. However, the % reduction from the base case is not as large as the % reduction in precipitation. For example, a 30% I/P ratio, typical for many coniferous forests (see earlier section), would only reduce respiration by about 11% (Table 11.1). This occurs because of the hyperbolic nature of the precipitation term so that at a precipitation of 10 cm/month, a 30% increase or reduction in precipitation does not yield a 30% change in respiration.

The effect of a reduction in precipitation by interception, however, becomes greater at lower rates of precipitation. In Table 11.2, we assume a 30% reduction in I/P ratios for all cases, but vary monthly precipitation from 10 down to 1 cm month^{-1} (typical of arid or seasonally arid ecosystems). The percentage reduction in respiration increases from 11.3 to 25.8% across this range. Again, the hyperbolic form of the precipitation term means that the slope is steeper at low rates of precipitation. Intuitively, we should expect that reductions on precipitation would result in greater impacts on respiration as water becomes more limiting. This principle could be illustrated with examples from seasonally arid communities such as the Pinyon-Juniper communities of the Western United States. Although the trees are widely spaced, the leaf area under the

Table 11.2 Effect of decreasing average precipitation, but with a constant I/P of 30%, and T = 25°C

Ave. T (°C)	Precipitation (cm month^{-1})	Net Precipitation (cm month^{-1})	Respiration without interception (mg-C m^{-2} d^{-1})	Respiration with interception (mg-C m^{-2} d^{-1})	% reduction in respiration due to interception
25	10	7.0	3.43	3.04	11.3
25	5	3.5	2.64	2.20	16.5
25	3	2.2	2.02	1.61	20.1
25	1	0.7	0.93	0.69	25.8

Table 11.3 Effect of decreasing average T (°C), but with a constant I/P of 30%, and precipitation of 10 cm/month

Ave. T (°C)	Precipitation (cm month^{-1})	Net Precipitation (cm month^{-1})	Respiration without interception (mg-C m^{-2} d^{-1})	Respiration with interception (mg-C m^{-2} d^{-1})	% reduction in respiration due to interception
25	10	7.0	3.43	3.04	11.3
20	10	7.0	2.61	2.31	11.3
15	10	7.0	1.99	1.76	11.3
10	10	7.0	1.51	1.34	11.3
5	10	7.0	1.15	1.02	11.3
0	10	7.0	0.88	0.78	11.3

evergreen canopies is quite dense and litter accumulates only under the canopy and decays slowly (author's personal observation). The accumulation of this litter becomes a fire management problem (https://www.unce.unr.edu/publications/files/nr/2003/cm0301.pdf). Owens et al. (2006) found that only 55% of the precipitation on Ashe juniper canopies in a semi-arid region of Texas reached the mineral soil surface and another 5% was diverted to stemflow. Owens et al. (2006) also speculated on the role of stemflow in delivering water to the root zone. The role of canopy interception plays a significant role in these types of semi-arid or seasonally arid ecosystems.

Table 11.3 presents the results of a 30% reduction in net precipitation as a function of average monthly temperature. While higher temperatures result in exponentially higher respiration (column 4), the percent reduction in respiration for the hypothetical reduction in precipitation of 30% is the same at all temperatures. This effect is a consequence of the fact that the precipitation term in the model is multiplied by the temperature term which is exponential. However, the more important point is that the difference in respiration, *with versus. without* interception, is much larger at higher temperatures (comparing columns 4 versus. 5). This simulation would suggest that a 30% interception under an evergreen canopy would have the same *percentage* reduction in soil respiration in the summer compared to the winter, but that the actual difference in units of g-C m^{-2} day^{-1} would be much greater in the summer because of the greater respiration at higher temperatures.

11.2.2 Studies that Experimentally Vary Precipitation

Given the absence of studies that specifically examine the effect of interception quantity on litter decomposition, we may examine studies in which precipitation is varied either by throughfall diversion or addition by artificial irrigation. Before reviewing these studies, it should be pointed out that the degree of exclusion or irrigation are in most cases greater than would be characteristic of interception effects. The goals of most studies were to simulate the effect of climatic change, e.g., droughts.

11.2.2.1 Rainfall Manipulation in Tropical Rain Forests

From the simulation shown in Table 11.2, it might be expected that rainforests would be less likely than other ecosystems to show a reduction in litter decomposition rate from the effect of interception. However, a throughfall exclusion experiment in a rainforest in Costa Rica demonstrated a 20% reduction in litter decomposition rate in a treatment in which throughfall was reduced by about 30% (Weider et al. 2009). The difference was significant during the early phases when leaching of dissolved organic matter may be expected to dominate weight loss and in the later stages when the authors believed microbial decomposition dominated. The actual interception under the canopy in the control area was difficult to estimate since the coefficient of variation was ±21%, but the mean was only 1.1% interception. The treatment probably may have excluded more throughfall than actual interception would. In a seasonally dry rainforest in the Amazon Basin, Nepstad et al. (2002) found no differences in litter decomposition rate in an experiment that excluded about 50% of rainfall. Litter decomposition rates were similar between the two plots, showing little treatment effect. In fine mesh litterbags, which excluded litter meso- and macrofauna, they found temporary slowing of decomposition following initiation of the throughfall exclusion but this effect disappeared by the next sample date. It is possible that the lack of effect of throughfall effect on decomposition may have been related to the greater influence of macrofauna. A study in the Eastern Amazon that had a pronounced dry season, used irrigation to simulate additional precipitation during the dry season and found that decomposition of litter was increased compared to controls (Vasconcelos et al. 2007). Using litter decomposition across a precipitation gradient ranging from about 50–500 cm per year in tropical forests of Hawaii, Austin, and Vitousek (2000) found that decomposition rates were linearly related to precipitation and precipitation continued to influence decomposition even at the wettest sites.

Another rainfall exclusion study was done along an elevation gradient in the rainforests of Ecuador (Krashevska et al., 2012). This study excluded all precipitation from an area of 1.5 m^2 and would thus be more extreme than the effects of interception, but it did show that throughfall exclusion reduced microbial biomass and respiration by about half, fungal biomass by 23%, and nearly all testate amoebae disappeared (91%). It was notable that fungal biomass was more tolerant to drier conditions than overall microbial biomass and may suggest that fungal biomass may be more tolerant to areas subject to high rates of canopy interception.

11.2.2.2 Rainfall Manipulation in the Temperate Zone

Several throughfall exclusion experiments in the temperate zone have been oriented toward the effects of summer drought. In a study in the Harvard Forest (Borken et al. 2003), throughfall was completely excluded during the summer of two years, but not excluded the rest of the year. There were large and significant reductions in soil respiration caused by the throughfall exclusion and this difference was mainly attributed to the O horizon. In a lab incubation, respiration increased immediately in response to a simulated precipitation event (Borken et al. 2003). Generally, similar results were obtained with a summer throughfall exclusion in a deciduous forest at Oak Ridge, TN, and USA (Cisneros-Dozal et al. 2007). While these experiments used complete throughfall exclusion only in summer, rather than the reductions that might be expected due to canopy interception, the immediate responses to wetting events may be applicable to precipitation events that are less than enough to saturate the canopy. Reasons for an immediate response may be due to a large stock of extracellular enzymes that are rapidly reactivated by moisture (Nadeau et al. 2007). In contrast, a study by Salamanca et al. (2003), using a 50% throughfall reduction, found no significant difference in litter decomposition in a forest in Japan, although 100% exclusion reduced decomposition rate by about 50%.

In a semi-arid steppe in Patagonia, Yahdjain et al. (2006) used precipitation exclusion at rates of 30, 55, and 85% to examine decomposition of grass litter. Decomposition was inhibited by the 30% exclusion and all exclusion rates. The significance of this study was that 30% is conceivably in the range of some canopy interception rates and that this occurred in a non-forested steppe environment.

11.2.3 Studies on Decomposition in Clearcut Forests and Experimental Gaps

Clearcutting and formation of forest gaps (experimental or natural) are disturbances that remove the canopy and potentially reveal the effect of a reduction in an interception. However, it should be emphasized that canopy removal by these disturbances not only reduce interception, but also expose the litter surface to radiation and temperature changes, higher wind speeds, decreased humidity, and increased soil moisture in the root zone caused by reduction in transpiration.

One of the best-known studies of the effects of clearcutting on decomposition was an experimental cutting of an entire watershed, adjacent to a control watershed with a temperate deciduous forest at the Coweeta Hydrologic Laboratory (Swank and Crossley 1988). Litter decomposition rates of the dominant oak species were 28% lower on the clearcut compared to the uncut watershed (Whitford et al. 1981) despite a rate of 12% interception reduction in the control forest (Swank and Crossley 1988). The authors noted that daily high temperatures at the litter soil interface averaged 40 °C during the summer (it was a south facing watershed), and they speculated that the inhibition may have been due to drying or inhibition of microarthropods. In another study in coniferous forests of British Columbia, decomposition rates of pine litter were lower, slower, and decomposition rates of aspen were similar to those in uncut plots (Prescott et al. 2003). Sites with colder microclimates responded similarly to those with warmer microclimates, suggesting that the rise in litter temperatures alone was not the sole factor. Another study (Binkley 1984) revealed the variety of differences in the Oa horizon of clearcut areas, compared to uncut plots (beyond the reduction in interception) in coniferous forest on Vancouver Island. Cellulose in litterbags decayed at a similar rate on the surface in clearcut versus uncut plots. But, cellulose placed at the bottom of the O horizon decayed much faster in clearcut plots and Binkley attributed the difference due to much higher concentrations of inorganic nitrogen (7–20 times) leaching from the clearcut forest floor.

Gaps in the forest canopy also offer the potential to examine the role of the canopy in the physicochemical characteristics of the forest floor. The most convincing of these type studies are those that vary the size of the canopy gaps. A study by Prescott et al. (2003) used gaps varying from a single tree gap, 0.1 ha, and others up to 10 ha. Despite the effects of reduced interception, forest floor moisture content was consistently *less* as gap sizes increased (including 0.1 ha) and summer temperatures in the forest floor were as much as 2–3 °C warmer in large gaps during the snow-free season. Thus, the authors concluded “drying of litter in gaps may offset the effect of higher temperatures, leading to little change in rates of litter decay even in gaps of only 0.1 ha.” They also cited a number of other studies with similar conclusions (e.g. Cortina and Vallejo 1994; Denslow et al. 1998).

11.2.4 Interception of Snow and Litter Decomposition

The interception of snow is treated as a separate case because of the many different variables concerned. The general ranges for interception of snow are covered in previous chapters of this volume. Besides reducing the volume of precipitation, the canopy may influence the litter by changing the distribution of snow, and snowmelt around the canopy, the extent of exposed litter, and the timing of melting. Snow itself may influence litter by insulating it from freezing, preventing drying between events, and creating long, slow periods of leaching.

The magnitude of interception and subsequent sublimation by coniferous canopies has been cited in the range of 19–25 or 30% (Broxton et al. 2014). Processes that occur during and after a snowstorm include accumulation of snow in the canopy, sloughing of snow, often to the outer edge of the canopy, snowmelt, and liquid throughfall as temperatures rise, and sublimation from snow in the canopy and snowpack (Storck et al. 2002). The lower snow depths under canopies, “snow wells”, is a very widely known phenomenon, even in the popular literature because of their danger (https://en.wikipedia.org/wiki/Tree_well, retrieved 12/17/2018). Broxton also found that areas beneath the canopy had less snow water equivalent than areas just outside the canopy, but that areas just outside the canopy had more snow water equivalent than areas greater than 15 m outside the canopy. The greater snow depth outside but near the canopy was interpreted as sloughing of snow. In a maritime Douglas fir forest, Storck et al. (2002) measured snow precipitation, storage in the canopy, subsequent snowmelt from the canopy and sublimation. They found that about 60% of snowfall was intercepted by the canopy (up to a maximum of about 40 mm water equivalent). Apparent average sublimation from the intercepted snow was less than 1 mm per day and totaled approximately 100 mm per winter season out of an average 2000 mm average winter precipitation. But 72% of the intercepted snow later fell as melted water and 28% of the intercepted snow was removed as large snow masses. The authors noted that sublimation would probably be more significant in drier, colder climates. The significance for litter decomposition in this site might be that most temporarily intercepted snow later fell as liquid on the forest floor although the sloughing effect might redistribute it.

Similar observations were made in a study of dissolved organic matter fluxes in a site at the Mount Shasta Mudflow Research Natural Area in California that also received most of its precipitation as winter snow. Although summaries have been published (Lilienfein et al. 2003, 2004) the following general observations on the fluxes during snow and snowmelt are unpublished observations (by R. Qualls). During a detailed study of the fate of snow interception and its fate during two large snow storms, most snow intercepted by the canopy was fell as liquid throughfall during three subsequent days, in fact the difference between the open area liquid plus snow water equivalent was not significantly different (with a S.E. of 7%). During the storm, snow accumulations on the ground were much greater between the densest portions of adjacent canopies. Liquid throughfall from the melting canopy snow reached the forest floor in areas with less snowpack. However, when snowpacks were deeper, the liquid throughfall tended to be absorbed in the interstices of the snowpack rather than reaching the forest floor and later froze at night to form much denser (more snow equivalent water per cm snowpack) in areas under trees, often forming layers of darkly stained snow/ice). Thus, much of the apparently shallower snowpack under trees contained more snow water equivalent than it appeared. Nevertheless, there was a significant accumulation of water in both lysimeters just above and under the forest floor during the periods of liquid throughfall from canopy snowmelt and throughfall collectors had high concentration of dissolved organic carbon (DOC) during these events. Forest floor litter under snow remained consistently wet, but unfrozen, throughout the winter. However, forest floor that was exposed was often observed to be frozen.

Although litter decomposition was not measured in the Mt. Shasta study, other studies from areas where most of the annual precipitation occurs as snow has found that much, if not most of the decomposition occurs under the snowpack (Stark 1973; Taylor and Jones 1990; Brooks et al. 1996). While it may be that litter under the snow remained at 0 °C or lower, apparently decomposers can remain active. Brooks et al. (1996) measured respiration (CO_2 efflux) which was significant when soil temperatures rose above −5 °C under the snowpack. One reservation may be made with some litter mass loss studies is the distinction between loss of dissolved material (e.g., DOC) and respiration. The constantly wet condition and slow, prolonged flux of water under snow may be ideal for leaching dissolved organic matter. Most of the annual flux of DOC from the forest floor at the Mt. Shasta site occurred during snowmelt (Lilienfein et al. 2004).

One study in a subalpine forest in the Sierra Nevada measured soil respiration at the litter surface litter at different distances from the trunks of Jeffrey pine trees (Stark 1973). Most precipitation fell as snow during the winter and early spring. The author observed that the area near the trunk was bare of snow a few days after a snowfall, but the author attributed this effect to radiation from the trunk rather than interception. Soil respiration was least near the trunk and increased progressively with distance from the trunk. The author also observed a stemflow effect: “The tree base is a harsh environment during rains or snowmelt because large quantities of water wash down the trunk and flood the litter at the base.” Also see similar observations by Van Stan and Gordon (2018). The accumulation of litter was also deepest near the tree base which the author suggested was due to slower decomposition.

11.3 Effects of Throughfall and Stemflow Chemistry on Litter Decomposition

11.3.1 Effects of Nutrients in Throughfall

Newly senesced plant litter is generally deficient in N, P and sometimes certain other nutrients compared to the optimal stoichiometry for decomposers (Berg and McClaugherty 2014). There are two possible sources for these elements for decomposers: the organic N and P compounds in the substrate itself, and external (exogenous) sources. The external sources include precipitation, throughfall, stemflow (Berg and McClaugherty 2014), or the surrounding water for aquatic environments (Qualls 1984; Webster and Benefield 1986), and possibly ingrowth of mycelia with external nutrient transport from the soil beneath (Qualls et al. 1991). Recently senesced litter typically gains net quantities of N and P on a basis of g element per g of original mass present and thus must come from sources other than the substrate. This phase of net uptake (i.e., net immobilization) for N often lasts for a year or more until the C/N ratio approaches a ratio of about 30–1 (Qualls 2016) eventually approaching a C/N ratio of about 20 during a subsequent phase of net N mineralization. Elements that are commonly observed to accumulate beyond the initial content in the substrate are: N, P, Ca, S, Mn, Cu, Zn, and Mg (after an initial leaching period on the case of Mg) and throughfall is widely believed to serve as a supply (Blair 1988; Berg and McClaugherty 2014). Although K is leached into throughfall from the canopy, generally it is also leached from plant litter and does not exhibit net immobilization. In streams, use of ^{15}N labeled litter has confirmed the uptake of nitrate from streamwater into microbial biomass in the decomposing litter (Cheever et al. 2013).

11.3.1.1 Elements Enriched in Throughfall

Several elements involved in the nutrition of decomposers are enriched in throughfall compared to bulk precipitation: N (sometimes), P, Ca, Mg, K, Cu, Mn, and other micronutrients (see Chap. 5 in this volume, Johnson and Lindberg (1992). In the case of inorganic nitrogen, the canopy can either be a source or a sink. For example, in a European wide gradient with a large number of sites (Kristensen et al. 2004) the ratios of throughfall nitrate to bulk precipitation nitrate were calculated. Most sites had ratios varying between 1:1 and 3:1, indicating that most sites had considerably higher concentrations in throughfall than in bulk precipitation. However, at sites with low levels of N deposition (less than about 5 kg-N ha^{-1} y^{-1}), assimilation of inorganic N by canopy leaves actually *decreased* the fluxes in throughfall. But at more polluted sites, the leaching of deposited N *increased* the concentrations in throughfall. Throughfall inputs include a large amount of dry deposition in addition to that in bulk precipitation including N forms in aerosols and gaseous phases (Johnson and Lindberg 1992). Conifers are generally more efficient at trapping dry deposition, and canopy roughness generally increases dry deposition (Kristensen et al. 2004). The ecosystem wide effects of this deposition on the forest floor were pervasive, resulting in increased soil solution and streamwater nitrate concentration. The role of the litter horizon was indicated by a correlation of forest floor C/N ratio and soil solution nitrate levels This correlation could indicate either the evergreen foliar litterfall contained higher N concentrations where N deposition is high or that high C/N ratios in litter were more effective in immobilizing N in deposited in throughfall. Phosphorus, calcium, and magnesium are also deposited in dust on the canopy leading to increased concentration in throughfall compared to bulk precipitation (Johnson and Lindberg 1992). For example, 70% of PO_4-P, and 21% of Ca was deposited in dryfall in a wet/dryfall precipitation collector in an open area at Coweeta Hydrologic Laboratory (Swank and Crossley 1988).

Van Stan and Gordon (2018) have pointed out that there is an area near stems that can be drier and have lower fluxes of nutrients than would otherwise be present in throughfall because the stemflow is being “funneled” from an extensive area. When voluminous, stemflow is generally considered to bypass most of the surrounding litter and preferentially infiltrate at the base of the stem (Johnson and Lemann 2006).

In an experiment using senesced litter of rye and crimson clover nutrients, Beare et al. (1989) applied simulated throughfall, containing only the inorganic ions. They found the simulated throughfall increased the decomposition rate of rye litter but not that of the more nitrogen-rich clover litter over that of deionized water controls, at least in the absence of microfauna. The total fungal hyphal length was greater during the early phases of decomposition of rye litter in the artificial throughfall treatment. In addition, the rye subjected to the artificial throughfall immobilized more N, P, and Ca than the deionized water controls. This experiment is one of the very few that purposely examined the effect of nutrients in throughfall and used control for moisture effects. The experiment is also important for its application to agro-ecosystems. Also, by excluding organic components of throughfall it was able to isolate the effects of inorganic nutrients leached into throughfall. In another study of the effect of simulated throughfall on decomposition of litter in a forest, additions of artificial throughfall alone had no effect on litter decay rates but presence of microfauna increased decomposition rates. Simulated throughfall did, however, increase the nutrient *concentrations* in the decomposing litter, and the treatment with both microfauna and simulated throughfall generally exhibited the highest nutrient concentrations.

Thus, the clearest effect of throughfall, and possibly stemflow, on litter biogeochemistry is in the contribution to net immobilization of nutrients in litter in the initial phases of decomposition (Beare et al. 1989). In experiments where N or P is supplied in greater concentration, greater amounts are immobilized on litter in the initial stages. Although aquatic studies do not involve throughfall directly, there are many examples of increasing decomposition rates and N and P immobilization with increasing concentrations in the surrounding water (Qualls 1984; Webster and Benefield 1986; Qualls and Richardson 2000; Cheever et al. 2013) although it is suspected that throughfall directly falling into headwater stream channels is a source of N and P since it is found in much higher concentrations during stormflows (Webster and Benefield 1986). In terrestrial fertilization studies of forest litter, N, and P are also immobilized in increased quantities (Hobbie 2005; Perakis et al. 2012; Emmett et al. 1995, McGill and Aber 1998) in response to increased N and P availability. In air pollution studies along gradients or experimental throughfall addition, N is also immobilized in increased quantities (Armentano and Loucks 1990; Berg and Matzner 1997; Boxman et al.1998; Kuperman 1999). Perakis et al. (2012) also showed that net immobilization of N from fertilized treatments was greater when N concentration in the initial litter substrate was lower.

11.3.1.2 What Is the Fate of Nutrients in Throughfall that Are Taken up in the Forest Floor?

The following example is taken from a study of fluxes of N, P, and C in precipitation, throughfall water percolation from the O horizon and litterfall from a deciduous watershed in the southern Appalachian Mountains at the Coweeta Hydrologic Laboratory, shown in Table 11.4 (Qualls et al. 1991, 2002). Canopy interception (computed from both throughfall and stemflow) was estimated at 12% of precipitation (reported in Qualls et al. 2002). As precipitation passed through the canopy it was enriched in nitrate N by about 20% and in ammonium N by about 26% although nitrate was present in higher concentrations. Other studies on adjacent watersheds have shown either net uptake or small leaching effect on ammonium by the canopy depending on season and condition (Johnson and Lindberg 1992). Although the site was affected by anthropogenic N deposition, it was below the threshold of about 5 kg/ha/y of inorganic N deposition given by Kristensen et al. (2004) for large increases in inorganic N in throughfall in the European gradient study. Phosphate P fluxes also increased by about 20% passing through the canopy, and about 70% of the phosphate P in bulk precipitation occurred in dryfall. However, the spatial variability in throughfall suggested that some canopy sites or trees were more efficient in trapping the dry deposition. With respect to the fate of inorganic N and P forms in both bulk precipitation and the net contribution of the canopy, much of the inorganic N and P was removed as it passed through the forest floor (a net removal of 70% of inorganic N in throughfall and a smaller percentage for inorganic P. In fact, the fluxes of inorganic N and P from the O horizon were

Table 11.4 Fluxes of N, P, and C forms in bulk precipitation, throughfall, and solution draining from the forest floor under the Oi and Oa horizons (from Qualls et al. 1991). DON is dissolved organic N, DOP is dissolved organic P, and DOC is dissolved organic C. Standard errors on the mean (±) reflect variability between 12 plots, not temporal variability. No error term is shown for bulk precipitation since it was from a single collector (bulk precipitation data from W. Swank, pers. communication)

Stratum	NH_4-N (kg ha^{-1} y^{-1})	NO_3-N (kg ha^{-1} y^{-1})	PO_4-P (kg ha^{-1} y^{-1})	DON (kg ha^{-1} y^{-1})	DOP (kg ha^{-1} y^{-1})	DOC (kg ha^{-1} y^{-1})
Bulk precipitation	0.85	1.9	0.18	0.29	0	0.08
Throughfall	1.07 ± 0.17	2.4 ± 0.92	0.22 ± 0.07	3.79 ± 0.31	0.19 ± 0.02	130 ± 8
Oi horizon	0.59 ± 0.04	0.80 ± 0.12	0.27 ± 0.08	10.2 ± 0.70	0.34 ± 0.07	412 ± 18
Oa horizon	0.39 ± 0.1	0.64 ± 0.13	0.16 ± 0.04	9.95 ± 1.07	0.29 ± 0.04	402 ± 20

Table 11.5 Comparison of nutrient fluxes in throughfall with those in litterfall, and the fate of nutrient input to the forest floor: (leaching or mineralization assuming the forest floor was at equilibrium between litterfall and decomposition). Taken from Qualls et al. (1991)

Process in designated stratum	C	N	P
Bulk precipitation (g m^{-2} y^{-1})	1	0.276	0.02
Throughfall (g m^{-2} y^{-1})	13	0.72	0.04
Litterfall flux (g m^{-2} y^{-1})	220	3.6	0.2
Foliar litterfall flux (g m^{-2} y^{-1})	171	2.1	0.15
Water-extractable litterfall content (%)	21.2	12	57
DOM flux from Oa horizon (g m^{-2} y^{-1})	40.5	1	0.029
[(DOM flux from Oa horizon)/(litterfall flux)] × 100%*	18.4	28	14
Net leaching from the forest floor (%)†	12.5	17.3	4.9
Estimated mineralization within O horizon	149‡	3.32	0.212

*The output in DOM from the forest floor is expressed as a percentage of the potentially soluble input in litterfall (which here includes throughfall)
†The net leaching from the forest floor was calculated as: [(dissolved organic flux from Oa horizon) − (throughfall dissolved organics)] × 100/litterfall flux
‡From Qualls (2016), 4 g-C m^{-2} y^{-1} was measured as fine particulate flux from the bottom of the O horizon

less than in bulk precipitation. The % removal of each species of inorganic N and P removed were the opposite of what might be expected on soil (i.e., $NO_3^- > NH_4^+ > H_2PO_4^{-2}$). There were large fluxes of organic forms of N and P, but these will be discussed in a succeeding paragraph.

What mechanisms might be responsible for the efficient removal of inorganic N and P from throughfall as it passed to the mineral soil surface? Solution collectors were located beneath the Oi horizon (litter from about 0 to 3 years old) and beneath the entire forest floor (Oa in Table 11.4). It is particularly remarkable that net removal from the percolating solution continued in the older layers of the forest floor (comparing Oi versus. Oa in Table 11.4). Litter from this watershed exhibits a net uptake of N in the initial stages but is expected to enter a net mineralization phase later. The maximum rate of net mineralization was found to occur after about five years of decomposition in another concurrent study at the same site (Qualls 2016). Thus, given the large inputs of litterfall N (Table 11.5) it is remarkable that the inorganic N and P fluxes do not increase from the Oi to the Oa horizon where net mineralization occurred. Possible mechanisms include (1) removal and translocation by roots in the forest floor, (2) ion-exchange, (3) transformation to organic forms, (4) uptake by mycorrhizal fungi and transfer from the forest floor. In the forest soil of the site, most roots were located in the A and B horizons. Within lysimeters that had no roots at all in the forest floor there was also net removal of nitrate, and ammonium N. As for ion exchange, although decomposing litter has abundant cation exchange sites formed during the process of humification (Qualls et al. 2003), negatively charged nitrate was removed to the greatest extent. Downward transport of fine particulate matter, often believed to be a major source of A horizon soils organic matter was minor (see Table 11.5 footnote) and bioturbation by earthworms was negligible (Qualls 2016). Transformations to organic forms were possible, but the large input of soluble organic matter from litterfall made it impossible to distinguish. The transformations more likely involved uptake by microbes, transformation into microbial biomass, and subsequent cycling. The forest in the study above had been undisturbed for over 60 years and given a turnover time of the forest floor on the scale of several years, the forest floor was believed to be in equilibrium (input equals output). However, the *net balance of all forms of N and P* input and export from the forest floor leaves a large gap (see Table 11.5). The net mineralization of N and P in the forest floor is estimated by difference of all inputs and outputs Table 11.5 but only a very small fraction appeared to leach from the forest floor.

11.3.1.3 The "Ectomycorrizal Export Hypothesis"

One way of explaining the fate of the N and P from throughfall and the larger amount from litter mineralization is uptake by mycorrhizae and translocation to roots in the A horizon. New studies involving DNA fungal community identification of the presence of ectomycorrhizal fungi, and other fungal taxa have confirmed the widespread presence or mainly basidiomycota ectomycorrizal fungi in the Oa horizon and top 5 cm of the A horizon at the Coweeta site (Veach et al. 2018). Of the 18 most common genera of fungi, 10 were ectomycorrhizal, while 6 were saprotrophs (with undefined substrate preference). There is also evidence that ectomycorrhizal fungi not only take up N and P but degrade hemicellulose, cellulose, and produce lignin-degrading enzymes (Lindahl and Anders 2014). Thus there is budgetary evidence (Table 11.5) and microbial evidence that could support the hypothesis for extensive mycorrhizal to root export from the O horizon to roots and trees for recycling in subsequent litter fall episodes. While throughfall comprises only part of the N and P flux from the forest floor, it is part of an extensive transformation and translocation of nutrients. Chuyong et al. (2004) hypothesized that cycling of P, Ca, and Mg in throughfall catalyzes the mineralization of litter and role of ectomycorrhizal in an African rainforest.

11.3.1.4 Organic Nutrients in Throughfall

Table 11.4 shows that organic N and P comprise about half of the total N and P in throughfall in the study described. Whether this N and P contributes to the immobilization of N and P during litter decomposition is difficult to determine since litter also contributes to the organic N and P leaching from the forest floor. Fluxes of DOP in throughfall were about 1/8 as large as those in foliar litterfall and fluxes of total N in throughfall were about 1/6 as large as those in foliar litterfall (Comparing Tables 11.4 and 11.5). But, DOP and DON in throughfall could account for 38 and 66%, respectively, of the observed flux in solution from the Oa horizon (Table 11.4), if it passed through without being consumed. However, the dissolved organic matter in throughfall was much more rapidly decomposed that draining from the forest floor (Qualls and Haines 1992) so it is likely that some are metabolized on the forest floor. For example, 58% of the dissolved organic N in an August throughfall sample mineralized during a 134-day incubation, and about half of the DOC was in a more rapidly decaying fraction of DOC of about 4% per day. It is a significant input to the forest floor even when litterfall is considered (Table 11.5). A study of throughfall in a *Juniperus virginina* forest also found that a large fraction was highly biodegradable (Howard et al. 2018). The composition of the dissolved organic N and P in the throughfall samples in the study shown in Tables 11.4 and 11.5 was evaluated by fractionation into hydrophobic or hydrophilic acids, base, and neutral substances (Qualls and Haines 1991). Throughfall was distinct from Oa horizon water and this was also linked to its biodegradability (Qualls and Haines 1992). Proteins and amino acids would be found in the hydrophilic base fraction and that comprised 25% of the DON in August throughfall and 7% in May. The C/N ratio for the base fraction was similar to that of proteins. Proteins and amino acids would be expected to be rapidly degraded and could be retained on the forest floor. In fact, most of this base fraction was removed before emerging in the Oa horizon drainage. The next largest fraction of the DON in throughfall was the hydrophilic neutral fraction, which might include amino-sugar carbohydrates. The hydrophilic neutral fraction was also the most labile one, at least for DOC, but other sugars and carbohydrates were probably the main components (Qualls and Haines 1992; Qualls 2005). In throughfall, the hydrophilic neutral fraction was also the largest one in terms of dissolved organic P. Phosphate ester carbohydrates, for example inositol phosphate, wound occur in that fraction.

11.3.1.5 Effects of Nitrate and Ammonia on Litter Decomposition: Carbon

The previous discussion has shown evidence that inorganic N and P in either bulk precipitation or throughfall can enrich the N and P content of decomposing litter. However, can it affect the decomposition of *carbon* (or general mass loss) in the litter? There have been many studies on the effects of inorganic nutrient fertilization on litter decomposition, but the purpose of most have been (1) to determine the impacts of nutrient enrichment in aquatic environments, (2) to determine effects of atmospheric N deposition in terrestrial environments, or (3) determine the effect on lignin decomposition.

Webster and Benfield (1986) summarized a number of aquatic studies of streams, rivers, and wetlands where inorganic N addition accelerated litter decomposition and also noted most studies found PO_4 addition did not. An exception was in a phosphorus-deficient wetland environment where P additions accelerated decomposition (Qualls and Richardson 2000). However, in terrestrial forests results of fertilizer additions have been mixed. For example, a study by Hobbie et al. (2012) found that additions of either NH_4 and NO_3 or amino acids accelerated the initial stages of decomposition but that it left a larger refractory fraction. The same study also reviewed a number of fertilization studies and found some that showed increased decomposition rate and others that found no difference. The authors concluded there may be some unknown site-specific effects. A literature meta-analysis of a number of studies by Knorr et al. (2005) led them to the conclusion that there was no consistent fertilization effect. They concluded that externally supplied N had negative effects on litter decomposition on average, but effects varied considerably. Negative effects were particularly evident where ambient N deposition rates were high, litter quality was low, or N fertilizer addition rates were high. There have also been several studies along gradients of atmospheric N deposition. For example, Kuperman (1999) found a strong positive correlation of litter decomposition rate, the over 19 months and N deposition rate. The C/N ratio of the forest floor as a whole decreased as N deposition increased. Net N mineralization from the litterbags was greatest at the site with the highest N deposition.

There is evidence that N fertilization or N deposition inhibits the decomposition of lignin, and thus the long term rate of decomposition (Berg and McClaugerty 2014, 2012). Perakis found that fertilization with either NH_4NO_3 or urea accelerated the decomposition of Douglas fir litter in the early stages (0.67 y) but had inhibited decomposition by three years. The litter was relatively high in lignin content (29–35%). But, addition of fertilizer also increased the net immobilization of N by the litter, even after 3 years. Lignin is the component of plant litter that is slowest to decompose with half decay times on the scale of years (Berg and McClaugherty 2014). It becomes concentrated in the decomposed residues but this residue becomes at least partially modified to resemble humic substances (Qualls et al. 2003). Elevated concentrations of inorganic N have been shown to repress the production of lignin-degrading enzymes (Mn peroxidase) by white-rot fungi (*Phanerochaete chrysosporium*) in culture (Kirk 1980). Hobbie et al. (2012) found that in plots fertilized with inorganic N or amino acids the activity of lignin peroxidase enzymes was reduced. Perakis et al. (2012) also suggested that this maybe the reason the late-stage decomposition of his pine litter, that had a high lignin content, was inhibited by N fertilization.

A study along an atmospheric deposition gradient in Sweden, concluded that N deposition in throughfall was the most important factor controlling ectomycorrhizal fungi production (Bahr et al. 2013). These ectomycorrhizal fungi were also very important in decomposition of carbon substrates from litter added in the form of maize leaves that left a 13 °C signature. They concluded that the amounts typically deposited in “moderately” polluted regions (1–25 kg-N ha^{-1} y^{-1}) can be sufficient to reduce ectomycorrhizal mycelial growth. Their proposed mechanism for the reduction in ectomycorrhizal fungi is different than that proposed for the effect on lignin decomposition and involved the decreased allocation of belowground resources by the tree roots to ectomycorrhizal fungi in nitrogen-rich environments.

The application of these findings to inorganic nitrogen in throughfall is that in forests where there is net leaching of inorganic N from the canopy, (e.g., regions with elevated atmospheric N), the later stages of litter decomposition may be inhibited because of inhibition of lignin decomposition and/or decreased activity of ectomycorrhizal fungi. This may occur even though additional inorganic N in throughfall may accelerate decomposition in the early stages when cellulose and hemicellulose are being decomposed in the Oi horizon.

11.3.2 Effects of Organic Constituents in Throughfall and Stemflow on Litter Decomposition

The effects of the organic forms of nutrients were discussed in the preceding section along with the effects of inorganic nutrients, but in this section, we will discuss other possible effects of organic substances in throughfall in either *stimulating* or *inhibiting* decomposition. First we will review the organic composition of throughfall (also see previous chapters for a more general review) with respect to several specific constituents (a) carbohydrates, (b) organic acids (c) polyphenols and tannins, (d) humic substances, and (e) allelopathic or antimicrobial substances. The most thorough review of dissolved organic matter concentrations and fluxes in the literature is in Van Stan and Stubbins (2018).

Carbohydrates, including sugars, are present in throughfall. McClaugherty (1983) measured significant quantities of carbohydrates in throughfall. McDowell and Likens in the year 1988 found that 8.7% of the DOC in throughfall, was monomeric carbohydrates and another 9% was polymeric carbohydrates. The previously discussed study of Qualls and Haines (1991) found that 25 and 30% of throughfall in May and August, respectively, was comprised of hydrophilic neutral substances that could include sugars, other carbohydrates, but could also include other neutral hydrophilic compounds such as alcohols. The content of these hydrophilic neutral substances was highly correlated with the more rapidly biodegradable fraction, compared among seasons, and compared with other sources such as soil and stream water (Qualls and Haines 1992). Howard et al. (2018) found that 36–73% of the DOC in throughfall samples was rapidly decomposed in incubations. They estimated that the impact of this throughfall and stemflow input on soil respiration could be equivalent to 33–47% of the average net ecosystem exchange estimated for forests in the state of Georgia.

Besides the respiration of labile organic substances originating from the throughfall itself, can the organic substances increase the decomposition rate of litter originating from litterfall or root mortality? It has long been realized that the addition of fresh organic residues can induce increased decomposition of older soil organic matter, the “priming effect” (Fontaine et al. 2003) but most studies involve agricultural soils. However, additions of glucose alone have failed to induce the priming effect in some soils that did respond to straw additions, so the authors concluded that soluble sugars alone did not induce the priming effect (Fontaine et al. 2003). Two theories of the mechanism of the priming effect may be consistent with the observed results (Fontaine et al. 2003). The first is that fresh organic matter supplies nutrients that stimulate growth of previously starved, or dormant microorganisms that then “turn” to older less available substrates. A second theory is that microbial growth on fresh substrates produces exoenzymes that induce co-metabolism of less available original organic matter. However, Fontaine et al. (2003) reasoned that *insoluble* organic matter was more effective in inducing the priming effect because it was more likely to be polymeric, and induce growth of “K selected” microorganisms (that is, adapted to slow growth rates, and unable to compete for short term supplies of very labile substances) that chiefly subsist on polymeric organic matter. If this theory of Fontaine et al. (2003) is true, then it might seem that dissolved organic matter in throughfall would be unlikely to induce the priming effect in litter because (a) it is soluble, (b) it contains relatively low to “intermediate” sized molecules and (c) contains at least significant quantities of carbohydrates and other labile components. The study of Stubbins et al. (2017) provides the most detailed structural study of dissolved organic matter in throughfall. The average molecular weight of formulas was in the range of 350–400 daltons for throughfall. This indicates that most of these dissolved organic molecules are unlikely to contain long polymers in the sense that Fontaine indicated for substances that have been used in some studies of the priming effect. For example cellobiose, with just two sugars linked together, has a molecular weight of 342 Daltons. The study also found a substantial proportion of structures were aromatic or could contain aromatic structures in addition to unsaturated structures (similar to the hydrophobic acid fraction in other studies). The study found less than 5% of the structures were sugars. But a large proportion of samples from a similar source contained a large, rapidly decomposing fraction (Howard et al. 2018). Perhaps most importantly, over 5000 structural formulas were identified and, considering the theoretical number of possible isomers per formula exceeds many millions (Hertkorn et al. 2007), consequently the suite of organics was very diverse. The diversity and presence of some lignin, polyphenolic-like structures may indicate that the assumptions of Fontaine (2003) about the ability of dissolved organic matter to elicit the priming effect might not apply to throughfall. It is possible that the lignin related breakdown products in throughfall might even provide some soluble nutrition to lignin-degrading microorganisms.

However, a study by Hamer and Marschner (2005a, b) directly addressed the question of the addition of labile soluble substrates to forest soils and the priming effect. They found that although glucose did not stimulate a substantial priming effect, fructose, an amino acid, and a low molecular weight organic acid did induce the priming effect in a forest soil. Repeated additions continued to stimulate the priming effect, suggesting that "the study shows that some of the priming mechanisms discussed by other authors such as co-metabolism and microbial biomass turnover are insufficient to explain the observed data." (quoted from Hamer and Marschner 2005b). Thus, there is no a priori reason to suspect that throughfall might not induce the priming effect. However, this review was not able to locate any studies that directly tested the ability of throughfall dissolved organic matter to stimulate the priming effect in litter or forest floor material.

Most current studies of the priming effect use some form of isotopic labeling to distinguish original soil organic matter from the added material. One way to perform such an experiment would be to use litter or soil organic matter from C4 plants (e.g. litter from a no-till cornfield), add naturally collected throughfall or a control of water containing only inorganic nutrients, and measure the 13 °C signature of respired CO_2.

11.3.2.1 Possible Inhibitory Effects of Throughfall on Litter Decomposition

Throughfall has been shown to contain some components that have, *in other contexts*, been implicated in the inhibition of litter decomposition: (a) acidity, (b) polyphenols and tannins, and (c) humic substances.

Throughfall and stemflow have significant concentrations of organic acids and they comprise about 60% of the DOC (Qualls et al. 1992; Guggenberger and Zech 1994). Most studies of the differences between bulk precipitation and throughfall have been in regions where anthropogenic pollution has been the motivation for the study (e.g., Kristensen et al. 2004). In general, for most studies, the pH actually increases as precipitation passes through the canopy, where H^+ ions are absorbed and cations are leached (Fillion et al. 1998). However, in a relatively unpolluted forest in the Cascades of the U.S., rainfall pH and throughfall pH were about the same, with a pH of 6.0–6.1 (Tarrent et al. 1968). However, in the same study, stemflow from conifers had an average pH of 5.0, while stemflow from alder had a pH of 5.8. Moreover, in a study of throughfall in several sites in France ranging from those affected by severe acid deposition to those less affected, the organic acid anions dominated the composition of all anions for throughfall with pH generally greater than 5.5 and that the dominance of non-marine sulfate corresponds mostly to throughfall with pH less than 4.5 (Fillion et al. 1999). Nevertheless, the DOC content seemed to play a determining role in the acidity even in samples of throughfall that had a pH value of between 4.5 and 5.5. In fact, in those with DOC content of 15 mg L^{-1} or greater, organic anions were higher in concentration than non-marine sulfate. The number of acid functional groups per mg of C were similar to those from other sources of DOC containing humic substances. Since the mean pKa (the pKa is the pH where 50% of the acids are dissociated) for the throughfall DOC acids was 4.9, there was still a pool of *undissociated* carboxylic acids in the throughfall, which would serve as a potent buffer against the pH falling lower.

Consequently, it seems in most cases that the organic acids contributed by throughfall may not lower the pH of the litter layer, but the organic acids may even exert a buffering effect in the range of pH 5, and other reactions in the canopy often buffer the effect of acid precipitation. Another point that makes it unlikely that the organic acids in throughfall would acidify the litter, that is the litterfall itself is acidic. For example, water draining from the Oa horizon used in the study of Qualls et al. (1991) had a pH of 4.0–4.6 and the solution draining from the Oi horizon was comprised of even higher concentrations of hydrophobic and hydrophilic acids than were present in the throughfall.

Polyphenols and tannins are another group of substances that have been studied for their inhibitory effects on decomposition of litter. Some studies have found that species with higher contents of polyphenols and tannins decay more slowly (Berg and McClaugherty 2014). Hättenschwiler and Vitousek (2000) reviewed studies showing inhibition of litter decomposition, inhibition of nitrification, and inhibition of ericoid mycorrhizae. Binding of enzymes and proteins has been suggested as a possible mechanism (Baldwin et al. 1983). Qualls et al. (1991) found about 6% of the DOC in throughfall was phenolic (but without carboxylic acids). McDowell and Likens (1988) found phenolic substances to comprise 8.6% of throughfall in the Hubbard Brook Forest. Hättenschwiler and Vitousek (2000) also speculated that the leaching of polyphenols from decomposing litter was probably a greater source than leaching from the canopy in throughfall. For example, in the study of Qualls et al. (1991) in newly senesced litterfall there was a "flux" of water-extractable phenolic substances equivalent to 3.5 g-C m^{-2} y^{-1} compared to a flux of less than 0.5 g-C m^{-2} y^{-1} of in throughfall. However, very little was found in water draining from the forest floor. It was speculated that this phenolic fraction was rapidly oxidized or condensed by phenoloxidase enzymes which then might have the properties of humic substances. Whether the concentrations in throughfall are enough to affect litter decomposition has not been tested, but it seems like litter itself would be a greater source as shown in Qualls et al. (1991). In fact, the two samples with the highest content of the phenol fraction (the August throughfall and the litter leachate) decomposed more rapidly than any other fractions on a biodegradability assay (Qualls and Haines 1992).

The humic substances that comprise a large portion of the dissolved organic matter in throughfall might also be suspected to inhibit microbial growth. However, in a test of the effects of humic and fulvic acid on litter decomposition in aerated solutions, there were no effects on leaf litter decomposition rates other than their effects on pH (Qualls and Haines 1990). However, decomposition was inhibited by pH levels of 4 and 5 compared to pH 7 whether they contained humic substances or were adjusted with HCl or NaOH. High concentrations of humic substances, however, could lower the pH to 5. The pH levels of leaf litter on the forest floor were pH 4.0–4.6 in the example of Qualls and Haines (1991) and that pH could be inhibitory to litter decomposition, but the source was the carboxylic acid content of the decomposing litter itself (Qualls et al. 2003) without the influence of throughfall.

11.4 Conclusions

11.4.1 Possible Effects of the Quantity of Canopy Interception on Litter Decomposition

Interception ratios are of the magnitude in many ecosystems to have possible effects in reducing decomposition rates due to moisture limitations. Simulations (Tables 11.1, 11.2, 11.3 and 11.4) indicate that these are especially likely to be limiting at higher temperatures, lower rates of precipitation and under evergreen canopies. Lower rates of precipitation (given equal leaf area indices) also accentuate the impact on decomposition because of the relationship of soil respiration to precipitation. Even at a given I/P ratio, interception occurring during higher temperatures in summer would also have more effect than in winter because absolute rates (in g-C m^{-2} day^{-1}) of litter respiration are higher.

However, this review has not located any experiments that directly test the hypothesis that canopy interception can reduce litter decomposition. There have been many observational surveys and experiments with different objectives, such as evaluation effects of climatic change, or drought. The most useful of these are throughfall exclusion, although exclusion rates less than 50% are few and these are, therefore, less likely to be in the range of observed interception rates. But, three studies using throughfall exclusion showed effects on decomposition, including one in a rainforest.

A less applicable set of experimental manipulations or observational studies are those that involve canopy *removal*, in most cases through clearcutting thinning or observations in natural gaps. Most clearcutting or gap studies have shown a slowing in decomposition rates, instead of what might be expected by increasing incident precipitation. The problem in applying canopy removal experiments to possible effects of interception is that other environmental variables also change, such as soil temperature, effects of direct radiation on drying or snowmelt, lower relative humidity, and UV radiation.

However, the outlook for demonstrating the role of interception quantity on litter decomposition is good with proper experimental design. One such design would be to use both irrigation and throughfall exclusion roofs at realistic rates of reduction in throughfall, and augmentation to simulate precipitation above the canopy.

11.4.2 Possible Effects of the Chemistry of Throughfall on Litter Decomposition

The most definite effects of throughfall chemistry on litter biogeochemistry are to increase the immobilization of N, P and, in the least one case Ca, in litter during the early stages. The two studies that directly address the effects of throughfall on litter decomposition showed that simulated throughfall containing inorganic nutrients increased the uptake of N and P and the subsequent rates of net mineralization. But the only the study with decomposition of rye litter showed that simulated throughfall increase rates of decomposition and the increase was small (Beare et al. 1989).

Many other studies that have not been aimed at evaluating the effects of throughfall have been done on the effect of fertilization with N and/or P. Some have shown that addition of N accelerated the early phases of decomposition, but others have not. The addition of N in fertilization experiments has been shown to slow the rates of decomposition in the later stages, probably by inhibiting the activity of lignin-degrading enzymes. But, the fertilization experiments do show increased net immobilization in N (and P when used) in the early stages and eventually higher rates of mineralization. The extension of the many fertilization experiments to nutrients in throughfall can only be speculative but they suggest that addition of N in throughfall might accelerate litter decomposition in the early stages but might tend to inhibit lignin degradation. Throughfall also contains labile organic N and P sources that may be rapidly decomposed and taken up in litter and these are present in comparable concentrations to those of inorganic N and P. However, one important qualification to the possible effects of inorganic N in throughfall is that there are often higher concentrations in precipitation above the canopy in regions affected by atmospheric N deposition.

There is an extremely diverse array of organic substances in throughfall that could hypothetically cause priming effects (see earlier discussion) or even inhibitory effects (e.g., polyphenols). However, these substances are also present in freshly senesced litter and maybe in higher concentration in the solid litter itself. Humic substances in throughfall decompose slowly but do not appear to inhibit decomposition of litter. However, experiments using realistic concentrations characteristic of throughfall appear to be lacking. A suggested experimental design in the field would be similar to the throughfall exclusion/supplementation design in the previous section, and utilize irrigation with isolated fractions of actual throughfall (inorganic and organic).

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