John T. Van Stan, II
Ethan Gutmann
Jan Friesen
Editors

Precipitation Partitioning by Vegetation

A Global Synthesis

Illustrated by Tyasseta and Siloy

Springer

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Foreword

As a hydrologist, I would like to know what happens in the terrestrial branch of the water cycle. The processes that return precipitation to the atmosphere as water vapor or to the oceans as river or groundwater flow are many and complex. If we ever want to be able to understand the hydrological cycle and the impacts that humans have on it, if we ever want to be able to manage our water resources in a sustainable manner, we need to understand these processes. For most raindrops that fall over land, the first thing that happens is that they hit a plant. Unfortunately, or in the present context, interestingly, this simple observation quickly leads to a large set of questions about what happens next: Does the drop stay on the leaf to evaporate back once the rain stops or does it fall through the canopy? Are drops that fall through concentrated, inducing relatively fast preferential flow through the soil, or is the rain dispersed? If we cannot get these very first processes right, how can we ever hope to come to grips with the next steps? These hydrological processes are relatively simple compared to the potentially even more relevant chemical and biological processes that take place when precipitation works its way through a canopy. From the movement of nutrients, spores, and bacteria to the functioning of epiphytes and decomposition of leaf litter, the movement of water through canopies governs a wide array of processes.

For a long time, these processes were not broadly recognized as significant or important. Over the last decades, precipitation partitioning and associated biogeochemical processes have received more of the attention they deserve. This book brings together, for the first time, the results of this recent work and provides a broad overview of what has become known. Now that the relevance of precipitation partitioning is well established, this monograph quickly brings every scholar up to date.

Precipitation partitioning is a highly interdisciplinary subject. One can look at the processes from a botanical point of view and wonder what the different evolutionary functions are that let plants “develop” certain mechanisms. One can also look at the ecosystem as a whole or one can look at it from a hydrological or meteorological point of view. In order to get it right, all these points of view will have to be brought together, something this book really brings to the fore. Similarly, in different ecosystems and landscapes, different partitionings take place with different biogeochemical results. For this reason, the large geographical diversity represented in the book is especially relevant. From American grasslands and croplands to forests in Europe and savanna in Africa, we see large variations that are captured by the widespread empirical evidence in the different chapters.

This geographical and disciplinary diversity is also reflected in the experiences and expertise of the editors. The three people making up the editorial team sufficiently overlap in their interests to ensure a coherent picture of the state of the art. To provide at the same time a comprehensive overview, they bring together a broad set of skills from LIDAR and satellite remote sensing to field measurements and hydrological and meteorological modeling. Personally, I really appreciate the fact that all editors contributed to new methods for measuring the complex processes of precipitation partitioning. I remember well how one of the editors, Jan Friesen, traveled through Ghana with John Selker and me to directly measure tree stem compression caused by canopy rainfall interception. As an example of how involved any of the measurements in this book can get, I just want to mention that to ensure a constant temperature around the clock, we wrapped the trees in electric blankets. Running generators to keep trees warm at night in Africa sounds like a silly thing to do, but it also exemplifies the subtle difficulties that had to be overcome for all experiments underlying the new insights presented in this book.

It is clear that this book is not the last word on precipitation partitioning, as the last chapter clearly explains. The book ends with an overview of the many unknowns that persist. The simplest question, how much rainfall is intercepted and evaporates before it can reach the root zone, has been around at least since the end of the nineteenth century. This monograph shows that there has been great progress, but that the enormous diversity of plants, ecosystems, and landscapes ensures that much research remains to be done.

As a final word of introduction, I must mention the great graphical summaries of the different chapters. The researchers have worked closely with cartoonists to make the essence of the findings clear with pictures that inform scholars and laypersons alike. The cartoons are rich in detail, further emphasizing the complexity and interrelatedness of all processes taking place. At the same time, they bring lightness and humor, which are so often lacking in scientific tomes.

Image credit: © A. Bagus Tyasseta

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Preface

Water is fundamental to life on Earth, including its dissolved and suspended materials, associated energy, and pathways through the land surface and atmosphere. Therefore, understanding and managing water resources is also fundamental to the sociocultural and economic underpinnings of human civilization. Given this importance, it is astonishing that, for the very first interaction between precipitation and the land surface (most of which is vegetated), there has been no comprehensive and global synthesis and evaluation of extant research. Although observations of precipitation–vegetation interactions have been reported since Theophrastus, over two millennia ago, the editors and contributing authors are not aware of a single volume that has since exclusively focused on these processes. Since Theophrastus, research on how vegetation "partitions" precipitation has become geographically extensive, but studies placing precipitation partitioning processes into global context are rare. The few studies that have considered the macroscale role of precipitation–vegetation interactions find significant influences over global hydrological processes, climate, and terrestrial ecosystem functioning (e.g., Miralles et al. 2010; Murray 2014; Porada et al. 2018). As such, *Precipitation Partitioning by Vegetation: A Global Synthesis* is not only timely but also a long overdue synthesis and evaluation—something often considered necessary for the progression of any discipline (Moldwin et al. 2017). This volume synthesizes research on precipitation partitioning by vegetation to date and globally contextualizes this knowledge with an explicit discussion of relevance and impacts to the climate and terrestrial ecosystem functioning, as well as direct socioeconomic effects. Our intention is for this to be a comprehensive reference for researchers and students seeking to discover what has been done and to inspire future research on both long-standing and new questions. Indeed, how can we manage water resources if we do not have an accurate accounting of, or even consistent accounting methods for determining, "how much precipitation *actually* reaches the surface?"

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Boulder, CO, USA	Ethan Gutmann
Leipzig, Germany	Jan Friesen

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About the Illustrators

Image credit: © A. Bagus Tyasseta

A. Bagus Jati Tyasseta (left), or Tyasseta (bagusseta1982@gmail.com), is an Indonesian artist working in the comic industry currently living in Jakarta with his family. He obtained a Master of Fine Arts in Sequential Art from Savannah College of Art and Design in Savannah, Georgia (USA) where he met Dr. Van Stan. He has published several comic titles in Indonesia and is currently working for an American comic publisher. His other artworks can be viewed in his artstation page: https://www.artstation.com/tyasseta.

Fredy Siloy (right), or Siloy (Siloyfredy@gmail.com), is a game developer at noon and color artist at night. He obtained a Bachelor of Fine Arts from Institut Teknologi Bandung in Bandung, West Java (Indonesia). He is currently developing a channel game for kids named *Tappy Taps* and casual game channel named *Ikan Asin Production.* Please check out more of his artworks: www.ikaanstudio.com.

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Image credit: © A. Bagus Tyasseta

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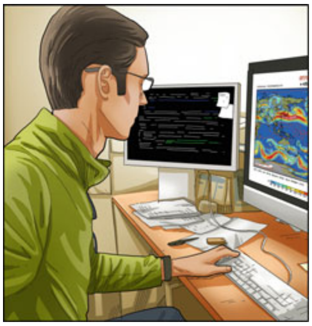

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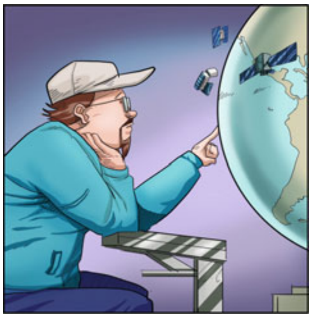
Ethan Gutmann, Ph.D. is a Hydrologist in the Research Applications Lab at the National Center for Atmospheric Research in Boulder, Colorado (USA). His background in hydrology, geology, and computer science found a happy marriage in remote sensing and hydrologic and atmospheric modeling. A passion for the outdoors has taken him to remote corners of the world, climbing mountains in Peru, Nepal, and Tanzania. He also enjoys scientific outreach, having dabbled in science blogging at Ars Technica and science videography with Earth Initiatives.



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Jan Friesen, Ph.D. is an Ecohydrologist at the Department of Catchment Hydrology, Helmholtz Centre for Environmental Research—UFZ, Leipzig (Germany). His research primarily focuses on forest ecohydrology, remote sensing, and sensor development where he applies and develops new monitoring solutions to bridge the gap between site studies and remote sensing. He has extensive experience in semiarid and data-scarce countries such as Ghana, Burkina Faso, Nigeria, and Oman and his work has a strong connection to water management issues.

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2018 So Far
Evaporation
The Last Century
1918 - 2017 CE
Early Observations
1850 - 1900 CE
Throughfall
Stemflow
Enlightenment
1750 - 1800 CE
The Origins
500 - 50 BCE

1

Precipitation Partitioning, or to the Surface and Back Again: Historical Overview of the First Process in the Terrestrial Hydrologic Pathway

John T. Van Stan, II and Jan Friesen

Abstract
This chapter presents a history of the interdisciplinary field focused on improving our understanding of the first step in the terrestrial hydrologic cycle: precipitation partitioning by vegetation. We describe the origins of interest, rooted in observations from "The Father of Botany," Theophrastus (350 BCE) and synthesize the early formal hydrologic and biogeochemical research (~1800–1917) that provided the foundation for modern precipitation partitioning investigation. To examine the field's publication and citation trends over the past century (1918–2017), a meta-analysis of precipitation partitioning research sampled from the Thompson Reuter's Web of Science is presented and discussed. Finally, a summary of research published on this topic through September 2018 (when this chapter was written) is used to discuss broad future directions as well as to introduce the overall structure of this book.

Keywords
Throughfall • Stemflow • Rainfall • Snow • Ice • Fog • History

1.1 Introduction

Any rain, snow, rime, or condensate (fog, mist or dew) attempting passage through a vegetated landscape will inevitably interact with its plant surfaces. These precipitation-vegetation interactions are the focus of a field called, "precipitation partitioning by vegetation," that has roots deep into the origins of natural science itself. Since precipitation partitioning is typically the first process to alter the amount and patterning of meteoric water, it affects all subsequent terrestrial hydrological and related ecological processes (Savenije 2004, 2018). The nature of any below-canopy precipitation (or "net precipitation") flux's hydrologic and ecological influence can depend on how that water penetrated the vegetation canopy, e.g., as a drip from surfaces and through canopy gaps (called "throughfall") or as a flow down the stem (called "stemflow"). The partitioning process also returns a portion of precipitation back to the atmosphere (called "interception") in the canopy, the understory and litter layer (Gerrits and Savenije 2011), which is of large enough magnitude to influence regional and global water (Porada et al. 2018) and energy budgets (Davies-Barnard et al. 2014; Van der Ent et al. 2014). Excellent historical reviews exist for fields with which precipitation partitioning overlaps—forest hydrology and biogeochemistry (Andréassian 2004; McGuire and Likens 2011)—but none have summarized and discussed historical aspects of the precipitation partitioning field itself. Thus, this chapter examines the historical origins, developments and major advancements of research seeking to improve our understanding of the first process in the terrestrial hydrologic pathway through vegetated landscapes.

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We first describe the origins of interest regarding interactions between vegetation and precipitation and, then, discuss the early formal research studies that provided the foundation for modern precipitation partitioning investigation. A meta-analysis of studies published in this field over the past century (1918–2017) is presented and discussed. Finally, a summary of research published in the first nine months of 2018 is used to discuss broad future directions as well as to introduce the overall chapter structure of this book project.

1.2 Origins

Processes governing the capture, storage, evaporation, and redistribution of precipitation by plants were little discussed before the nineteenth century. However, as early as 350 years BCE, Greek naturalists began recording the effects of precipitation partitioning at the surface, and many of these observations fascinated scientists through the Age of Enlightenment and into modern times.

Beginning with the first-known scientific publication on plants, *Historia Plantarum* (350–287 BCE), the Greek naturalist and philosopher Theophrastus (371–287 BCE) described many of the ecological effects now attributed, in part or in whole, to precipitation partitioning. His first discussion of these effects touched on rainfall redistribution by throughfall, although this term and other modern hydrologic terms (e.g., stemflow and interception) were not yet explicitly used. Early in the third volume, Theophrastus reviews observations from Anaxagoras (510–428 BCE), Diogenes (412–323 BC), and Cleidemos (fifth–fourth century BCE) on the role that rainfall redistribution plays in the dispersal of seeds (section i, 3), concluding with his own observations that throughfall "brings down many of the seeds with it, and at the same time causes a sort of decomposition of the soil and of the water" (section i, 11) (Theophrastus 1483). Regarding stemflow, *Historia Plantarum* (volume IV, section iii, 4–5) reports observations related to the now well-recognized capability of trees (Hildebrandt and Eltahir 2006), shrubs (Whitford et al. 1997), herbs, like thyme (Belmonte Serrato and Romero Díaz 1998), and grasses (Roth-Nebelsick et al. 2012) to survive in arid environments through funnelling dew, fog, and scant amounts of rainfall to their root systems. Theophrastus hypothesized that plants situated "in the land where no rain falls" were sustained "by the dew" for he considered it to be "sufficient [water], considering the size of such plants and their natural character." The idea that precipitation intercepted by plant canopies was taken up by the plant was also discussed by Leonardo da Vinci, in his notebooks (1478–1518 CE), where he states that "the [rain] water which falls upon the shoot can run down to nourish the bud, by the drop being caught in the hollow [axil] at the insertion of the leaf." Water uptake by canopy surfaces has now become a widely-observed phenomenon (see Chap. 10). It was also reported that fig trees can "become diseased if there is heavy rain; for then the parts toward the root [where stemflow infiltrates] and the root itself [where stemflow can preferentially flow: Johnson and Lehmann (2006)] become, as it were, sodden" (volume IV, section xiv, 6).

Even the interception, storage and evaporation, of rain and snow is briefly addressed in Theophrastus' observations of silver fir (*Abies alba*) trees. He describes this species' foliage as being "so dense that neither snow nor rain penetrates it" (volume III, section ix, 6–7). The effects of rainwater entrained on, and flowing across, plant surfaces were also described during his studies of infestation and pollination. Infestation of olive trees was described as being "prevented from appearing under the skin [of the fruit] if there is rain after the rising of Arcturus [the northern springtime star]" (volume IV, section xiv, 9). We now understand that within-canopy transport of rainwater can affect the spread of pathogens (Garbelotto et al. 2003), see also Chap. 14 of this volume. Theophrastus notes the importance of avoiding rainfall during artificial pollination of fig trees (volume II, section viii, 1–3), as rainwater entrained on the canopy surfaces can wash away pollen, as observed by Lee et al. (1996), and may reduce available pollen for insect pollinators.

Theophrastus' observations impressed Pliny the Elder (23–79 CE), who called him "the most trustworthy of the Greek writers" (Parejko 2003). Thus, it is no surprise that Pliny was the next naturalist to observe and report the effects of precipitation partitioning by vegetation. In Pliny's *Naturalis Historia* (77–79 CE) he not only describes rainfall interception and throughfall, but even qualitatively compares the droplet size distributions of throughfall between tree species! "The drops of water that fall from the pine, the *Quercus*, and the holm-oak are extremely heavy, but from the cypress fall none" (volume XVII, chapter xviii) (c.f., Hall and Calder 1993). In the same chapter, Pliny confirms Theophrastus' observations that substantial interception is likely due to "foliage being densely packed." Then, he describes an effect of precipitation partitioning that was not quantitatively observed until the twentieth century: the canopy's ability to "smooth" rainfall intensity (Keim and Skaugset 2004; Trimble and Weitzman 1954), "the alder [canopy] is very dense … it serves as an effectual protection against heavy rains." Pliny also sparked scientific and public interest about the chemical composition of throughfall and stemflow through his observation of allelopathy, or the chemical inhibition of the establishment and growth of competing plants, in the shadows cast by certain trees, especially *Juglans* (walnut) species: "The shadow of the walnut tree is poison to all plants within its compass" (volume XVII, chapter xviii). Modern work has not only identified that allelopathic compounds are leached from walnut leaves during rainfall (Jose and Gillespie 1998) but that this process occurs in the canopies of other species, like *Fagus sylvatica* (European beech) (Bischoff et al. 2015). Pliny advocated for future natural scientific inquiry on processes within the "shadows of trees," concluding that "in the case of every variety of plant, the shade is found to act either as a kind of nurse or a harsh step-mother." During the 1350s, the Moroccan Islamic scholar, Ibn Baṭṭūṭah, gave perhaps the harshest account of rain-plant interactions during his travels through southern Tibet, stating that there were "poisonous grasses growing, such that when the rains fall upon it, and run in torrents to the neighboring rivers, no one dares of consequence drink of the water during the time of their rising: and should anyone do so, he dies immediately." (Ibn Baṭṭūṭah 1356). Despite this shocking account and Pliny's prior urging for greater study of the processes at play in the black box enshrouded by the canopy's shadow, no known attempts to measure, estimate or monitor the storage, evaporation, and redistribution of precipitation by plants occurred for centuries.

1.3 The First Observations and Development of Conceptual Foundations

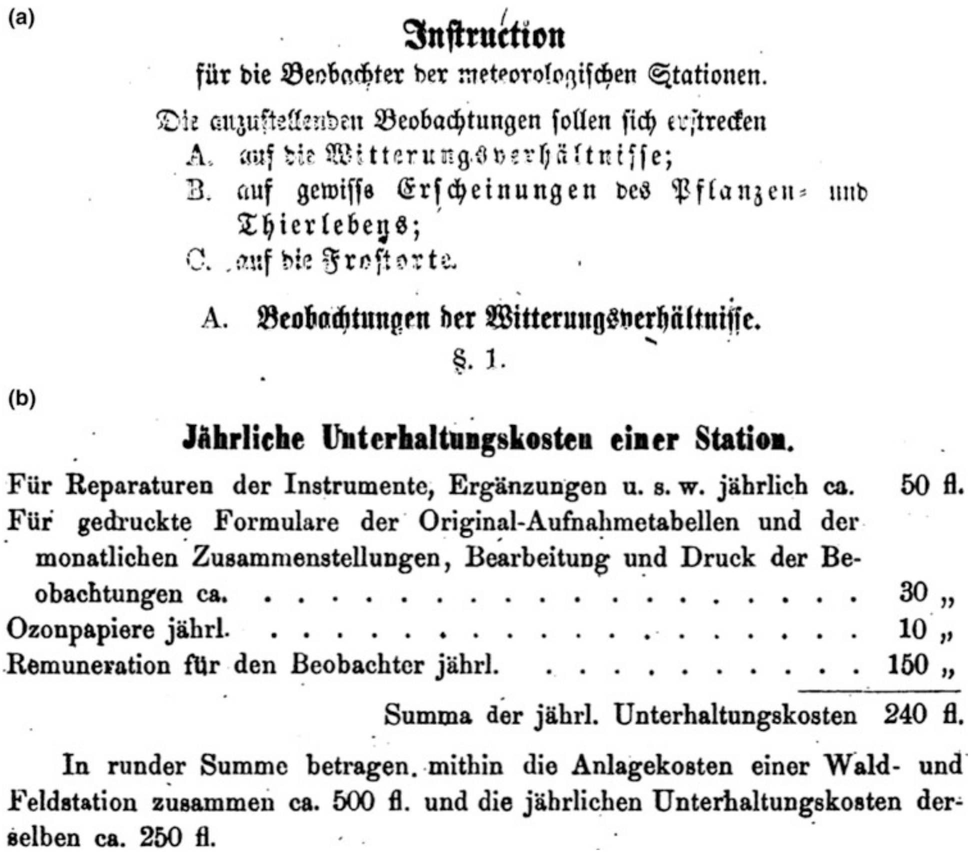
1.3.1 Foundational Hydrologic Observations

European adventurers during the eighteenth century reported on the links between precipitation and vegetation (von Humboldt and Bonpland 1807) and cases where indigenous peoples used precipitation-vegetation interactions to their benefit (De Galindo and Glas 1764). Both von Humboldt and Captain George Glas witnessed, in particular, the people of the Canary Islands using fog capture by vegetation canopies to significant supplement their water resource needs (De Galindo and Glass 1764; Kunkel 2012). The account of Captain Glas is particularly detailed and has been used to introduce the relevance of fog interception in early research (Kerfoot 1968):

> In one of the Canary Islands grows a tree which furnishes water to the inhabitants and beasts of the whole place … its leaves constantly distill such a quantity of water as is sufficient to furnish drink to every creature in [El] Hierro, nature having provided this remedy for the drought of the island. … On the north side of the trunk are two tanks or cisterns. One of these contains water for the drinking of the inhabitants, and the other that which they use for their cattle, washing and such like purposes. Every morning, near this part of the island, a cloud of mist arises from the sea, which the south and easterly winds force against the fore-mentioned steep cliff so that the cloud … advances slowly … and then rests upon the thick leaves and wide-spreading branches of the tree from whence it distills in drops.

No quantitative observations of precipitation partitioning were made by these eighteenth-century European adventurers. Interest in precipitation partitioning within the scientific community fully awakened in the mid-nineteenth century when Dove (1855), after analyzing rainfall observations in the temperate zone, posed the question of how changes in forest cover may influence rainfall patterns. Thus motivated, Krutzsch (1855) reviewed Swiss and French deforestation work to develop a conceptual description of forest canopy interception processes and their potential influence on rainfall intensity, soil organic matter content, infiltration and erosion. Although he describes forest canopy interception, no direct observations are reported or cited in 1855. Nearly a decade later, Krutzsch (1863, 1864) reports the first-known direct observations of canopy precipitation partitioning after updating his monitoring network to observe below-canopy precipitation (throughfall) in Tharandt, Saxony, Germany. To our knowledge this was the first national, at that time associated to the Kingdom of Saxony, monitoring network dedicated to forest-meteorological observations. These throughfall observations were used to estimate canopy saturation point for the first time: 0.2 mm (Krutzsch 1864). A direct relationship between relative throughfall and storm size across storms was also first reported, with relative throughfall being 9–57% of storms ranging 1.1–14.8 mm in magnitude. Although multiple insights were gained by Krutzsch's (1864) throughfall observations, more questions (and, as a result, more interest) arose in the scientific community. Broader measurements of canopy precipitation partitioning, including stemflow, were begun in 1868 in Bavaria, Germany by Ebermayer (Ebermayer 1873; Bühler 1918) after visiting Krutzsch's meteorological monitoring stations in Tharandt (Hölzl 2010). Similar to Krutzsch's monitoring network, Ebermayer also set up a series of national (Kingdom of Bavaria) long-term observatories. Similar field campaigns, although on more local scales (e.g., experimental forests, botanic gardens, or single trees), for precipitation partitioning were begun by researchers throughout mainland Europe, e.g., France [Mathieu in 1866 per Clavé (1875)], Switzerland [Frankhauser in 1869 per Maurice and Frécaut (1962)], and the Czech Republic (Johnen and Breitenlohner 1879).

Interestingly, both Krutzsch and Ebermayer published details regarding instrumentation as well as costs per station for their observatories. For example, Fig. 1.1 shows the annual maintenance and observer costs as well as the overall installation costs for the Bavarian observatory. For the Saxon observatory installed in 1862–1863, the investment costs were estimated to 87 Thaler and 4 Neugroschen (Saxon currency around 1862) whereas the annual cost for observation amounted to 30 Thaler



(a)

Inſtruction

für die Beobachter der meteorologiſchen Stationen.

Die anzuſtellenden Beobachtungen ſollen ſich erſtrecken

A. auf die Witterungsverhältniſſe;

B. auf gewiſſe Erſcheinungen des Pflanzen- und Thierlebens;

C. auf die Froſtorte.

A. Beobachtungen der Witterungsverhältniſſe.

§. 1.

(b)

Jährliche Unterhaltungskosten einer Station.

Für Reparaturen der Instrumente, Ergänzungen u. s. w. jährlich ca.	50 fl.
Für gedruckte Formulare der Original-Aufnahmetabellen und der monatlichen Zusammenstellungen, Bearbeitung und Druck der Beobachtungen ca.	30 „
Ozonpapiere jährl.	10 „
Remuneration für den Beobachter jährl.	150 „
Summa der jährl. Unterhaltungskosten	240 fl.

In runder Summe betragen mithin die Anlagekosten einer Wald- und Feldstation zusammen ca. 500 fl. und die jährlichen Unterhaltungskosten derselben ca. 250 fl.

Fig. 1.1 Costs for the **a** Saxon forest-meteorological observatory (Krutzsch 1863) and **b** annual maintenance and observer costs per station for the Bavarian observatory network (Ebermayer 1873)

(Krutzsch 1863). This equates to approximately $160 (nineteenth century, i.e., unadjusted for inflation). Observers that worked at any study site location experiencing sub-zero temperatures were paid an extra 20 Thalers, amounting to 50 Thaler per station. For the Bavarian observatory, installed in 1866, Ebermayer estimated an investment cost of 500 guilders (Bavarian currency at the time) and annual maintenance and observer costs of 250 guilders per station (Ebermayer 1873).

Throughfall observations began without spatial replication, comparing measurements of one open field gauge and one below-canopy gauge (Ebermayer 1873). Despite this limitation, Ebermayer (1873): (1) reported that annual relative throughfall varied significantly across forest types (68–75% of rainfall) and across four seasonal leaf states; (2) estimated the first snow interception amount (38% of snowfall); and (3) provided detailed instrumentation information. The first discussion of throughfall spatial variability was based on observations from Groß Karlowitz (now Velké Karlovice, Czech Republic) by Johnen and Breitenlohner (1879)—although the number of gauges deployed was not specified. This study also first reported the effect of event duration on interception capacity (i.e., short, low intensity rainfall produces greater interception and the opposite conditions increase throughfall). Aware of the need to account for interstorm and spatial throughfall variability but limited by costs and logistics, Bühler (1892) distributed gauges under different degrees of canopy cover and differently aged trees in two Swiss forests (including snow, but not stemflow) and recorded discrete storm size and intensity. Under this sampling design, Bühler (1892) first found the asymptotic relationship between relative interception and storm size, where relative interception is highest for small storms (<5 mm), decreasing until large storms (>10 mm) and remaining more-or-less stable. Hoppe (1896) conducted what is considered to be the first high-resolution throughfall study where 20 gauges were distributed along two crossing lines at a distance of 2 m in Brunneck and Farnleite, Austria (Fig. 1.2a). Impressively, this first high-resolution throughfall study also included meticulous photogrammetric analyses of canopy closure and density (Fig. 1.2b). These past results inspired Ebermayer's comprehensive manuscript (synthesizing data from Bavaria, Prussia, France and Switzerland) and clearly influenced his discussion as he noted that his throughfall results should be treated as "minimal crown influence" (i.e., lower boundary conditions) rather than an average (Ebermayer 1897).

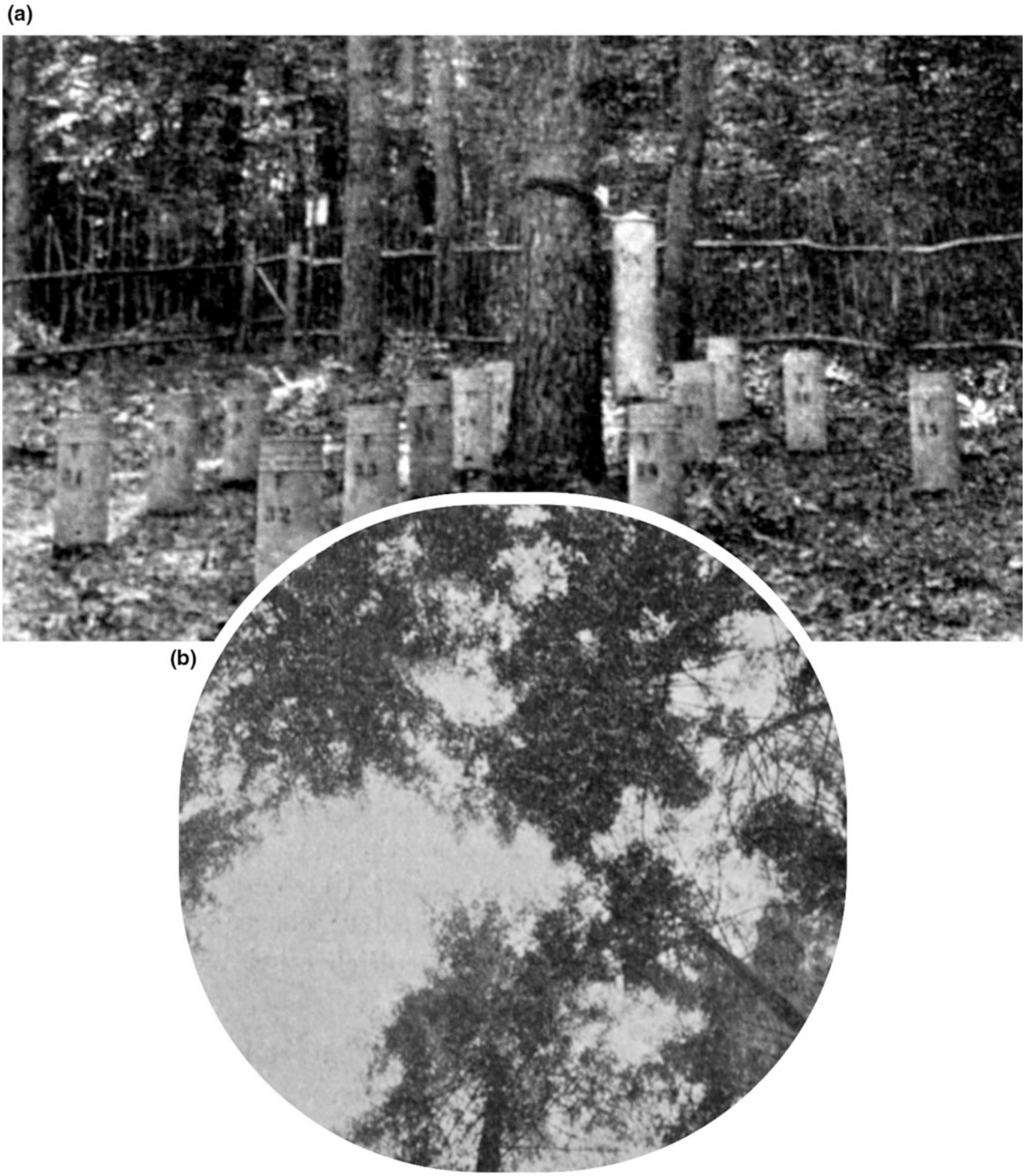


Fig. 1.2 Photographs taken by Hoppe (1896) showing **a** the first high-resolution throughfall monitoring campaign and **b** canopy closure above an example throughfall gauge. A detail worth noting is the presence of stemflow monitoring (see the collar connected to trunk in the photograph center)

Stemflow was, reportedly, not measured until 1868 at Ebermayer's Johannes-Kreuz site; however, based on later publications it seems these stemflow observations were never published (Bühler 1892; Ebermayer 1873; Ney 1894). The first published stemflow observations were by Riegler (1881) alongside a conceptual discussion of the stemflow process.

Stemflow was measured from four isolated trees, each a different species with unique canopy structuring: *Fagus sylvatica*, *Quercus robur*, *Acer platanoides*, and *Abies excelsa* (Riegler 1881). His discussion was more robust than his sampling campaign, synthesizing the scant stemflow data available at that time to support hypotheses about stemflow's relationship with branch angle and bark roughness (Riegler 1881). He cites an interesting personal communication with Professor Kerner (likely Anton Josef Kerner at the University of Vienna from 1878 to 1895) about experiments that involved pouring small grist grains onto branches and leaves to visualize water flow (i.e., stemflow) patterns (Riegler 1881). We could not find the results of these experiments. Riegler (1881) also collected throughfall and open rainfall, ultimately concluding that previous work (i.e., Ebermayer 1873) required correction for stemflow and recommending future work include stemflow in the canopy water balance. Ney (1893, 1894) was the first to comprehensively measure and estimate stand-scale stemflow and may actually have been the first stemflow observer, as Ebermayer (1873) mentioned that Ney made the stemflow observations at Johannes-Kreuz from 1868 to 1871 (that, as mentioned earlier, were not published). Ney (1893) included stemflow measurements across forest types, leaf states and precipitation types—namely rain, snow and even dew. Surprisingly, his analysis extends even further, into the influence of stand age, interspecific traits, canopy density (Ney 1893). His proceeding publication summarized previous stemflow observations and emphasized stemflow's importance to net precipitation calculations (Ney 1894). Although rarely cited, the results of Ney (1893, 1894) confirm many of the late twentieth century and early twenty-first century ecohydrology literature (Friesen and Van Stan 2019).

By the end of the nineteenth century, scientists had achieved a profound understanding of most processes underlying the hydrological aspects of precipitation partitioning, how to measure these processes, and how to estimate those that were not directly measurable at that time (like canopy water storage). Enough observations and discussions had been published by the early twentieth century that Zon (1912) and Bühler (1918) were able to develop comprehensive reviews of precipitation partitioning studies with reference to both rain and snow. These reviews highlighted throughfall and stemflow measurements and the indirect estimate of interception, leaving the interception components, water storage and evaporation, understudied. Horton (1919) then closed this gap by presenting direct estimates of rainwater storage capacity for different leaf structures, discussing how to disentangle storage and evaporation components of interception, and placing these interception components into context alongside net precipitation measurements and wind conditions. Horton's (1919) seminal paper, being cited copiously since and continuing to be cited today, thus completed the conceptual foundation upon which modern precipitation partitioning work began to build.

1.3.2 Foundational Biogeochemical Observations

Quantitative observations of the exchange (leaching or uptake), transformation, and wash-off of deposited nutrients during precipitation partitioning began in croplands. These agricultural roots stem from nutrient content analyses becoming key to studies on the efficacy of fertilizer application methods during the mid-to-late 1800s (Johnson 1869). Indeed, conservation of fertilizer was of significant socioeconomic and cultural importance to both farmers and nations before development of the Haber-Bosch method for synthesizing ammonia (Erisman et al. 2008). Despite conjecture on nutrient exchange between leaves and precipitation by Stephen Hales (1727), where his observations of submerged leaves (Fig. 1.3) prompted the hypothesis that "nourishment … is conveyed into vegetable thro' the leaves, which plentifully imbibe the dew and rain, which contain salt, sulphur, etc.," research on biogeochemical aspects of precipitation partitioning did not mature until the mid-twentieth century. In fact, chemical leaching between precipitation and plant surfaces was not generally accepted by the publishing biogeochemical community until its experimental confirmation via isotopically labeled nutrients in the 1950s (Long et al. 1956; Silberstein and Wittwer 1951). Of course, the loss of internal solutes from damaged or dead plant materials into water has been known since the dawn of human civilization (q.e.d., popular plant-based beverages, like beer, tea, or coffee). The delay in recognizing and quantifying nutrient exchanges between precipitation and living plant surfaces appears to be, in large part, due to an extensive and sometimes contentious debate that began in the 1870s—as summarized by Le Clerc and Breazeale (1908). The debate seems to have been rooted in the Earl of Dundonald's (1795) hypothesis that solutes within plants are protected by their "outward surface," preventing "their being acted upon by rain or moisture." This hypothesis was oddly foundational to his overarching theory of natural science, stating that "the insolubility, to a certain degree, of this system [plant surfaces], adopted by nature, is undoubtedly preferred … for it is evident that if putrefaction or oxygenation had possessed the power of rendering all the vegetable matter, by a speedy process, soluble in water … the rains would have washed down such extracts and soluble matters, as fast as formed, into the rivers and springs, contaminating the waters and rendering them unfit for the existence of fishes, or for the use of terrestrial animals" (Dundonald 1795). Dundonald (1795) goes on to describe the "pernicious consequences" that would result should plant surfaces chemically

Fig. 1.3 An illustration of a branch submersion experiment performed by Hales (1727). Observations of the leaves during long-term submersion inspired Hales to hypothesize about the possibility of nutrient exchange between precipitation and leaf surfaces (image from Hales 1727)

interact with precipitation, including "the sea, in the process of time, would thereby receive all the [dissolved] vegetable produce of the dry land and the Earth would ultimately become barren." Thus, the world's first authoritative treatise on plant biogeochemistry argued that precipitation and internal plant solutes could not interact without catastrophic consequences.

Major leaps in chemical and agricultural science throughout the mid-1800s, due primarily to Germany's Agricultural Experimental Stations, debunked many of Dundonald's theories on plant biogeochemistry (Johnson 1869). However, the Earl's theory that chemical leaching between plants and precipitation was impossible, remained an ingrained belief of the scientific community. This theory even persisted despite experiments showing that in-tact leaves (albeit detached from the stem) could enrich purified water with soluble salts, in eight successive trials, and that the mass of salt dissolved into the water was similar to the mass lost in the leaves' ash-ingredients (de Saussure 1804). Nineteenth-century plant scientists ascribed de Saussure's (1804) observations of solute leaching to the leaves being damaged. In fact, only damaged plants were thought to lose solutes to precipitation (Guilbert et al. 1931; Ritthausen 1856). By the late 1800s, the most famous plant physiologist of the time, Dr. Samuel W. Johnson of Yale, still downplayed de Saussure's (1804) foliar leaching observations, stating "all experiments which indicate great loss [of solutes] in this way [i.e., interaction with precipitation], have been made on the cut plant, and their results may not hold good to the same extent for uninjured tissues of plants" (Johnson 1869). Still, observations were mounting that perplexed plant biogeochemists (who denied precipitation-related solute exchange), beginning with the first observations of crop nutrient contents at various growth stages (Norton 1847). Norton's (1847) perplexing observation was that certain nutrients in crops did not continually accumulate until ripening; rather, they maximized around the heading period then diminished until harvest (Le Clerc and Breazeale 1908). Many scientists asked, "where are these nutrients going?" and most believed they were being translocated back to the roots or soil, but they could not be found there (Le Clerc and Breazeale 1908).

Liebscher (1887) hypothesized that this loss of nutrients in healthy crops was due to portions of the plant withering and decaying; however, nutrient losses of this kind only accounted for a portion. After reviewing the nineteenth-century plant biogeochemical literature, Wehmer (1892) posited that "plant food" was removed from leaves by precipitation. Although he did not collect data himself, both the estimate of the potential nutrient loss from rain-related leaching and a conceptual process of leaching were provided (Wehmer 1892). Le Clerc and Breazeale (1908) state that Wehmer's (1892) review and hypothesis were opposed by his contemporaries to "so great an extent that it seems to have been relegated to the background.” Indeed, even Le Clerc and Breazeale (1908), who observed rainfall enrichment with salts after passing through various crop canopies, still concluded that only wash-off processes occur, “plants exude salts upon their surfaces, and the rain then washes these salts back to the soil,” and stopped short of indicating that solute leaching could occur between precipitation and plant surfaces. Another notable work on the enrichment of rainfall by plant exudates is the review by Arens (1934). Thus, the application of isotopically labeled nutrients to biogeochemical research was required to confirm uptake and leaching from plant leaves experimentally (Long et al. 1956; Silberstein and Wittwer 1951).

Le Clerc and Breazeale (1908) were not the first to observe and discuss the wash-off of plant exudates by precipitation—this, like leaching, was first observed by de Saussure (1804). During observations of cucumber leaves, he noticed exudations that formed crusts across the leaf surface (de Saussure 1804). He tested the exudate crust and found that, although it was not deliquescent, a portion was soluble in water and likely to be washed off by precipitation (de Saussure 1804). Johnson (1869) discusses these, and similar findings on other crops, and indicates that the wash-off of exudates during precipitation may represent “a considerable share of the variations in percentage and composition of the fixed ingredients of plants.” It was not realized that precipitation wash-off also includes “dry” deposited atmospheric materials, or that these materials had biogeochemical importance, until the mid-twentieth century (Ingham 1950; Meetham 1950). Shortly after Ingham’s and Meetham’s (1950) publications, scientists recognized dry deposition contributions to net precipitation chemistry (Eriksson 1952; Tamm 1951). Thus, it was in the 1950s that a robust conceptual foundation of precipitation partitioning biogeochemical aspects (that included elemental leaching, uptake, transformation and wash-off) was achieved. This decade also produced the first comparative observations of throughfall chemistry beneath various forest canopies, specifically pine, oak and birch (Tamm 1951). Tamm (1951) compared throughfall Ca, K, Na and P concentrations to open rainfall to highlight the significant enrichment of these nutrients in throughfall (by 4–70 times). The first annual throughfall nutrient yields were reported as 25–30 kg K, 11 kg Ca, 9 kg Na, and nearly 900 kg of carbohydrates ha^{-1} year^{-1} for an apple orchard (Dalbro 1955). In the same year, Will (1955) roughly estimated throughfall nutrient yields for select solutes, but did not publish the full study until a few years later (Will 1959). These nutrient yields surprised many plant biogeochemists and placed throughfall, particularly leaching by throughfall, into the standard research methodology for nutrient budgeting (Tukey 1966). However, biogeochemical aspects of stemflow were still unexamined. Stemflow properties (acidity and particulate content) were first reported by Pozdnyakov (1956), but stemflow nutrient concentrations and fluxes, including interspecific and seasonal variability, would not be reported until Voigt (1960). Then, the potential for stemflow nutrient fluxes to exert significant localized ecological effects was not recognized until Eaton et al. (1973) and Mahendrappa and Ogden (1973).

1.4 The Last Century: A Bibliometric Analysis from 1918 to 2017

Since the hydrological and biogeochemical foundations of precipitation partitioning research were laid, the new research topics raised and addressed over the last century in this field have been substantial and diverse. Rather than attempt a complete summary of key advancements in this field, which would likely require much more space than available for this chapter, we perform a meta-analysis of publication and citation trends from Thompson Reuter’s Web of Science (WoS). Certainly, WoS represents only a portion of the full corpus of literature on any subject, placing some limitations on our bibliometric analyses—see recent discussions on this topic (Harzing and Alakangas 2016; Mongeon and Paul-Hus 2016). The WoS sample of publications and citations on precipitation partitioning is assumed to provide sufficient coverage and stability of coverage (i.e., Harzing and Alakangas 2016); however, we acknowledge a bias in WoS toward English publications, which did not become the dominant language of science until after the Second World War (Gordin 2015). Besides missing some early works in other languages, we are unsure of the exact impact of over-sampling English publications on the bibliometric analyses. Another consideration regarding language: although key terms for precipitation interception processes—canopy/leaf and stem/trunk evaporation and water storage—were used by the research community prior to 1918, key terms for net precipitation fluxes—throughfall and stemflow—are not to be found in the WoS publication database until Ellison and Coaldrake (1954). Notwithstanding, use of WoS enables assessment of the disciplines (or “Research Areas” per WoS) where precipitation partitioning research has been published and cited.

Queries over the past century, excluding patents and limited to titles, abstracts and keywords, resulted in the following total number of publications for bibliometric analysis: 3666 for throughfall, 2405 for rainfall interception, 1494 for stemflow, 387 for snow interception and 136 for fog interception. Search results were manually reviewed to remove unrelated publications from the dataset. Of the 252 research areas categorized by WoS, rainfall interception and throughfall studies represented the greatest diversity across disciplines, being published in over 90 research areas. Despite stemflow research having the latest start, it has been published in 77 research areas. Snow and fog interception studies were represented in

63 and 50 research areas, respectively. The dominant research area for publication of all precipitation partitioning topics over the past century was “Environmental Sciences & Ecology,” representing 80–90% of publications. For throughfall and stemflow, journals in the “Forestry” research area ranked second, having published at least 70% of research. A significant portion of studies on all interception topics were published in “Meteorology & Atmospheric Sciences” outlets. The dominance of forestry journals in throughfall and stemflow aligns with net precipitation fluxes having primarily been investigated for their role in forest water and nutrient budgets over the past century (Parker 1983; Van Stan and Gordon 2018; Will 1955). On the other hand, studies on vegetation water storage and evaporation of precipitation have primarily been motivated by an interest in moisture return to the atmosphere—explaining the dominance of meteorology and atmospheric science journals over the past century (Horton 1919; Lundberg and Halldin 2001; Rutter et al. 1971; van Dijk et al. 2015). Over one-quarter of snow interception papers were published in the mathematics research area, consisting of work with a modeling focus (Hellström 2000; Liston and Elder 2006; Pomeroy et al. 1998). Nearly one-third of fog interception publications are published in the biodiversity and conservation research area, likely because many fog-reliant ecosystems are biodiversity “hot spots” in need of conservation science (Bruijnzeel et al. 2011).

Precipitation partitioning research has been frequently cited by the broader scientific community between 1918 and 2017. The number of studies in WoS that cite precipitation partitioning literature over the past century was 10 times (stemflow) to 25 times (snow interception) the number of publications on the subject! These citations yielded 100-year H-indices (not including self-citations) ranging from 35 (fog) to 117 (throughfall). Research areas citing precipitation partitioning research over the past century were more diverse than the publication research areas, by 1.5–2 times. The number of research areas citing each topic was 106 (fog interception) to 140 (throughfall), but the environmental science and ecology arena dominated the citations for all topics.

In total, studies from all keyword searches in WoS represented author affiliations from 121 different countries in every world region. A pictograph of these results per country (for the top 25 countries) shows the dominance of European, North American, East Asian, and Oceanian countries in publication output over the past century (Fig. 1.4). However, in examining international publication trends, it is important to recognize that multiple socioeconomic, political, and physical geographic factors underly “why” scientists start investigating precipitation partitioning processes and interact to determine “how” these investigations are enabled and supported. We also reiterate that our bibliometric analysis under-represents native language scientific publication, which could increase the number of publications represented in Fig. 1.4. A few major world regions are strongly represented by a single country in the precipitation partitioning literature: Brazil (South America), India (South Asia), and Mexico (Central America) (Fig. 1.4). Although South African researchers were active from the early days of precipitation partitioning research in forests and grasslands (Beard 1955; Phillips 1926, 1928; Wicht 1941), their work in the field slowed through the century, resulting in their ranking 29th (*n* publications = 48)—tied with Chile. Of all Middle Eastern countries, Iran produced the most publications on this topic over the past century (31st, *n* publications = 36), which

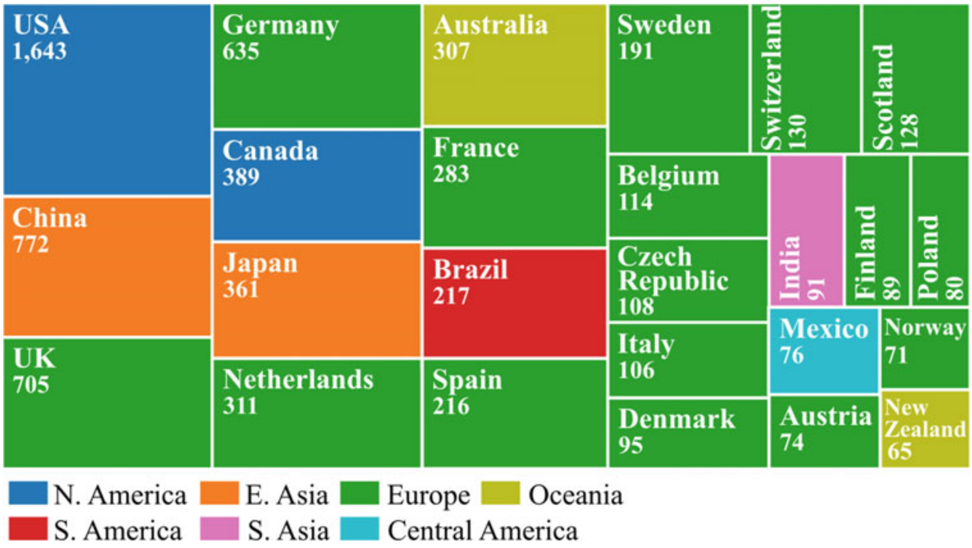


Fig. 1.4 Pictogram of the 25 countries that have published precipitation partitioning research according to the Web of Science database, where box size is weighted by number of publications and the color indicates each country’s world region

appears to have been principally motivated by concerns about the degradation of the Caspian Oriental Beech Forests over the past decade (Ahmadi et al. 2009). For Southeastern Asia, Indonesia has produced the most publications on this topic per the WoS database (32nd, *n* studies = 31), generally rooted in the work of Calder et al. (1986). However, the first English publication on precipitation partitioning from Southeastern Asia appears to be an assessment of five Malaysian catchments (Low and Goh 1972). To date, no work in English on this subject has been reported for Central Asia or the Congo, areas with quite different vegetation, each equally meriting precipitation partitioning research in order to close regional data gaps and achieve a macroscale to global-scale understanding.

1.5 Current Relevance

Nine months into 2018 (at the time of writing this chapter), over 100 papers have already been published examining precipitation partitioning and its relationships with ecosystem functions, showing the growing relevance of the field. We focus this review of recent research on publications and presentations that have described new processes and estimates of states or fluxes. Thus, studies which report data on previously known processes, states or fluxes for new plant species, vegetation covers, etc., have been excluded from the following discussion. There is also not enough room in this chapter to fully describe the processes underlying each of these highlights; as such, the intention is that the reader will refer to the cited publication or presentation for greater detail. Not all results indicate that precipitation partitioning significantly influence the studied ecosystem properties; for example, no influence was found for throughfall on root biomass (Qi et al. 2018), contradicting long-cited semi-quantitative work regarding throughfall patterns and root patterns (Ford and Deans 1978). The oft-cited work on stemflow's role in generating "fertile islands" around plant roots in arid environments (Whitford et al. 1997) has also been challenged by meticulous manipulation experiments that found the stemflow influence alone was inadequate to engender fertile islands (Li et al. 2017). Some natural and plantation forest systems' may even be resilient to changes in precipitation partitioning (Orság et al. 2018), and their canopy ecohydrological processes, themselves, may be resilient to climate changes (Gimeno et al. 2018). Identifying the degree to which ecosystem elements, processes and the entire ecosystems, themselves, are resilient or sensitive to interception, throughfall and stemflow is a complex and critical pursuit.

Regarding rainfall interception research, global estimates of rainfall storage and evaporation from vegetation have been revised to include nonvascular vegetation (lichens and bryophytes), increasing global vegetation water storage capacity, from 0.4 to 2.7 mm, and evaporation by 61% (Porada et al. 2018). Savenije (2018) commented on the Porada et al. (2018) interception estimates, stating they "suggest that water balance computations need to be revisited." Indeed, much work thus far in 2018 has examined rainwater storage and evaporation controls in vegetation. One highlight in this research vein includes work by Klamerus-Iwan and Witek (2018) that quantifies and characterizes the effects of leaf pollutant uptake and infection on leaf water storage capacity. Significant work has been done on intercepted water taken up by leaves and redistributed within plants—and a new review article summarizes these foliar water uptake pathways, the biophysical conditions underlying them, and provides quantitative assessment of this process within plant water budgets (Berry et al. 2019). There is also a growing awareness of the importance of storm events and precipitation routing within the canopy to plant–microbe interactions, especially regarding the "disease triangle" between hosts, pathogenic microbes and their environment (Aung et al. 2018).

For throughfall, significant work continues to focus on the effects of its reduction on multiple ecosystem functions, like net ecosystem productivity, soil moisture dynamics or soil gas emissions (e.g., Bracho et al. 2018; O'Connell et al. 2018; Samuelson et al. 2018). Understanding of throughfall kinetic energy and soil erosion in forests was recently revised to recognize the importance of understory vegetation influences (Lacombe et al. 2018). New insights into fine-scale spatial variability in throughfall amount and intensities have also been gained, revealing the importance of patterns in storage "refilling" due to within-storm evaporation (Keim and Link 2018). Fine-scale temporal variability in throughfall generation processes is on the horizon, as near real-time observations systems are being tested in the field that yield water stable isotope measurements every few minutes (Herbstritt et al. 2018). In geomorphology, recent findings indicate throughfall measurements may be important for fallout radionuclide-based methods used to determine stream suspended sediment source and age (Karwan et al. 2018). Soil aggregate stability and associated organic carbon stocks appear to rely, in part, on throughfall (Zhang et al. 2018). For stemflow, an "alternative water transport system" for plants was recently identified and described that relies on stemflow (Biddick et al. 2018). Stemflow from forests' fog water harvesting may play an important role in water resources along the arid Omani coast, having been estimated to increase precipitation available for recharge by 20% (Friesen et al. 2018). Debate has recently arisen regarding stemflow research, where scientists are asking what metrics (stemflow percentage, yield, input, or funneling ratio) under which circumstances should researchers report for stemflow (Carlyle-Moses et al. 2018). This question was, in part, motivated by a recent global analysis of stemflow in forests that indicates stemflow may exert significant ecological influences on near-stem soil biogeochemical processes via resource limitation (Van Stan and Gordon 2018).

There have also been many new insights from studies investigating all precipitation partitions. Recent work indicates that dissolved organic matter in throughfall and stemflow (called “tree-DOM”) can be significantly concentrated compared to other terrestrial hydrologic fluxes (Van Stan and Stubbins 2018), that tree-DOM is structurally diverse (Stubbins et al. 2017), and that it may provide a highly biolabile C subsidy to soil microbes (Howard et al. 2018). In the tropics, a comprehensive evaluation of DOM optical and isotopic properties indicated that tree-DOM may reach stream networks, where it may be rapidly metabolized (Osburn et al. 2018). Regarding agricultural science, recent work has elucidated throughfall’s and stemflow’s role in pesticide transport (Glinski et al. 2018), and it was found that precipitation partitioning should be considered when managing crop canopies for rainfed agriculture (Hakimi et al. 2018; Niether et al. 2018).

Finally, significant progress has been made at the intersection of microbiology and precipitation partitioning. The first report of bacterial cells transported from the canopy to the soils during storms found that this flux can equal quadrillions of cells ha^{-1} year^{-1} (Bittar et al. 2018). Analysis of the bacterial community structure via high-throughput sequencing, found for the first time that throughfall and stemflow fluxes can carry taxa known to engage in soil and litter biogeochemical processes, and that their community composition may be principally controlled by atmospheric deposition and storm synoptic patterns (Teachey et al. 2018). These bacterial hitchhikers share their hydrologic highway with a large quantity of metazoans: 1.2 million rotifers; 216,000 nematodes (many being bacterial feeders!); 160,000 tardigrades; 73,000 mites; and 25,000 collembolans year^{-1} tree^{-1} (Ptatscheck et al. 2018). Considering the abundance of fungal spores (Gönczöl and Révay 2004), archaea (Watanabe et al. 2016), particulates (Bischoff et al. 2015), and so on, the latest findings show that throughfall and stemflow may best be analogized as ephemeral, but congested, hydrologic highways between the plant canopy and any receiving surface or subsurface ecosystem. Future research will, undoubtedly, shed fascinating insights into whether these compounds and creatures survive their interactions with precipitation partitioning, where they end up, what they do there, and how much it matters at various ecosystem scales.

1.6 Conclusions: The Structure of This Volume

We began this chapter and, thereby, this book, by familiarizing our readers with the Peripatetic origins and foundational observations of precipitation–vegetation interactions. It was the impacts of precipitation partitioning at the surface, in the “shadows” cast by plant canopies, that caught the eyes of the “Father of Botany” (Theophrastus) and Pliny the Elder over 2000 years ago. Contrary, however, to the chronological order of discovery in this field, this book will address the impacts of precipitation partitioning only after a thorough description of the underlying processes behind the “shadow,” or, put more scientifically, within the black box: water storage on vegetation (Chap. 2) and evaporation (Chap. 3). We follow the remaining precipitation that drains from the canopy to the surface as throughfall and stemflow (Chap. 4) and, then, examine the dissolved and particulate composition of these net precipitation fluxes (Chap. 5) as well as their spatiotemporal patterns at the surface (Chap. 6). To contextualize, for the first time, all precipitation partitioning processes into the global hydrologic cycle and climate system, Chap. 7 describes common parametrizations and applies land surface models to estimate the impacts of precipitation on regional and global hydrologic forecasts and land-atmosphere energy exchange. Precipitation interception, throughfall, and stemflow are also placed into context within vegetated ecosystem processes, starting with the C cycle (Chap. 8), and then vertically through the ecosystem itself: starting with the plants inhabiting plant canopies, epiphytes (Chap. 9), then examining the water and nutrient balance of plants rooted in soils (Chap. 10), impacts on litter biogeochemistry (Chap. 11) and soil physicochemistry (Chap. 12), then concluding with the relevance of precipitation partitioning to subsurface waters (Chap. 13). As precipitation partitioning interacts across all habitats of vegetated ecosystems, a discussion is provided regarding its interactions with microbiota in habitats throughout the plant microbiome (Chap. 14). Finally, the importance of precipitation partitioning to the human environment is highlighted via description of the economic valuation of its ecoservices (Chap. 15). To be as comprehensive a text as possible on its subject, the final chapter concludes with currently unanswered questions that the field considers to be key to the illumination of processes at the conceptually shadowed intersection of hydrologic, ecological, and climate theory. It is our hope that this book will add fuel to the fire that Theophrastus and Pliny ignited and make it brighter—bright enough to concentrate its beams toward the darker reaches of current theory while keeping conspicuous the lessons of past research.

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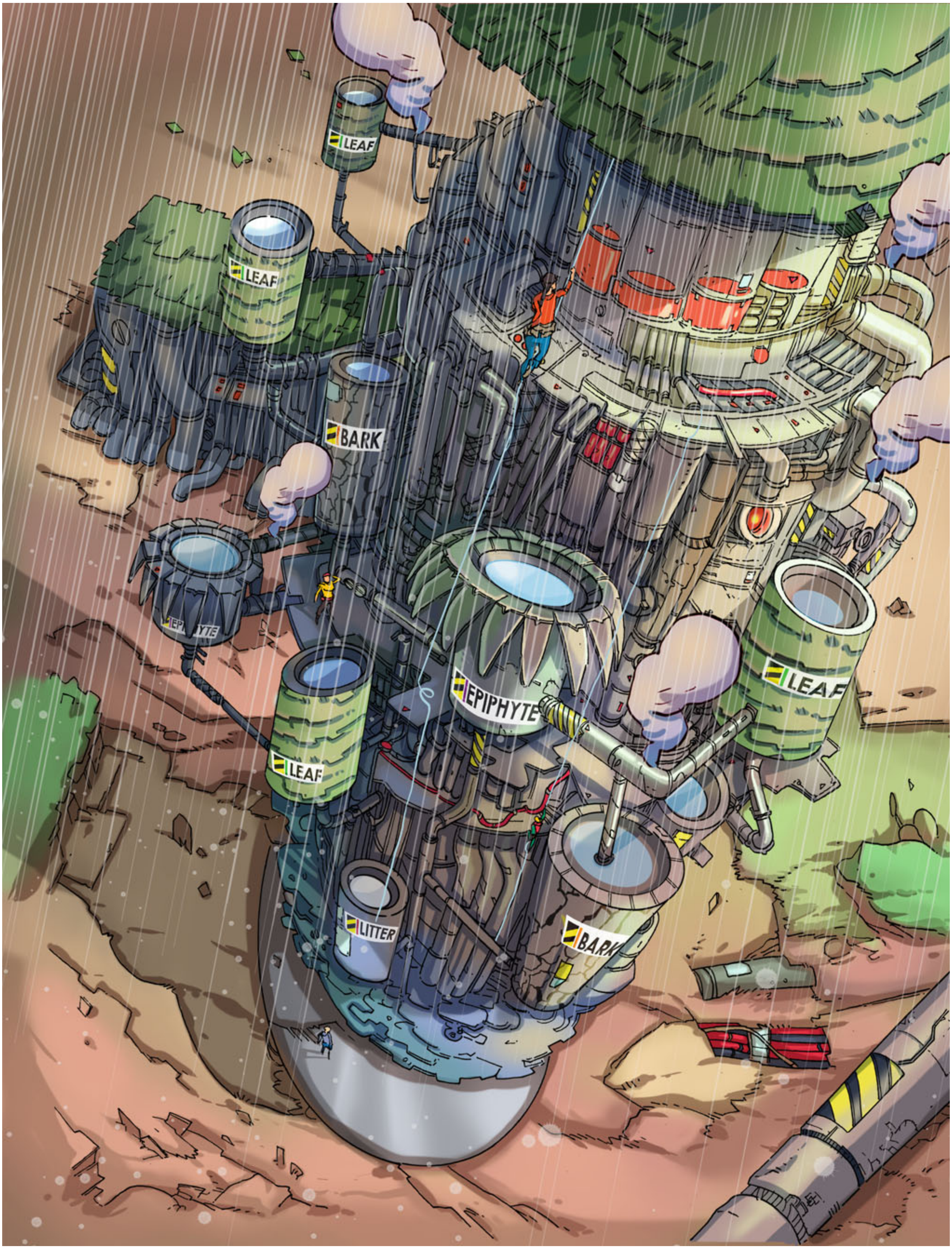
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2

Storage and Routing of Precipitation Through Canopies

Anna Klamerus-Iwan, Timothy E. Link, Richard F. Keim,
and John T. Van Stan, II

Abstract

Water storage on tree crowns, trunks, the understory, and litter is, in many respects, one of the simplest water balance components of vegetated ecosystems, but one that is rarely parameterized in detail. Interception processes are often analogized and parameterized as the dynamic (filling and emptying) of static reservoirs, but canopy storage reservoirs and dynamics are more complex, and hence are not fully represented in most ecohydrological models. Each reservoir is itself dynamic in its spatial extent, temporal persistence, and interconnection to other reservoirs throughout the canopy space. Total water storage in the canopy depends in part on how much surface area is affected by water flowing along, and drops among, vegetative surfaces. These flow pathways and their connectivity to other canopy reservoirs also determine drainage rate, i.e., flow to stems and drip from all surfaces as throughfall to the understory or litter. Traversing the canopy in this way could take rainwater $\sim 10^{-2}$ to 10^{2} h (and potentially 10^{3} h for frozen precipitation), depending on intrinsic characteristics of canopy surfaces and extrinsic meteorological factors. The aim of this chapter is therefore to describe how precipitation storage in vegetated ecosystems is measured, the major water storage reservoirs, and intrinsic and extrinsic factors affecting these reservoirs; and discuss the extent and limitations of our current knowledge about the distribution network between reservoirs.

Keywords

Ecohydrology • Leaf texture • Bark • Litter • Wettability • Water storage capacity • Snow

2.1 Introduction

Before precipitation reaches the mineral soil of vegetated ecosystems, it is intercepted by plant canopies and their litter layer. Once intercepted by plant surfaces, solid and liquid precipitation waters are “stored” until evaporated and/or sublimated (Chap. 3) or until they drain along leaf and branchflow pathways to the surface as throughfall and stemflow, or release as masses of snow (Chap. 4). This initial step in precipitation partitioning can exert profound impacts on all subsequent hydrological processes—impacts valued at tens to hundreds of millions of dollars (US) at the headwatershed to municipal

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scale, respectively (Chap. 15). Water storage and distribution within plant canopies, however, is typically not managed to maximize pecuniary or non-pecuniary benefits (i.e., human health and wellness), or, if it was managed, the design likely had other aims than water management, like timber yield, safety, landscaping aesthetics (Van Stan et al. 2018), or reduction of potential damage from snow loading (Miller 1964).

Hydrologically, vegetated ecosystems may be conceptualized as a water distribution network with distinct interconnected storage components. Thus, land cover change that alters these storage components, or the conceptual "pipelines" between them, may impact the terrestrial water balance. For example, the impact of altering canopy and trunk interception "reservoirs" during forest thinning can be so large that the typical interception models are no longer valid (Shinohara et al. 2015). The epiphytic and parasitic plant reservoir in canopies has recently been found to influence global evaporative partitioning (Porada et al. 2018). Beneath the canopy, the understory and litter act as a reservoir for sub-canopy precipitation that can reduce net rainfall to the soil by 6–84% (Gerrits and Savenije 2011). Indeed, many studies over the past several decades indicate the need to improve our understanding of this intercepted precipitation distribution system in vegetation (Black 1957; Friesen et al. 2015; Helvey and Patric 1965; Moul and Buell 1955). These calls have a diversity of justifications, as interactions between precipitation reservoirs and pipelines in vegetation influence spatiotemporal throughfall (Keim and Link 2018; Keim et al. 2005) and intensity patterns (Keim and Skaugset 2004; Keim et al. 2006b), and the chemical composition (Raat et al. 2002; Rosier et al. 2015) of net precipitation.

Factors affecting the water storage capacity of vegetation, and particularly the wettability of leaves, are of growing interest to ecohydrologists (Aryal and Neuner 2010; Berry et al. 2019; Helliker and Griffiths 2007; Limm and Dawson 2010; Rosado and Holder 2013). Nevertheless, the full suite of factors controlling water adherence to plant materials is still not fully understood (Burkhardt and Hunsche 2013; Fernández and Eichert 2009), and is considerably more complicated for snow storage processes (Miller 1964), which may partly explain the over-simplified representation of precipitation storage in land surface models. Nearly all land surface models represent precipitation water storage and redistribution on vegetation as a simple reservoir of universal size (Dolman and Gregory 1992; Sellers et al. 1996), or more recently, varying directly with Leaf Area Index (Fig. 2.1a) using a daily phenology multiplier for plant functional types (Gerten et al. 2004; Murray 2014). These water storage capacities are typically low (0.2–2 mm), compared to field observations (1–16 mm) (Gerrits and Savenije 2011; Porada et al. 2018; Van Stan et al. 2015), probably because LAI alone does not account for the various other reservoirs in vegetated ecosystems (Fig. 2.1b). At a smaller scale, nearly all process-based models of canopy interception physics also depend on canopy storage as a parameter. The surprisingly poor understanding of the controlling factors thus limits predictive capability at multiple scales. The aims of this chapter are therefore, to describe (i) how both liquid and solid (snow) precipitation storage in vegetated ecosystems can be measured, (ii) the major precipitation water storage reservoirs (leaves, bark, epiphytes, understory, and litter), (iii) intrinsic and extrinsic factors affecting these reservoirs, and (iv) discuss the extent and limitations of our current knowledge about the distribution network between reservoirs.

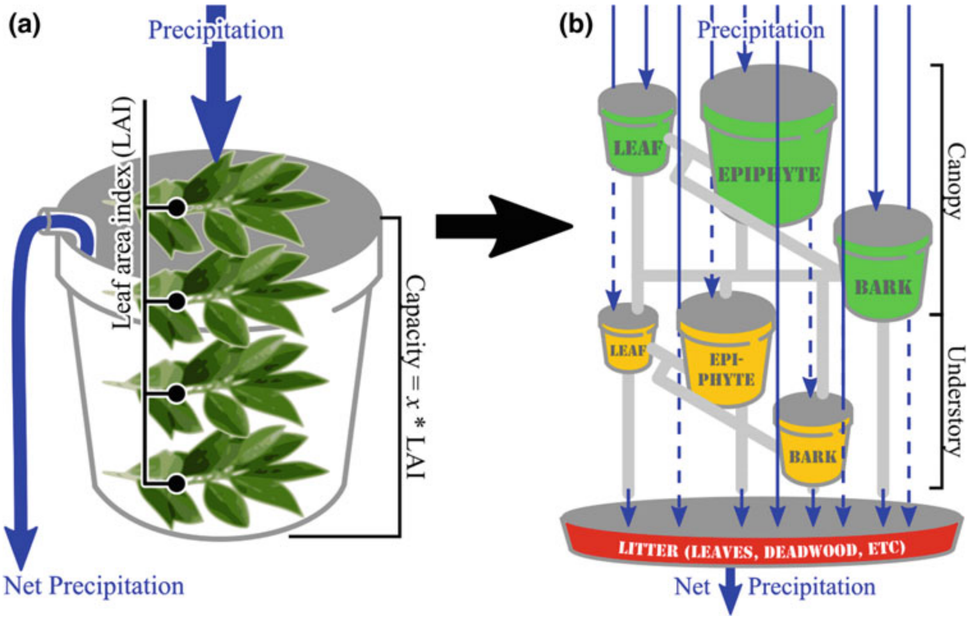

Fig. 2.1 **a** Typical representation of precipitation water storage and distribution systems in land surface models as a single reservoir (represented as a bucket), whose capacity is some multiplier of leaf area index (*x* * LAI) and resulting net precipitation is the overflow. **b** There are multiple interconnected reservoirs in vegetated ecosystems and nearly all other reservoirs (epiphytes, bark and litter) have greater capacities than leaves and operate at different timescales than leaf phenology

2.2 Measurement of Precipitation Water Reservoirs on Vegetation

The earliest methods for estimating the storage of intercepted precipitation in the overstory canopy relied on relationships between above-canopy or open (hereafter, gross) precipitation and net (or subcanopy) precipitation (Bühler 1892; Dove 1855; Ebermayer 1873a; Horton 1919; Krutzsch 1863). These authors plotted gross precipitation [mm] against the water that dripped from the canopy or through gaps, called “throughfall” [mm], or net precipitation. Capacity of the canopy reservoir [mm] was estimated by an upper envelope regression or simple linear regression with gross precipitation and the water that ran down stems to the soil surface, called “stemflow” [mm]. With these fitted lines (Fig. 2.2a), the canopy and stem reservoirs could be estimated in a variety of ways: (1) by finding an inflection point in the upper-envelope line among storms where reservoirs were saturated or unsaturated; or (2) by using the absolute value of the *y*-intercept of the simple linear regression for all storms with minimal during-event evaporation (Leyton et al. 1967) or (3) for only the storms that saturated these reservoirs (Klaassen et al. 1998). The limitations of these indirect estimates are various and well-researched (Friesen et al. 2015). Most fundamentally, throughfall and stemflow are highly spatiotemporally heterogeneous and require large sampling campaigns (Hoppe 1896; Kimmins 1973) to produce representative estimates of spatial means (to regress with gross precipitation). As a result, ecohydrologists began seeking more direct ways of estimating and monitoring canopy and stem precipitation reservoirs.

The field began direct measurement of precipitation storage with monitoring weight changes in entire plants over time (Fig. 2.2b), which enabled monitoring of all reservoirs throughout a plant on a lysimeter (Fritschen et al. 1973; Shidei et al. 1952; Storck et al. 2002), hung from a frame system (e.g., Fig. 16 in Kinar and Pomeroy 2015; Schmidt et al. 1988; Watanabe and Ozeki 1964; Hedstrom and Pomeroy 1998; Satterlund and Haupt 1967), or affixed to a stand and placed on a load cell (Storck et al. 2002). Monitoring water storage of whole plants, however, is inherently limited in scale (i.e., observations of individual plants require up-scaling, both from measureable individual trees to larger individuals and/or entire stands) which prevents investigation of each storage sub-reservoir, their relationships, and eventual effect on where and how much precipitation is transferred from the canopy to the understory and through the litter layer. To resolve these details, researchers began to sample various components—leaf litter (Helvey and Patric 1965), leaves and bark (Herwitz 1985; Liu 1998), epiphytes (Pypker et al. 2006; Veneklaas et al. 1990), whole branches (Keim et al. 2006a), and coarse

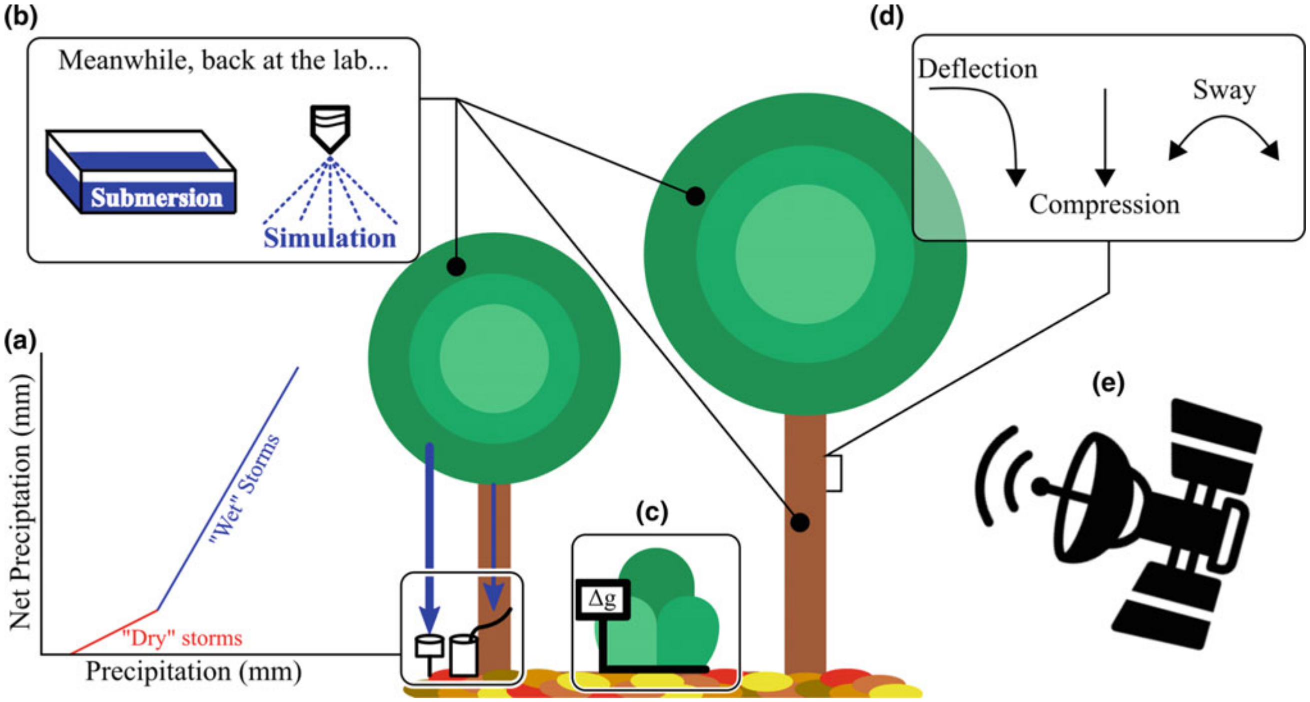

Fig. 2.2 Various methods for monitoring or estimating water storage capacity and water storage dynamics in vegetation: **a** indirect estimates via throughfall and stemflow monitoring; **b** testing samples in the lab via submersion or precipitation simulation; **c** whole plant lysimeters; **d** relating mechanical properties, like strain or sway, to mass changes; and **e** remote observations via photographic analyses or signal attenuation

woody debris (Sexton and Harmon 2009)—to develop ex situ estimates of the capacity for each of these reservoirs (Fig. 2.2c). Liquid water storage capacities for each sampled element can then be estimated per two principal laboratory methods: submersion until saturation (Liu 1998; Pypker et al. 2006; Van Stan et al. 2017a; Veneklaas et al. 1990) or exposure to simulated precipitation until saturation (Calder et al. 1996; Hutchings et al. 1988; Keim et al. 2006a; Klamerus-Iwan and Witek 2018). Submersion of samples until saturation, although easy to do, exaggerates an element's water exposure and results in an estimated upper bound for water storage capacities. Precipitation simulation can be more representative of field conditions, but may not represent realistic intensities, velocities, droplet sizes, or reduce droplet splash loss, still potentially inflating water storage capacities (Friesen et al. 2015).

Similar research utilized physical models (Pfister and Schneebeli 1999; Kobayashi 1987) to represent differing structures and inclinations and excised tree branches (Schmidt and Gluns 1991) to understand the mechanisms that control variations in snow storage dynamics at the branch scale. The storage dynamics of model and excised branches were assessed using both naturally occurring snowfall events and artificial snow in both laboratory (Suzuki et al. 2008) and outdoor (Pfister and Schneebeli 1999) environments. Snow storage at the branch scale was quantified by directly weighing branches and snow (Pfister and Schneebeli 1999) or mechanically removing and weighing intercepted snow (Schmidt and Gluns 1991). In the case of snow, artificial precipitation can also differ in crystal structure and dramatically different environmental conditions relative to actual deposition events, since snowfall events are frequently associated with higher windspeeds than occur in laboratory environments (Suzuki et al. 2008).

Recently, field-durable strain sensors and other sensors have been used for in situ methods of monitoring water storage dynamics and capacities. As a storm loads water onto a plant canopy or branch, that mass change will produce "mechanical displacement" (or, strain), compressing the plant stem or deflecting an individual branch (Fig. 2.2d). To date, the application of strain sensors has resulted in water storage capacity measurements for whole trees during rain (Friesen et al. 2008; Hancock and Crowther 1979; Huang et al. 2005; Van Stan et al. 2013) and snow (Bründl et al. 1999; Bründl and Schneebeli 1995; Martin et al. 2013; Pomeroy and Schmidt 1993). Another mechanical variable that can be monitored and related to water storage (and other phenomena related to mass/stiffness changes) is a plant's sway frequency. If the stiffness of a plant stem is considered to be constant and the stem is loaded with intercepted storm water, its sway frequency should decrease proportionally—for example, snow water storage for a single event was found to decrease sway frequency by 30% (Papesch 1984). Sway-to-mass has since been applied to estimate rainwater storage (Selker et al. 2011) and its variability between species (van Emmerik et al. 2018; van Emmerik et al. 2017). Interestingly, strain and sway frequency could be monitored simultaneously using strain sensors at very high temporal resolution (~ 10 Hz), allowing cross-comparison validation of these methods; however, to our knowledge, this has not yet been done. Monitoring strain and/or sway requires installation of sensors directly into plant stems or branches at points of interest, which can limit the scale of a field campaign, because of the cost of sensor networks, data logger limitations, and data management, combined with the required careful scaling techniques (see discussion by Friesen et al. (2015) required to derive canopy storage).

Multiple remote sensing methods have been applied to monitor water storage capacity (Fig. 2.2e), including image processing (Floyd and Weiler 2008; Garvelmann et al. 2013; Parajka et al. 2012; Pomeroy et al. 1998; Stähli et al. 2009; Tennyson et al. 1974) and signal attenuation (Bouten et al. 1991; Calder and Wright 1986; Fowler 1970; Franz et al. 2013; Gutezeit 2006; Schneebeli et al. 2011). Photographic methods began with manual analysis of film frames every 60 min to monitor snow accumulation (Hoover and Leaf 1967) and 5 min for rainfall (Tennyson et al. 1974), but has since progressed to computer processing of digital imagery (Floyd and Weiler 2008; Garvelmann et al. 2013; Parajka et al. 2012; Stähli et al. 2009). Signal attenuation methods initially monitored radioactive attenuation to measure rime (Fowler 1970). Later, gamma ray and microwave attenuation were successfully applied to estimate rainwater storage in forests (Olszyczka and Crowther 1981; Bouten et al. 1991; Calder and Wright 1986) and for a spinach field (Gutezeit 2006). A microwave radiometer has been used to relate canopy opacity to rainfall interception and dew formation in forest canopies (Schneebeli et al. 2011). Also in forests, cosmic gamma radiation has been used to estimate snow water equivalent (Fritzsche 1983). High-resolution terrestrial laser scanning (TLS) has also shown promise for monitoring canopy snow storage, but significant challenges remain including occlusion of canopy elements, accurate estimation of canopy snow density, and temperature-dependent changing canopy structure due to branch deflections under heavy loads (Russell et al. 2019). Although precipitation reaches vegetation surfaces in various forms, including rainfall, occult deposition, rime and snow, most methods for estimating or monitoring precipitation storage in leaves, bark, epiphytes or litter have been designed and applied for rain and snow. Estimates of rime and ice storage on plants are especially scarce (Berndt and Fowler 1969; Fowler 1970) likely due to the fairly limited spatial extent and/or temporal frequency and hence limited hydrological importance relative to rain and snow.

No single method has emerged as the standard for measuring precipitation storage. Choice of technique remains dependent on the reason for measuring storage and the concept of storage itself is not easy to define. The demarcation between storage in and on canopy surfaces is not always simple, nor is the demarcation among liquid, solid, and vapor-phase water, and between water stored for short periods that only affect timing of throughfall delivery to the soil (i.e., dynamic storage: Keim et al. 2006a, b; Reid and Lewis 2009) versus longer periods that are relevant to, for example, evaporative losses or biogeochemical processing. For example, direct uptake of intercepted water into plants can be an important component of the water budget for some ecosystems such as drylands and fog-associated ecosystems (Breshears et al. 2008; Limm et al. 2009; Berry et al. 2014). In these cases, some or all water ablated from surface storage may not evaporate until subsequent transpiration and thus should not be considered "storage" from the perspective of some canopy interception budgets. As another example, isotopic evidence has revealed that throughfall frequently bears the signature of exchange with intracanopy vapor (Allen et al. 2017), and the water vapor pressure within the canopy also strongly affects evaporation rate, so that the total relevant volume of water "stored" in the canopy space includes vapor for some applications.

2.3 The Canopy Reservoir

Throughout this chapter, water storage will, per hydrologic standards, be reported as depth equivalent [mm] over land area—i.e., 1 L (or kg or 0.001 m^3) of water per m^2 of land area, or mm of water. The type of leaves, variability of leaf phenology, and storm conditions to which leaves are exposed (even between overstory and understory plants in the same location) all vary across plant types, resulting in a wide range of water storage capacities for the canopy reservoir: 0.07–4.3 mm (André et al. 2008; Crouse et al. 1966; Leyton et al. 1967; Link et al. 2004; Llorens and Gallart 2000; Ochoa-Sánchez et al. 2018; Pypker et al. 2011; Wallace et al. 2013). Importantly, although canopy liquid water storage capacities are generally <4 mm, they exceed the depth of precipitation for many low intensity and short duration storms. How large the leaf reservoir is for any vegetated ecosystem depends on several major intrinsic factors, including leaf structure (Pypker et al. 2011), seasonality (Sadeghi et al. 2018), and surface characteristics—particularly those that determine leaf wettability (Klamerus-Iwan and Witek 2018; Rosado and Holder 2013); and extrinsic factors, including storm conditions (Keim et al. 2006a), pollution exposure (Adriaenssens et al. 2011; Klamerus-Iwan et al. 2018a), and disease (Klamerus-Iwan and Witek 2018).

Solid (snow) water storage capacities for the canopy reservoir are larger and have been noted to span a much wider range from relatively small values, ~4 mm for low density snowfall occurring during very cold conditions in a boreal black spruce forest, to considerably higher values, approaching 40 mm for high density maritime snow occurring close to the freezing point in a mature coniferous forest (Storck et al. 2002). Most research on canopy snow storage has focused on coniferous forests, in part because storage on leafless deciduous vegetation is commonly assumed to be low due to rapid unloading under dry snow conditions. However, it may be as large as conifers where intercepting areas are similar, due in part to denser intercepted snow relative to coniferous forests (Miller 1964). Similar to the interception storage of liquid water, the magnitude of the canopy snow reservoir depends on both intrinsic factors including crown and branch structures (Pfister and Schneebeli 1999) and vegetation stiffness (Schmidt and Pomeroy 1990), and extrinsic factors including hydrometeorological conditions that control crystal form, adhesion of snow to vegetation, cohesion of snow (Satterlund and Haupt 1967), and interactions between extrinsic (temperature) and intrinsic (e.g., branch flexibility) factors (Schmidt and Pomeroy 1990).

2.3.1 Canopy Precipitation Storage: Intrinsic Factors

The greatest variability in the capacity of the canopy reservoir appears to be explained by general leaf structure: broadleaf, max ~2.0 mm (Leyton et al. 1967), versus scaleleaf, max ~3.7 mm (Van Stan et al. 2017b), versus needleleaf, max ~4.3 mm, (Link et al. 2004). The lower bound of leaf liquid water storage capacities in the literature for all leaf types is around 0.1 mm—see reviews discussing the topic in regard to canopy structural variability (Pypker et al. 2011), measurement methods (Friesen et al. 2015), and urban forestry applications (Van Stan et al. 2018). This difference in leaf water storage capacity is intuitively connected to the "depths" of branch-scale reservoirs between these leaf structures: broadleaves have but a single surface per leaf on which water can pond, yet scaleleaves have greater structural variability that provides shelter to entrained precipitation and, finally, needleleaves can have several layers of needles per branch that enable the greatest chance of water capture and retention due to capillary attraction between closely spaced needles.

The capacity of the leaf reservoir can also vary within each of these general leaf structural categories, depending on overall morphology and other intrinsic traits (like surface characteristics). For broadleaves, generally the wider the leaf or greater the total leaf area, the greater the precipitation storage reservoir. For scale or needle-leaved plants, greater total leaf

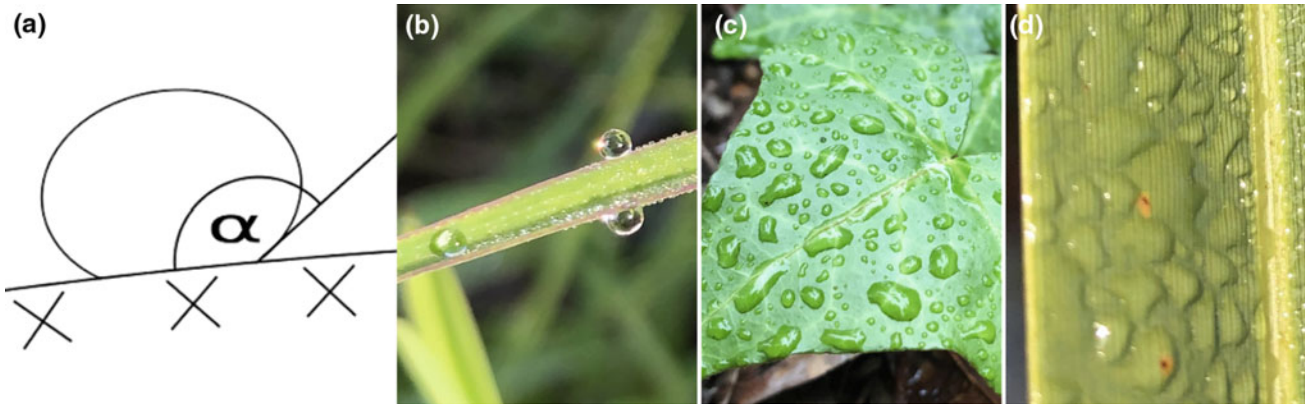

Fig. 2.3 **a** Illustration depicting the measurement of water drop inclination angle to the leaf surface. This is the standard metric for reporting the degree of hydrophobicity (see Table 2.1). Examples of droplets on leaves considered **b** highly hydrophobic, **c** moderately hydrophobic, and **d** hydrophilic. Photographs for panels **b**–**c** taken by John T. Van Stan II

area should increase water capture; additionally, larger or denser scales or needles may also increase water storage capacity. Surface traits can alter these relationships, especially if the surface traits alter the ability to retain or shed water (Rosado and Holder 2013). Aryal and Neuner (2010) developed the method most commonly applied for estimating a leaf surface's hydrophobicity, where the contact angle at which a water drop adheres to the leaf surface (Fig. 2.3) is used to classify the wettability on a scale ranging from superhydrophilic to superhydrophobic (Table 2.1). Undoubtedly, the waxes in leaf cuticles strongly influence hydrophobicity and, thereby, the amount of water retained on the leaf (Klamerus-Iwan and Błońska 2018). Other specialized leaf surface microfeatures, such as hairs, resinous excrescences, vesicular papillae—collectively called "micromorphology," can influence hydrophobicity-related water storage (Cheng et al. 2006; Neinhuis and Barthlott 1998). Finally, leaf shape affects storage and release of water. For example, drip-tips common in tropical forests release water is smaller droplets and may cause leaves to dry faster (Malhado et al. 2012)

Substantial variability in leaf hydrophobicity has been observed between plant species and seasonally for individual species (Brewer and Nunez 2007; Holder 2011, 2013; Holder and Gibbes 2017; Koch and Barthlott 2009; Neinhuis and Barthlott 1998). Changes in the chemical composition of leaves themselves can be an adaptation to life under differing seasonal conditions (Deguchi et al. 2006). Chemistry and thickness of the cuticular wax layer that directly interacts with water drop adhesion is particularly variable with aging leaves (Fernández et al. 2014). Wax content in the cuticle per unit of leaf area tends to be less in young leaves (Fernández et al. 2014), but this may vary depending on species. For healthy common oak leaves, Klamerus-Iwan et al. (2018a, b) observed an increase in average water storage capacity from 6.2% of the total simulated precipitation in May to 20.6% in September, illustrating that leaf age and phenological state cannot be disregarded. There is also a significant influence of leaf age on the contact angles between water drops and leaves. When analyzing exclusively healthy leaves in May, the average inclination angle was 153° while for samples collected in September it was 30° (Klamerus-Iwan et al. 2018a, b).

Unlike the storage of liquid precipitation, the interception storage of snow is controlled by a complex combination of adhesion of falling precipitation to canopy elements, cohesion and mechanical bridging of snow particles, and alteration of canopy structure as loading increases. Under relatively cold (<−3 °C) and dry snow conditions there is little adhesion of ice crystals to canopy elements and hence very low interception efficiency (Hoover and Leaf 1967; Hedstrom and Pomeroy 1998), whereas efficiency increases dramatically within several degrees of 0 °C (Kobayashi 1987; Pfister and Schneebeli

Table 2.1 Classification of wetting "degree" according to Aryal and Neuner (2010)

Water drop adhesion angle (α) [°]	Degree of hydrophobicity
<40	Superhydrophilic
40–90	High wettability
90–110	Good wettability
110–130	Hardly wettable
130–150	Very hardly wettable
>150	Superhydrophobic

1999). Under cold (air temperature ≪ 0 °C) conditions, initial snow interception occurs by crystals bouncing and sliding down toward junctions of canopy elements where canopy elements slope upwards, or preferentially sliding off where elements slope downwards (Hoover and Leaf 1967) thereby resulting in low interception efficiencies under light snow loads. Snow bridging by cohesion gradually occurs between intercepted masses which eventually causes the intercepting surface area to increase rapidly, thereby resulting in high interception efficiencies when snow loads are moderate. As snow loads become heavier, branches bend downwards causing additional snow crystals to bounce off intercepted masses and/or dislodge particles causing the interception efficiency to decline (Schmidt and Gluns 1991). Branch flexibility is an intrinsic function of species and branch architecture, including thickness, taper, length, and arrangement of branch elements (Schmidt and Pomeroy 1990). This sequence of processes, whereby snow interception efficiency cycles from low to high and back to low, produces the characteristic sigmoidal snow interception efficiency curves that resemble autocatakinetic growth curves in colder snow environments (Satterlund and Haupt 1967; Schmidt and Gluns 1991), and emphasizes why canopy snow storage can vary greatly between both species and hydrometeorological conditions.

2.3.2 Canopy Precipitation Storage: Extrinsic Factors

Several extrinsic factors alter the capacity and response of the canopy reservoir—storm conditions being chief among them. Cuticular wax thickness can be eroded by intense rainfall (Baker and Hunt 1986), especially if that rainfall is persistently acidic (Turunen and Huttunen 1990). Rainfall and snow storage capacity for leaves can substantially differ, depending on the water equivalent of the intercepted snowfall, but such comparisons are rare (Ebermayer 1873b). Since ice storms can coat leaves in a thick layer of rime (Fowler 1970), events where ice or rime accretes in the plant canopy likely result in the greatest leaf water storage capacity, especially when heavy rime occurs after snowfall. For liquid water, droplet temperature affects the capacity of the leaf reservoir by altering wettability: as temperature increases, the contact angle between water drops and the leaf surface decreases (becoming more hydrophilic by 3.44° per 1 °C, and the effect on water storage per leaf biomass ranges from 1.7 $\mathrm{g\ g^{-1}\ {}^{\circ}C^{-1}}$ for spruce to 1.3 $\mathrm{g\ g^{-1}\ {}^{\circ}C^{-1}}$ for oak (Klamerus-Iwan and Błońska 2018).

Canopy snow storage is even more strongly related to precipitation temperature, because wet snow close to the freezing point (>−3°C) readily adheres to leaves and coheres to intercepted snow mass. This produces relationships between event snowfall amounts and interception storage that are linear or asymptotic in warmer, maritime snow environments (Storck et al. 2002) and sigmoidal in colder, more continental snow environments (Satterlund and Haupt 1967; Schmidt and Gluns 1991). The upper limits of snow storage capacity are partly controlled by the degree of branch bending which is strongly controlled by temperature up to the freezing point because branches become increasingly flexible as temperatures warm and crystals within branch cells melt (Schmidt and Pomeroy 1990). Thus, canopy snow storage capacity can vary even in the absence of variations in plant area or adhesive properties.

The texture of the leaf surface, and thereby leaf water storage capacity, is also influenced by disturbances to the atmospheric environment, such as pollution. For example, a broad group of organic air pollutants produced from fossil fuel burning, polycyclic aromatic hydrocarbons (PAHs), deposit onto, and over time penetrate into, plant leaves (Popek et al. 2013). Plant species differ in terms of the amount of pollutants retained on their surface (Dzierżanowski et al. 2011; Sæbø et al. 2012), but long exposure to PAH changes the surface texture and chemistry of leaves for all species to date, and has recently been linked to shifts in water storage capacities for Scots pine and silver fir along an urbanization gradient in Poland (Klamerus-Iwan et al. 2018b). Although PAHs are strongly hydrophobic, long-term exposure to pollutants leads to erosion of leaf surfaces, removing waxes, increasing leaf wettability and, thereby, leaf water storage capacity. Short-term exposure to PAHs appears to briefly transfer their hydrophobic properties to leaves. The effect of PAH-induced leaf damage was confirmed in images obtained from the scanning electron microscopy, where the amount of pollutants accumulated around the stomatal apparatuses can be seen at higher magnifications (Sgrigna et al. 2016).

Leaf pathogens may also play an important role in the capacity and dynamics of the leaf precipitation storage reservoir. Substantial work has focused on the role of precipitation in leaf pathogen life cycles and transmission (e.g., Kiss et al. 2004; Liyanage et al. 2017) and their impacts are oftentimes visible on the leaf surface, but the authors are only aware of a single study on the effect of leaf pathogens (oak powdery mildew) on water storage capacity (Klamerus-Iwan and Witek 2018). Oak powdery mildew infection develops a mycelium that increases leaf wettability and water storage capacity from 1% up to 35% of the total precipitation for mycelium coverage of 80% (Klamerus-Iwan and Witek 2018). This is not only a significant change in water storage, but a significant advantage for the fungal infection, as by retaining more rainwater, the pathogen provides itself with favorable conditions for the development of mycelium (Kiss et al. 2004). Scanning electron microscopy has also confirmed textural shifts in the leaf surface between the uninfected oak leaves and those covered in mycelium.

Interestingly, the pathogenic impact on leaf wettability and water storage may be compounded by urban air pollutants, as the mycelium capture greater air pollution, further diminishing leaf hydrophobicity and increasing the capacity of the leaf reservoir (Klamerus-Iwan and Witek 2018). These examples highlight how precipitation water storage capacity of leaves is crudely parametrized in models of canopy interception from the stand to global scale, because storage capacity is neither static in time nor related to surface area metrics alone (like leaf area index) as it often is treated in models.

2.4 The Stem (Sometimes the "Bark") Reservoir

Any plant with a stem has a precipitation reservoir distinct from the leaf canopy reservoir. Most research on the capacity and dynamics of bark water storage in woody plants has focused on intrinsic factors, like thickness, porosity, microrelief, or roughness, and species-specific variability in each property (Ilek et al. 2017; Levia and Herwitz 2002; Levia and Wubbena 2006; Sioma et al. 2018; Van Stan and Levia 2009; Van Stan et al. 2016). For herbaceous vegetation, the stem reservoir is likely related epidermal outgrowths, like hairs, spines, thorns, and desiccated leaf remnants (Fig. 2.4a–d), though these stem reservoirs have rarely been examined. Greater effort is merited on this topic as, for example, the stem water storage capacity (areal mean total depth, per m^2 ground area) of dogfennel stems is 0.43 mm (Gordon et al. 2018), which exceeds some leaf water storage capacities (previous section). This occurs because dogfennel stems are coated in desiccated leaves (Fig. 2.4d) and can achieve large densities, >700,000 stems ha^{-1} (Dias et al. 2018). Indeed, understory plants' water storage capacity, when measured, has generally exceeded the storage capacities of overstory trees (Breuer et al. 2013). Bark and stems of woody plants and structurally diverse (Fig. 2.4e–h). Its storage capacity is often higher than leaves, 0.2–5.9 mm (Liu 1998; Pypker et al. 2011; Van Stan et al. 2018), typically due to bark's rougher surface structure and porosity (Ilek et al. 2017; Sioma et al. 2018; Van Stan et al. 2016); however, when bark is thin and smooth, like for *Fagus* species (Fig. 2.4h), its water storage capacity can be equal to, or less than, that of leaves (Van Stan et al. 2016). An example comparison between the capacity of bark and leaf storage for a single species can be found for Scots pine, where Llorens and Gallart (2000) found water storage capacities per unit needle area were 0.04–0.10 mm, depending on simulated wind condition (by removal of droplets formed after saturation), whereas the corresponding value per unit bark surface area was 0.62 mm.

A limitation of past work on bark storage is that observations and estimates primarily rely on measurements at or below breast height of 1.4 m. bark is texturally variable with height, where the bottom bark tends to be rough with numerous fissures and the top bark is smoother (Levia and Wubbena 2006). This results in vertical variability in bark water storage. In addition, bark morphology varies depending on tree age, tree size, and site conditions (Legates et al. 2013), likely resulting in age-related variability in bark water storage capacity. Little hydrologic research has focused on bark in general, compared to leaves or epiphytes; however, bark storage is of ecological relevance. For example, it is a key resource for corticolous organisms living on tree boles such as corticolous lichens and bryophytes (Franks and Bergstrom 2000). Bark storage can also be important for some plants as a pathway for water uptake (Earles et al. 2016).

2.5 Water Storage on the Plants on Plants

Water storage capacity of the plants living in the canopy and understory (i.e., epiphytes and parasites) can be, depending on plant structure and abundance, the largest reservoir: 0.4–16.6 mm (Jarvis 2000; Porada et al. 2018; Van Stan et al. 2015), in part because mosses and lichens can absorb an amount of water that vastly exceeds their dry weight, by factors ranging from 6 to 10 (Van Stan and Pypker 2015). Even in grasslands, bryophytic epiphytes have been estimated to store more than most forest leaf and bark reservoirs combined: 4.3 mm (Michel et al. 2013). The large capacity is because epiphytes absorb substantial amounts of water (Van Stan and Pypker 2015), related to anatomical elements that epiphytes have developed to survive despite being detached from soil- and groundwater sources (Zotz 2016b). Many of these anatomical elements are quite absorbent, for example: leaves with trichome scales (Stuart 1968; Van Stan et al. 2015), absorbent lichen and bryophyte thalli (Kranner et al. 2008; Proctor et al. 2007), velamen radicum layers in the aerial roots of orchids (Zotz and Winkler 2013), and many others (Zotz 2016a). In the tropics, there is an abundance of vascular plants that use specialized leaf structures to impound water, storing about 0.4 mm of rainfall in these "tanks" (Hölscher et al. 2004). Although epiphyte "tanks" perform ecophysiological functions for the plant (Schmidt and Zotz 2001), they do dry out between storms (Zotz and Thomas 1999).

Several estimates of the epiphyte reservoir are available, and at least one study has placed a portion of epiphyte water storage into global hydrologic context, that of lichens and bryophytes (Porada et al. 2018); however, broad fundamental

Fig. 2.4 Photographs of various botanical elements that can contribute to the stem precipitation storage reservoir in vegetated ecosystems. Stem water storage capacities are rarely estimated for herbaceous plants, yet their stems can be densely covered in **a** hairs (Starr and Starr 2016), **b** thorns (Starr and Starr 2011), **c** spines (Delso 2013), and **d** desiccated leaves (credit: John T. Van Stan II). The bark structures that determine stem water storage capacity for woody plants are also diverse, including **e** scaled (PumpkinSky 2017), **f** furrowed (Ramsey 2016b), **g** flaky (Atanassova 2019), and **h** smooth (Ramsey 2016a). Species information is provided for each photograph in the citation information

knowledge gaps remain. Nonvascular epiphytic cover on boreal and tundra forests and as groundcover elsewhere can be substantial (Porada et al. 2013) and snowfall and mixed precipitation events occur frequently there, but no research has reported the storage capacity or dynamics of these epiphyte communities. It is commonly believed that epiphyte storage persists between storms and, therefore, has little influence over the precipitation storage dynamics of vegetated ecosystems (Hölscher et al. 2004; Zotz 2016b) but may contribute to temporal persistence in chemical signatures in throughfall (Allen et al. 2014). However, there are few studies that report how much of epiphyte storage is available immediately before storms, or how often (the frequency and duration) epiphyte reservoirs are empty or nearly empty. Another knowledge gap includes the precipitation water storage of parasitic plants, which are diverse and can be abundant (Press and Phoenix 2005), yet no estimates of their water storage capacity have been reported.

2.6 Pathways and Residence Times of Water Flux Through Canopy Storage

Precipitation makes its way through canopies along varied pathways that depend on meteorological conditions and canopy structure. The beginning of these pathways is the location of precipitation incidence on the canopy, which depends largely on wind speed and direction, precipitation type (frozen, liquid, or condensing vapor; intensity), and plant architecture and phenology (Crockford and Richardson 2000). Once on the canopy, residence times of water also depend on similar factors, and with the added possibility that the water may be partitioned into direct evaporation, mechanical removal, or foliar or bark uptake that remove it from canopy storage. In the case of snow storage, water is partitioned into sublimation, large mass release, or in situ melt that is hence partitioned into evaporation or meltwater drip to deeper canopy layers and the ground. The interaction of these multiple factors leads to a wide array of flowpaths to the ground, many of which remain described only as isolated empirical observations.

The net effect of these flowpaths on the mean and distribution of canopy transit times has only been examined in a few cases. Keim and Skaugset (2004) reported mean hydraulic residence times in the canopy (i.e., residence of the hydraulic response, not necessarily particle transit time) of 8–30 min in moderately complex or highly complex stands of coniferous trees. Subsequently, Keim and Link (2018) suggested storms with longer hydraulic residence times are likely caused by intermittency leading to partial evaporation of stored water, and that mean hydraulic residence times in a highly complex stand of coniferous trees is more likely ∼8 min. So far, no similar analyses have been attempted for other canopy types. Residence times are likely much smaller in less-complex canopies, although canopies with greater dominance of stem flowpaths may retain precipitation longer. No similar studies have been conducted to understand intra-canopy snow movement in detail, and primarily focus on the duration and release of stored snow (e.g., Storck et al. 2002).

The effects of meteorological conditions on canopy storage and flowpaths are better understood for some factors than others. The effects of wind have been widely investigated because of its obvious role in delivering rainfall as well as disturbing storage. The incidence angle of wind-driven precipitation or fog leads to spatially varying precipitation within the canopy (Herwitz and Slye 1995; Fan et al. 2015), and also controls which canopy surfaces are wetted (Herwitz 1985) or impacted by rime and snow (Miller 1964). Wind-driven precipitation can at least sometimes be responsible for increased stemflow (Van Stan et al. 2011), although that phenomenon has not been extensively investigated. Wind can release stored water from leaves and small branches, but the finding that wind-driven rain can sometimes increase stemflow suggests that a portion of that released water may be diverted to pathways that include flow along surfaces for some period of time (relatively long residence) rather than immediate drip (short residence).

Canopy storage and the deportment of intercepted snow are likewise strongly controlled by meteorological conditions. In sub-freezing, dry snow conditions, unloading of stored snow is effected by mechanical disturbance of the canopy and intercepted snow by wind (Hedstrom and Pomeroy 1998; Schmidt and Gluns 1991; Hoover and Leaf 1967). In maritime snow environments and during above freezing periods, unloading of snow tends to be synchronous with meltwater production in the canopy (Storck et al. 2002). There are limited analyses of the proportions of snow removed by meltwater drip and large mass releases, but observations of maritime snowcover dynamics for several events indicated 70% by drip and 30% by mass unloading (Storck et al. 2002). Similar results were found using numerical simulations for a melting continental snowcover, where 70–80% of snow was released as meltwater and 20–30% as mass releases (Mahat and Tarboton 2014). Understanding of how snow canopy storage and flowpath dynamics are affected by meteorological conditions are important because the amount and residence time of stored snow controls the amount of sublimation losses, mass releases contribute to the development of the sub-canopy snowpack and reduce snow sublimation losses, and meltwater drip may pass directly through the sub-canopy snowcover if it is ripe and enter the litter and/or soil reservoirs.

Rainfall intensity also affects storage, residence, and pathways. Intense rain can dislodge stored water, but also causes temporary buildup of water on the canopy (Keim et al. 2006a, b) that likely affects flowpaths as evidenced by the frequent observation that stemflow delivery to the ground increases with rainfall intensity (e.g., Dunkerley 2014). Greater rainfall intensity also increases splash droplet formation (Dunkerley 2009), which may also contribute to wetting of canopy surfaces with long subsequent pathways to the ground.

Plant phenology and morphology also affect flowpaths through the canopy. The most frequently cited examples of this effect are crown architecture that may promote or suppress stemflow delivery to the ground (e.g., Liang et al. 2009), bark texture that may promote stem pathways (smooth bark) or drip (rough bark), and the different incidence of stemflow delivery to the ground in leaf-on as compared to leaf-off conditions (e.g., Carlyle-Moses and Schooling 2015). Unlike the effects of phenology and morphology on liquid water pathways, in general, the release of intercepted snow is much more strongly affected by hydrometeorological conditions than individual tree characteristics (Satterlund and Haupt 1970; Schmidt and Gluns 1991) although these relationships have not been studied extensively.

2.7 The Litter Reservoir

The litter layer represents a transition between the canopy and the soil, and it can sometimes be unclear how to conceptualize water storage in this zone. Here, we consider the litter layer to be composed of the uppermost forest floor, generally free of roots, where water outflow is dominated by gravity and direct evaporation, and transpiration is not an important pathway.

The litter layer is composed of various plant-derived elements, like leaves, stems, fallen trees, deadwood, bark molts, fallen epiphytes, seeds and seedpods, etc., however, the leaf component is the most comprehensively studied part of the litter precipitation reservoir (Gerrits and Savenije 2011). The most recent review of precipitation interception by litter reported a range of water storage capacities of 0.2–8 mm (Gerrits and Savenije 2011). Of the various litter components, water storage capacity has been estimated for several independently (Table 2.2). Contrary to the leaf reservoir (in the overstory and understory), broadleaves in litter typically store greater precipitation than shed needleleaves, if the thickness of the litter layer is similar (Table 2.2). For any leaf type, thicker layering of leaves due to senescence or disturbance events increases water storage capacity (Guevara-Escobar et al. 2007; Sato et al. 2004). Bark shed from tree stems does not store as much water in the litter layer as has been measured on stems (Table 2.2) because shed bark is generally only thin flakes (Van Stan et al. 2017a). The coarse fruiting bodies of two tree species studied to date (Levia et al. 2004; Van Stan et al. 2017a) store more precipitation than all other litter components (Table 2.2). Fallen branches and wood also store enough precipitation to merit their investigation (Table 2.2). Only one study known to the authors estimated the water storage capacity and temporal dynamics for all litter components throughout the year, and interestingly, fruiting head production exerted a strong influence over the capacity of the litter reservoir (Van Stan et al. 2017a).

Precipitation type and characteristics influence litter water storage capacity. Only one study reports the effect of precipitation type, finding that snow can flatten leaves and diminish storage capacity (Gerrits et al. 2010). Throughfall patterns can influence litter storage, with intermittent throughfall increasing water storage throughout a storm because the spatial heterogeneity leads to increased localized drainage (Gerrits et al. 2009, Gerrits and Savenije 2011). Simulated throughfall experiments have also demonstrated that a direct relationship exists between intensity and storage (Gerrits et al. 2007). However, wind, which is a major driver of evaporation and storage in plant canopies, is not often a major factor in litter water storage dynamics due to the attenuation of wind speeds by vegetation cover. However, radiation can drive evaporation sufficient to reduce litter storage during intermittent storms and enable more throughfall to be stored over the course of the event (Gerrits et al. 2009).

Forest treatments change the microclimate and the availability of litter elements, particularly dead wood. Dead wood content in the litter can affect the species composition and growth rate of both insects and fungi, which affects the rate of decomposition of wood and to its physical properties (Jacobs and Work 2012). There is a marked increase in wood moisture and a decrease in wood density in subsequent stages of decay (Paletto and Tosi 2010; Pichler et al. 2012). As wood decomposes, its structure changes, which causes variable water retention capabilities (Błońska et al. 2018). There is interspecific variability, for example: Błońska et al. (2018) found that minimally decayed ash logs stored the least water compared to aspen and fir logs at a similar level of decomposition, and that the highest moisture in highly decomposed wood was in ash wood and the lowest in aspen wood. Water drop penetration time (Täumer et al. 2005), showed even stronger

Table 2.2 Water storage capacities (S_{Lmax}) estimated in previous work for various individual elements of the litter reservoir

Litter element	Site information	S_{Lmax} (mm)	Study
Broadleaves	European beech forest	1.0–2.8	Gerrits et al. (2010)
Needleleaves	Scots pine forest	0.6–1.7	Walsh and Voigt (1977)
Scaleleaves	Japanese cedar forest	0.3–1.7	Sato et al. (2004)
Bark flakes	Slash pine forest	0.2–0.3	Van Stan et al. (2017a)
Fallen branches	Slash pine forest	0.1–0.4	Van Stan et al. (2017a)
Fallen logs	Mixed evergreen forest	0.9–1.5	Sexton and Harmon (2009)
Deadwood	Mixed broadleaf forest	0.1–0.5	Błońska et al. (2018)
Fruiting heads	Sweetgum forest	3.9–4.2	Levia et al. (2004)

interspecific variability. For example, Błońska et al. (2018) found water penetration time was relatively short for moderately decomposed fir and aspen logs (mean ∼10 s), but much slower for the wood of other species (∼1000–1650 s). For logs in advanced decomposition, the water penetration times for wood of all tested species was very short (1–4 s), emphasizing the strong relationship between degree of decay and potential throughfall absorption. Dead wood, similar to soil, has a critical drying point above which it becomes hydrophobic. This finding has methodological and ecological implications. Since many water storage capacity estimates involve saturation of materials after drying (see Sect. 2.2), caution should be taken to ensure that this critical drying point is not reached prior to attempting saturation. Ecologically, long-term or seasonal droughts that thoroughly dry dead wood may drive down water storage capacity of dead wood in the forest (Błońska et al. 2018).

2.8 Conclusions

Vegetation is regarded as a critical component in both urban and wildland areas that enhances the resilience of social–ecological systems. The amount and duration of intercepted precipitation retained by the vegetation canopy is an important component of the water balance, which has a major impact on the climate and hydrology of vegetated watersheds and is an important component of global climate and hydrologic cycles. However, it is one of the simplest and least-often parameterized water balance element. Factors that affect the water storage capacity of vegetation and mechanisms that control the deportment of intercepted precipitation, including the wettability and effects of pollutants on the wettability of plant material, cannot be disregarded in ecohydrological research. More experimental evidence is needed to better understand the physical and hydrological properties of plant materials and canopies overall, including the effects of pollution and/or different canopy structures. Research on water storage should consider as many factors as are able to affect significant changes in the amount and temporal persistence of canopy intercepted water.

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ENERGY HOTEL

3

Evaporative Processes on Vegetation: An Inside Look

Miriam Coenders-Gerrits, Bart Schilperoort,
and César Jiménez-Rodríguez

Abstract

While evaporation is the largest water consumer of terrestrial water, its importance is often (limitedly) linked to increasing crop productivities. As a consequence, our knowledge of the evaporation process is highly biased by agricultural settings, and results in erroneous estimates of evaporation for other land surfaces and especially for forest systems. The reason why crop and forest systems differ has to do with the vegetation height and what is happening in the space between the plant top and surface. Forests are multi-layered systems, where under the tallest tree species, lower vegetation layers are present. These lower vegetation layers transpire, but at a different rate then the main vegetation, since the atmospheric conditions are different under the canopy. Additionally, the sub-vegetation layers, and also the forest floor, intercept water. Next to different atmospheric conditions per layer, the interception process is highly complex due to differences in interception capacity and a time delay caused by the cascade of water when water flows from the top canopy down to the forest floor. Lastly, forests also have the capacity to store heat and vapor in the air column, biomass, and soil. While this energy storage can be up to 110 W/m^2 it is often neglected in evaporation models. To get a better understanding of what is happening inside a forest, for the purpose of evaporation modeling, we should make use of new sensing techniques that allow identifying the rainfall, energy, and evaporation partitioning. This will help to improve evaporation estimates for tall vegetation, like forest, and allow spatial up scaling.

Keywords

Evaporation • Heat and vapor storage • Remote sensing • Interception • Forest

3.1 Evaporation: Farmers' Wisdom or not?

Evaporation is, after precipitation, one of the largest fluxes of the water balance: globally 55–80% of the annual rainfall evaporates from the land surface (Gleick 1993). Nonetheless, hydrologists historically tend to focus on the relationship between rainfall and streamflow and consider evaporation as a residual flux (Harrigan and Berghuijs 2016). The result of this strong focus on rainfall–runoff relations, combined with the difficulties of measuring evaporation at the right temporal and spatial scale, is that knowledge on evaporation is underdeveloped (Brutsaert 1986; Oki 2006; Zhao et al. 2013). For agricultural areas this knowledge gap is smaller. Since farmers want to optimize crop production, information on crop behavior in relation to atmospheric conditions, soil moisture conditions, and supplied irrigation is required. Therefore, many extant evaporation studies focus on (well-watered) crops and they form the basis of many evaporation equations that are still used to date (e.g., Doorenbos and Pruitt 1977; Hargreaves and Samani 1982; Monteith 1965; Priestley and Taylor 1972). These crop-derived relations are, after some minor adjustments, used for other land surfaces as well and directly or indirectly incorporated into models that provide evaporation estimates (e.g., Allen et al. 1998; de Bruin and Lablans 1998; Konukcu 2007; Thom and Oliver 1977; Wright 1982). This approach seems to work reasonably well for most short vegetation covers

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but not for forested ecosystems, as will be shown on the basis of some studies that validate their evaporation estimates with other (independent) evaporation estimates. For these purposes, we distinguish two types of evaporation models: hydrological models and meteorological (RS) models (where RS refers to remote sensing, since these models often use RS data as input).

To assess the performance of these models, preferably independent "ground truth" data is used as a benchmark. Eddy covariance (EC) systems are currently seen as the best method to continuously measure evaporation (Wang and Dickinson 2012) and are used worldwide, e.g., FLUXNET (Baldocchi et al. 2001). EC-systems should be installed far above the vegetated surface (e.g., on a tower) and links high frequency measurements (>20 Hz) of water vapor and CO_2 concentrations to deviations in vertical wind velocity to estimate an ecosystem-scale flux. Depending on the slope, wind speed, and direction, the upwind area (i.e., footprint) where vapor originates from varies, which is problematic when the land cover is not uniform. Although it is commonly acknowledged that EC-systems have problems with varying footprints (Mu et al. 2011) and the non-closure of the energy balance (Stoy et al. 2013; Twine et al. 2000; Wilson et al. 2002), they are frequently used for calibrating and validating evaporation models as it is the best method available. Another frequently used method to assess model performance is to cross-compare evaporation estimates. Hence, in this case we compare the outcome of hydrological and meteorological models with EC observations and each other.

- **Hydrological and meteorological models versus EC**
  Morales et al. (2005) compared four process-based models (RHESSys, GOTILWA+, LPJ-GUESS, and ORCHIDEE) to EC observations in 15 European forests. They looked both at the water and the carbon fluxes and concluded that model performance varied greatly per location (RMSE[1]: 10–100 gC m^{-2} $month^{-1}$ and 50–300 mm/month, respectively) and that there was not a universal model that performed for all cases. Furthermore, they found that frequently the models overestimated the latent heat flux by a factor 1.3–2 (±20–80 W/m^2). This overestimation for forests was also found by Wang et al. (2015), who compared (among others) evaporation estimates of a VIC-model (Liang et al. 1994) to EC observations for different land types. For most forests an overestimation of a factor of 1.1–1.7 was found. In Ershadi et al. (2014), the remotely sensed SEBS model (Su 2002), Priestley and Taylor, Penman-Monteith (Brutsaert 2005), and an advection-aridity model (Parlange and Katul 1992) were compared with EC-data for different land cover types. They found that all models overestimated the evaporation flux (RMSE: 64–105 W/m^2) and that for different model performance metrics, all models performed worst for evergreen needle forest in comparison to, e.g., grassland or cropland. Also Hu et al. (2015) found for Europe that the operational MOD16 (Mu et al. 2011) and LSA-SAF MSG Eta (Ghilain et al. 2011) models performed best for crop- and grassland (RMSE: 0.47–0.72 mm/day) and overestimated the evaporation flux in complex canopies in summer (RMSE: 0.34–1.57 mm/day). Similar results are found by Ha et al. (2015), who found large uncertainties (R^2: 0.60–0.84) in four pine forests in the USA and showed that most models overestimate evaporation (RMSE: 15–23 mm/month). More recent Land Surface Models (LSMs), who implemented complex modeling schemes to model the water and energy fluxes, still show large uncertainties for forests. For example JULES (Best et al. 2011) compared their results to 10 FLUXNET sites and found that JULES overestimates evaporation in temperate forests with a RMSE varying between 15 and 30 W/m^2 (Blyth et al. 2011). Similar results are found by the CLM4 land surface model (Lawrence et al. 2011), where forest had on an hourly basis a RMSE of 34–49 W/m^2.
- **Intermodel comparison**
  Several hydrological models show discrepancies between simulated evaporation estimates and the SEBAL-algorithm (Bastiaanssen et al. 1998) for forests. For example, Immerzeel and Droogers (2008) compared (monthly) evaporation estimates of a SWAT model (Arnold et al. 1998) for a catchment in India and found the largest bias for (evergreen) forests (bias of –50 to 100 mm/month and average 40 mm/month). Similar results are found by Schuurmans et al. (2011), who ran a coupled groundwater and unsaturated zone model (MetaSWAP) for the Netherlands and found differences up to 4–5 mm/day for forests in comparison to 0–4-mm/day for other land classes. And Winsemius et al. (2008) tried to constrain the model parameters of a semi-distributed conceptual HBV-like model (Bergström 1995) with the SEBAL-algorithm and found that for forested areas this was difficult, indicating that forest systems are likely not yet modeled correctly. For testing the performance of Land Surface Models, special benchmarking platforms have been developed (e.g., ILAMB (Luo et al. 2012), PILPS (Pitman 2003), SUMMA (Clark et al. 2015a), CLASS (Verseghy et al. 1993)). As mentioned before, LSMs try to represent many biophysical and hydrologic processes. The downside of this is that parameterizing these LSMs becomes difficult, and therefore PILPS was initiated. But also in PILPS they found larger deviations in latent heat of ±50 W/m^2 for forests in comparison to ±20 W/m^2 for grass (Henderson-Sellers et al. 1995).

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[1] RMSE: root mean square error.

Hence, overall we see the common observation that short vegetation and cropland is often reasonable well-modeled, while the latent heat flux above forests is not well-modeled and often overestimated in comparison to EC observations. The hydrological models (VIC, SWAT, MetaSWAP) vary between –45 W/m^2 and 142 W/m^2, the meteorological models (SEBS, MOD16) between 10 and 105 W/m^2, and the LSMs (JULES, CLM4, PILPS) have a discrepancy of ±50 W/m^2. Thus the "farmers wisdom" on crop evaporation clearly cannot be transferred one-to-one onto forest systems.

3.2 By the Way, Which "Evaporation" Do We Mean?

The causes for the errors and mismatches between major evaporation models and the observations can originate from conceptual errors in the models as well as drawbacks in the measuring technique. However, to understand the causes it is important to first clearly define what is meant by evaporation, since in the literature many misconceptions exist whether only transpiration is meant, or that interception and soil evaporation are included as well (Savenije 2004).

Here we define total evaporation (E_{tot}) as the sum of transpiration (E_t), interception evaporation (E_i), soil evaporation (E_s), and open water evaporation (E_o), all with dimension [L T^{-1}] (Shuttleworth 1993)

$$E_{\text{tot}} = E_t + E_i + E_s + E_o \tag{3.1}$$

Although transpiration is the most dominant evaporative flux (Coenders-Gerrits et al. 2014; Schlesinger and Jasechko 2014; Sutanto et al. 2014; Wei et al. 2017) interception evaporation should not be underestimated, and at times it may be the dominant flux, especially in forested areas (see e.g., Fig. 5 in Wang-Erlandsson et al. 2014). A literature review by Miralles et al. (2010) has shown that the canopy can intercept 8–34% of rainfall.

Interception is present in both crops and forests; however, it can already partly explain the mismatch between the evaporation models and EC observations. First, neglecting interception will lead to an underestimation of evaporation in hydrological models. The results found by Mueller et al. (2013), Liu et al. (2016) showed that especially wet catchments perform worse. Neglecting the interception process in hydrological models causes an underestimation of total evaporation if not compensated by an increase in transpiration. Since more water enters the unsaturated zone than in reality or by any calibration, transpiration can be overestimated (Van den Hoof et al. 2013). But that would mean the model is conceptually wrong, which has large consequences for studies dealing with, e.g., carbon exchange and climate and/or land use change models. The second reason for the mismatch is that, next to hydrological models that often overlook interception, many eddy covariance systems also ignore interception. Many EC-systems are open-path systems, which measure the gas concentrations in situ by an optical sensor (as opposite of closed-path systems that draw air through an intake tube and analyze the sample not directly at the sample location). These optical open-path sensors do not work properly if the optical path is obscured like in the case if they are wet (Hirschi et al. 2017), resulting in the evaporation shortly after a rainfall event not being observed so long as the open-path analyzer is wet.

However, as said, interception is both present in croplands and forests, so it cannot be the only reason why evaporation models show worse model performance for forest systems. Hence the question remains: why can we not use the farmers' wisdom to model forest evaporation? Are not trees basically supersized crops?

3.3 Why Don't Forests Act like a Giant Crop Field?

Yes, in a way trees are just supersized crops; but, only when one looks at the transpiration of the main tree species, and even then differences occur due to different water use strategies (rooting depth, crop rotation). In forests, the space between the canopy and the ground allows other vegetation species to grow (Fig. 3.1). These species transpire and intercept water; however, since the atmospheric conditions under the main canopy are different, quantifying its magnitude is not straightforward for understory and ground vegetation. On top of that, heat and vapor can be stored in the space between the canopy and ground, which affects the entire water and energy balance. Both the effect of additional understory and ground vegetation, and heat and vapor storage are not (or less) present in crop systems and explain (at least partly) why crop-concepts cannot be used directly for forest systems.

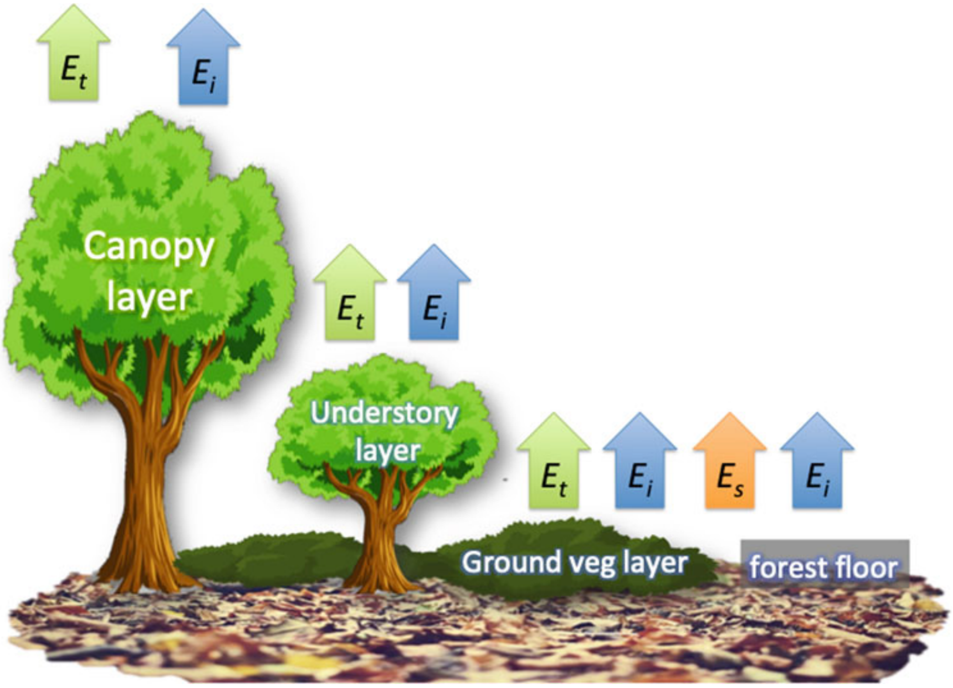

Fig. 3.1 Schematization of forest layering and its sources of transpiration (E_t), interception evaporation (E_i), and soil evaporation (E_s). *Note* forest floor interception evaporation is distinguished from soil evaporation by the fact that soil evaporation refers to water that is stored in the root zone (De Groen and Savenije 2006)

3.3.1 The Waterfall of Interception Storages

Canopy interception is often well modeled by Rutter-like models (Rutter et al. 1971; Valente et al. 1997), where the interception process (I) is modeled by a simple threshold model, whereby interception evaporation (E_i [L/T]) takes place as long as the interception storage (S [L]) is not emptied

$$I = E_i + \frac{\mathrm{d}S}{\mathrm{d}t} \tag{3.2}$$

Often the interception storage capacity (S) is derived from vegetation characteristics like LAI and the interception evaporation is a function of the potential evaporation.

If one wants to include the interception of the understory and forest floor as well, one cannot simply increase the interception storage capacity for two reasons. First, there is a sequence in the storages. Once a storm begins, the canopy "bucket" must be filled to initiate throughfall (including splash losses, see Chap. 12), then throughfall can fill the understory "bucket", followed by the "bucket" of the ground vegetation and lastly the forest floor (Fig. 1.2). This filling and spilling, causes a cascade of interception storages, which causes a shift in time (Gerrits et al. 2010). For more details on water storage of vegetation see Chap. 2. Second, the potential evaporation below the canopy is lower than above. Radiation is less (Jarvis et al. 1976; Rauner 1976), wind is often reduced, and some energy is already consumed by evaporation of the intercepted canopy water, thus changing the air temperature and humidity the understory is exposed to. This lower potential atmospheric demand is often used to argue that forest floor interception is negligible; however, this lower atmospheric demand is compensated by the often-larger storage capacity of the forest floor (see values in Fig. 3.2) (Breuer et al. 2003; Bulcock and Jewitt 2012; Gerrits and Savenije 2011a, b; Kittredge 1948). This results in residence times of several hours to days for forest floor interception in comparison to less than an hour for intercepted canopy water (Baird and Wilby 1999; Gerrits et al. 2007, 2009; Li et al. 2017; Wang-Erlandsson et al. 2014). The interaction between the canopy and forest floor interception, also results in a reduced effect on the phenology. Often it is thought, that in winter time interception is zero for deciduous trees, because the trees do not have leaves; however, the leaves are on the forest floor where water can still evaporate (despite its low potential evaporation), because of the high water content (Gerrits 2010; Gerrits and Savenije 2011a, b; Van Stan et al. 2017).

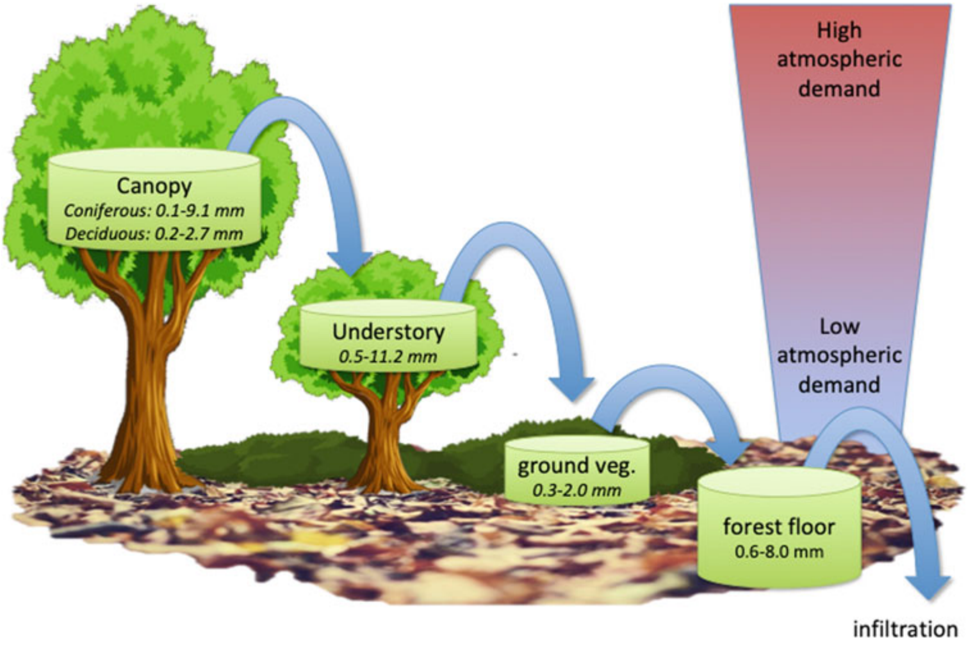

Fig. 3.2 Cascade of interception storages (S) in relation to atmospheric demand. Values in 'buckets' indicates minimum and maximum storage capacity as summarized by (Breuer et al. 2003) and (Gerrits and Savenije 2011a, b)

An elegant attempt to model both canopy as forest floor interception at the global scale, that also takes into account the reduced potential evaporation, has been done by Wang-Erlandsson et al. (2014). In their STEAM model they showed that globally for different forest types. 16–20% of the rainfall was intercepted by the canopy and 4–14% by the forest floor, resulting in a total interception of 22–34% of rainfall. For crop systems these values were much lower: 13%, 3%, and 16% for canopy, forest floor, and total interception, respectively. This indicates that in forest systems the below-canopy interception is more important in comparison to crop systems.

3.3.2 Energy Hotel

Remotely sensed evaporation products use different algorithms to estimate the latent heat flux, although they share some similarities. The basis of most products is the energy balance

$$R_n = \rho\lambda E + H + \frac{\mathrm{d}}{\mathrm{d}t}\left(\sum Q\right) \tag{3.3}$$

where R_n is the net radiation, $\rho\lambda E$ the latent heat (or evaporation expressed in W m^{-2}), H the sensible heat flux, and $\frac{\mathrm{d}}{\mathrm{d}_t}(\sum Q)$ the storage flux, all with unit (W m^{-2}). Generally, the $\sum Q$-term is set equal to the ground heat flux $(\mathrm{d}Q_g/\mathrm{d}t)$. However, studies that investigated the non-closure of the energy balance of EC-systems, already indicated that only considering the ground heat flux is not sufficient. Following Oke (1987) two terms are missing: advective energy and a storage term. If we consider extensive forested areas, the advective energy is usually neglected, hence only the storage term remains. Foken (2008) and McCaughey and Saxton (1988) considered three types of storages:

- storage of heat and vapor in the air below the flux measurements (Q_h and Q_e, respectively),
- storage in the vegetation (Q_b), and
- energy required for photosynthesis (Q_p).

This was confirmed by several other studies (Mayocchi and Bristow 1995; Meyers and Hollinger 2004; Oliphant et al. 2004).

Hence, after neglecting advected energy and including the storage terms the energy balance above a forest at height z (m) can be defined as (e.g., Barr et al. 1994; McCaughey 1985):

$$R_n = \rho\lambda E + H + \frac{\mathrm{d}}{\mathrm{d}t}(Q_g + Q_h + Q_b + Q_p) \tag{3.4}$$

all with units W m^{-2}.

To estimate the first four storage terms, information on the thermal properties and state of the ground, air, and biomass is required. For the ground heat flux ($\mathrm{d}Q_g/\mathrm{d}t$) these are the ground temperature gradient ($\mathrm{d}T_g$, [K]) over depth (dz, [m]) and λ the soil thermal conductivity [W K^{-1} m^{-1}] and z [m] the measuring depth and C the soil heat capacity [J m^{-3} K^{-1}] (Brotzge and Crawford 2003):

$$\frac{\mathrm{d}Q_g}{\mathrm{d}t} = -\lambda\frac{\mathrm{d}T_g}{\mathrm{d}z} + zC\frac{\mathrm{d}T_g}{\mathrm{d}t} \tag{3.5}$$

The heat and latent heat storage rates are defined as (Barr et al. 1994; McCaughey 1985)

$$\frac{\mathrm{d}Q_h}{\mathrm{d}t} = \int_o^z \rho_a c_p \frac{\mathrm{d}T_a}{\mathrm{d}t}\mathrm{d}z \tag{3.6}$$

$$\frac{\mathrm{d}Q_e}{\mathrm{d}t} = \int_o^z \rho_a \lambda \frac{\mathrm{d}q}{\mathrm{d}t}\mathrm{d}z \tag{3.7}$$

with ρ_a the density of air [kg m^{-3}], c_p the specific heat of air [J kg^{-1} K^{-1}], T_a air temperature [K], λ the latent heat of vaporization [J kg^{-1}], q the water vapor mixing ratio [kg kg^{-1}], and t the time [s].

And similar for the biomass heat storage rates (McCaughey and Saxton 1988):

$$\frac{\mathrm{d}Q_b}{\mathrm{d}t} = \int_o^{h_c} \rho_b c_b \frac{\mathrm{d}T_b}{\mathrm{d}t}\mathrm{d}z \tag{3.8}$$

where ρ_b the density of the biomass [kg m^{-3}], C_b the specific heat of biomass [J kg^{-1} K^{-1}], T_b biomass temperature [K].

The last storage term in Eq. 3.4 is related to the energy used for photosynthesis Q_p is estimated as ±422 kJ per mole fixed CO$_2$ (Masseroni et al. 2014; Meyers and Hollinger 2004; Nobel 1974). Although Blanken et al. (1997) illustrated that Q_p can be 23% of $\sum Q$ on clear sunny days, it is often neglected, since it is difficult to measure and it was found to be less than 3% of $\sum Q$ in the middle of the day (Jarvis et al. 1976; Tajchman 1981; Thom 1975).

In Table 3.1 an overview is given of the magnitude of the other storage terms. The difficulty with the individual storage terms is that–unlike the sensible and latent heat flux– the storage terms do not follow the net radiation pattern. Only the ground heat flux is a percentage of the net radiation once a time lag is included; however, the biomass storage peaks before noon. And the sensible and latent heat storage are peaking just before sunrise, where the latent heat storage becomes already negative two hours after, and the sensible heat storage just before sunset (Lindroth et al. 2010; Oliphant et al. 2004).

Hence the space between the top of the canopy and the forest floor is like a hotel, where energy can be stored during the day. For EC-systems these storage terms are not the primary cause of incorrect evaporation estimates, since only wind and vapor information is used (it is only partly responsible for the non-closure of the energy balance (Foken 2008)). However, it is important for RS-products. Ignoring the storage terms implies that more energy is attributed to the latent and/or sensible heat. Especially, for forests the storage terms can be significant, since there is a large air column where heat and vapor can be stored in comparison to, e.g., crop or grassland. As shown in Table 3.1 these storage terms have the same order of magnitude or even bigger than the ground heat flux. This might then also explain why RS-algorithms compare better to ground observations in non-forested areas.

Table 3.1 Literature study overview from magnitude of daily minimum and maximum storage rate terms

Vegetation type	Height [m]	Country	$\mathrm{d}Q_g/\mathrm{d}t$ [W m^{-2}]	$\mathrm{d}Q_h/\mathrm{d}t$ [W m^{-2}]	$\mathrm{d}Q_e/\mathrm{d}t$ [W m^{-2}]	$\mathrm{d}Q_b/\mathrm{d}t$ [W m^{-2}]	$\mathrm{d}Q_p/\mathrm{d}t$ [W m^{-2}]	$\mathrm{d}\sum Q/\mathrm{d}t$ [W m^{-2}]	R_{net} [W m^{-2}]	References
Eucalyptus forest	40	Australia	–10 to 48	–75 to 50	–25 to 25	–50 to 61	NA	NA	NA	(Haverd et al. 2007)
Maize crop Soybean	3 0.9	Illinois, USA	–15 to 25 –5 to 17	NA NA	NA NA	–5 to 20 0 to 7	10 to 25 5 to 10	±80 ±35	±500 NA	(Meyers and Hollinger 2004)
Maple, beech, oak	27	Indiana, USA	–10 to 30	–10 to 20	–5 to 0	–10 to 20	NA	–30 to 60	NA	(Oliphant et al. 2004)
Mixed forest	20	Ontario, Canada	–25 to 90	–30 to 45	–70 to 30	–10 to 17	NA	–60 to 110	–60 to 720	(McCaughey and Saxton 1988)
Mixed forest	26–30	The Netherlands	–5 to 15	–50 to 70	–40 to 30	NA	NA	–50 to 70[a]	–80 to 650	(Schilperoort et al. 2018)
Mixed pine and spruce	28	Sweden	–5 to 15	–15 to 15	–8 to 6	–20 to 22	NA	–35 to 45	–50 to 400	(Lindroth et al. 2010)
Sorghum	1.14	Texas, USA	–25 to 60	–5 to 5	–5 to 10	–10 to 10	–10 to 13	NA	–25 to 600	(Kutikoff et al. 2019)
Tropical forest	14–25	Brazil	–25 to 0	–20 to 40		–20 to 40	NA	–50 to 70[a]	–20 to 700	(dos Santos Michiles and Gielow 2008)
Tropical forest	35	Brazil					NA	–80 to 80[a]	NA	(Moore and Fisch 1986)
Young larch	10.6	Eastern Siberia	0–50				NA	–25 to 100	–50 to 550	(Tanaka et al. 2008)

[a] Excluding Q_g

3.4 Outlook

To improve our knowledge on forest evaporation we should invest in studying what is happening in and underneath the forest canopy, and not neglect the space where water, vapor, and heat can be stored and released. However, this is not easy to achieve, as often observation techniques are limited or extremely expensive (Arya 2001; Tajchman 1981). Some attempts have been made to measure turbulent fluxes of momentum, heat, and vapor directly within forests (Baldocchi and Meyers 1988; Bergström and Högström 1989; Verma et al. 1986). However, the vertical spatial resolution was limited to a few points in height, while the space between the top of the canopy and forest floor is highly variable (Allen and Lemon 1976; Arya 2001; Patton et al. 2010; Rauner 1976). On top of that, this space is also interacting in a complex way with the air above the canopy. So can it be that at certain times of the day vapor originating for the understory is simply transported vertically through the canopy, while at other times it is stored in this space or is transported horizontally and finds another way to the atmosphere, e.g., near a forest edge or gap. Meaning that sometimes the below and above canopy air are entirely decoupled from each other, and at other times turbulent exchange takes place (Alekseychik et al. 2013; Belcher et al. 2008; Göckede et al. 2007; Thomas et al. 2017). This complex turbulent behavior is difficult to model, and even Large-Eddy Simulations (LES), which are currently the best numerical tool to simulate this, has shortcomings in dealing with these complex flows (Dellwik et al. 2019; Patton et al. 2010). The importance of detailed information on turbulent fluxes follows from the work of Clark et al. (2015b) where they showed how sensitive their model was for changes in below-canopy wind parameters.

Fortunately, new opportunities have arisen with new sensing techniques. Distributed Temperature Sensing (DTS) is one of these techniques, whereby continuously (up to 1 Hz) temperature is measured at a high spatial resolution (0.25 m) along a fiber optic cable (Selker et al. 2006). As shown by Euser et al. (2014) and Schilperoort et al. (2018), DTS can also be used to measure vertical temperature and moisture profiles, from which the latent and sensible heat flux can be derived as well as heat storage. And more recently, Van Ramshorst (2019) and Sayde et al. (2015) showed the application of wind profile measurements, by actively heating the fiber optic cable like a hot wire anemometer. Combining the temperature, vapor and wind profiles allows studying turbulence fluxes of momentum, heat and vapor within the forest layer at a high spatial and temporal resolution.

Additionally, LiDAR-information can help to better understand forest structure to estimate turbulent flows (Boudreault et al. 2015), vegetation characteristics like LAI (Zhao and Popescu 2009), DBH, height (e.g., Brede et al. 2017), interception storage capacity (e.g., Berezowski et al. 2015; Roth et al. 2007) and/or the heat stored in the biomass. For the latter objective thermal infrared imagery might also be a possible tool (Garai et al. 2010; Pfister et al. 2010; Voortman et al. 2016).

In addition to looking at the turbulence structure within and underneath the canopy, knowing how evaporation is partitioned between transpiration, interception, and soil evaporation is a key element to improve understanding of forest evaporation processes (Blyth and Harding 2011; Dubbert et al. 2013; Lawrence et al. 2007; Van den Hoof et al. 2013; Wang and Yakir 2000). One of the main methods to achieve this is by means of stable water isotopes either sampled from the surface (Kool et al. 2014; Soderberg et al. 2012) or derived from satellites (Steinwagner et al. 2007; Sutanto et al. 2015). Stable water isotopes are considered to be ideal tracers because of their natural occurrence and their ability to distinguish water evaporated from the soil and/or wet surface (i.e. canopy or forest floor) and water that has been transpired (Ehleringer and Dawson 1992; Fekete et al. 2006; Gat 2010; Kendall and McDonnell 1998). The first process causes physical fractionation (kinetic), while with root water uptake this isotopic fractionation does not occur (Williams et al. 2004). Hence after reaching steady state, the isotopic signature will be similar to the soil water. This methodology appears to work rather well for both canopy as the forest floor (Giuditta et al. 2018; Griffis 2013; Moreira et al. 1997; Rothfuss et al. 2010, 2015; Sutanto et al. 2012; Wenninger et al. 2010); however, it is costly and laborious, has a low temporal resolution, and some of the model assumption are questioned (Farquhar and Cernusak 2005; Lai et al. 2006; Rothfuss et al. 2010; Sutanto et al. 2014). Fortunately, with current developments in isotope measuring devices like improved accuracy and direct air samplers, where uncertain cold trap systems become redundant (Jiménez-Rodríguez et al. 2018; Rhee et al. 2004), new opportunities arise to disentangle the various evaporation components. A great example of the added value of isotopes is the study of Wei et al. (2018), where they included isotopes information in a combined LSM-LES-Cloud Modeling System model.

Combining knowledge on rainfall, energy, and evaporation partitioning will help to model the complex system that is present from the top of the vegetation to the forest floor. This model can explain how heat, energy, and water are transported from the top of the canopy to the unsaturated zone and vice versa. In the end, this will lead to improved evaporation estimates for tall vegetation, like forests, and allow upscaling by means of (thermal) remote sensing algorithms that can only observe the top of the canopy.

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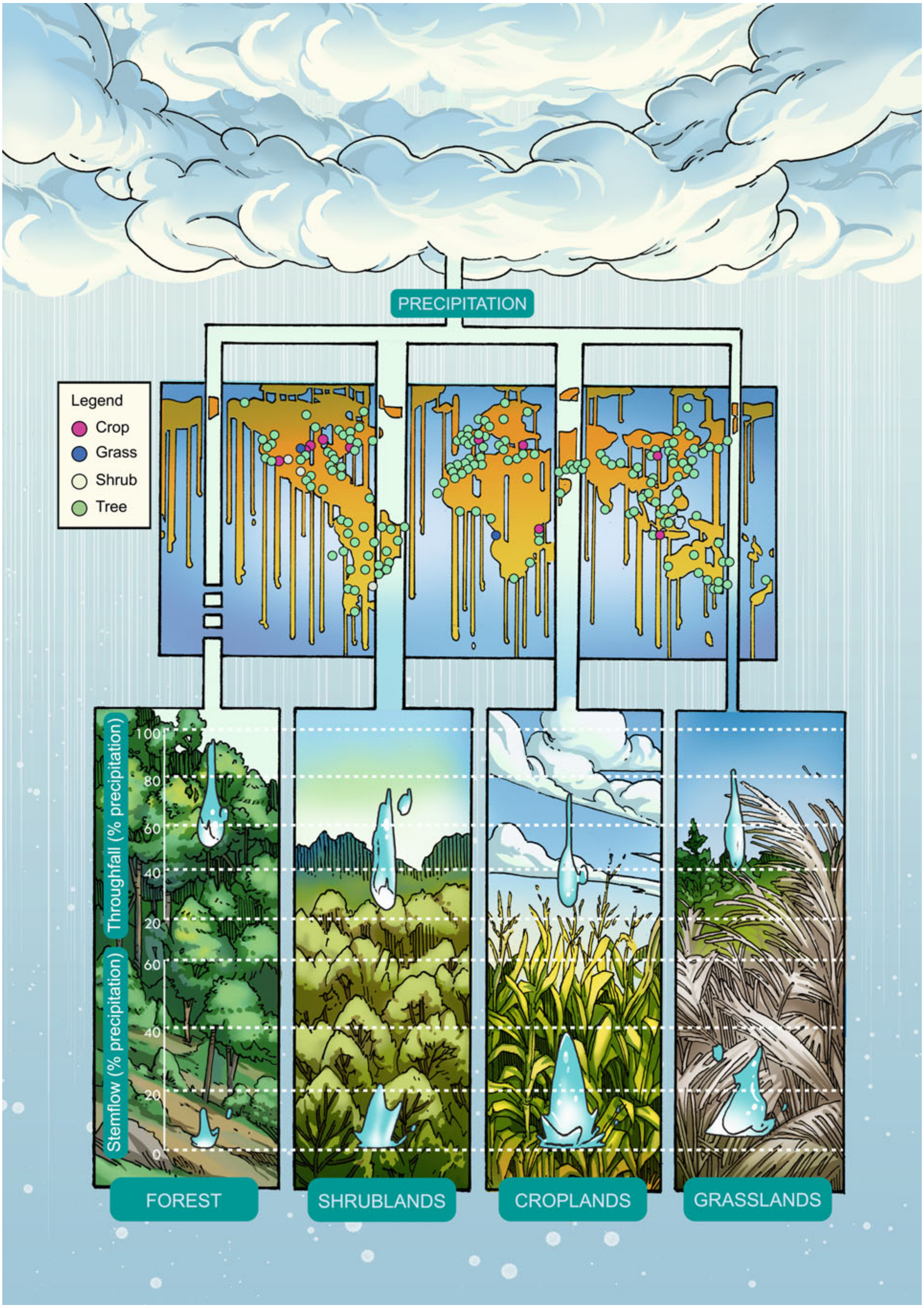
PRECIPITATION
Legend
Crop
Grass
Shrub
Tree
Throughfall (% precipitation)
100
80
60
40
20
Stemflow (% precipitation)
60
40
20
0
FOREST
SHRUBLANDS
CROPLANDS
GRASSLANDS

4

A Global Synthesis of Throughfall and Stemflow Hydrometeorology

Seyed Mohammad Moein Sadeghi, D. Alex Gordon, and John T. Van Stan, II

Abstract

The amount and patterning of precipitation beneath vegetation is determined by throughfall and stemflow. Throughfall is the portion of precipitation that falls through, or drips from, the canopy; whereas, stemflow is the portion that drains down the stem. This chapter briefly synthesises throughfall and stemflow methods, data and major drivers of variability from all studies returned from Web of Science that reported relative annual or seasonal throughfall and stemflow (% of precipitation across the canopy) to date: 644 observations spanning broad climate (boreal, temperate, Mediterranean, subtropical and tropical) and plant types (forests, shrublands, croplands and grasslands) around the globe. Relative throughfall was greatest for forests followed by shrubs > crops > grasses; whereas, relative stemflow was greatest for grasses followed by crops > shrubs > forests. This synthesis identified challenges to integrating net precipitation into large-scale (regional-to-global) hydrologic and climate processes and estimates, including: (1) under-sampling at sites; (2) lacking data for solid and mixed precipitation events' throughfall and stemflow; (3) very few throughfall and stemflow observations for herbaceous vegetation (compared to woody plants) despite croplands and grasslands representing 11% and 27% of the land surface, respectively, as well as understory herbaceous vegetation being present in nearly all forests; and (4) the current focus on fine-scale drivers of highly localized patterns.

Keywords

Crops • Ecohydrology • Fog • Forests • Grasses • Net precipitation • Rain • Shrubs • Snow

4.1 Introduction

The volume and spatiotemporal pattern of precipitation above plant canopies differ significantly from observations at the surface. This is because plant canopies redistribute precipitation as throughfall and stemflow. Throughfall is any precipitation that passes through canopy gaps, drips, or (in the case of snow) unloads and melts from canopy surfaces. Stemflow is any precipitation channeled by outlying canopy areas and drained to an individual plant's stem base. Hence, the actual amount of precipitation that reaches the forest floor is "net precipitation" (throughfall plus stemflow). Net precipitation is crucial to vegetated ecosystem functioning, being the precipitation water supply that supports soil physicochemical and biological processes (Chang and Matzner 2000; Lacombe et al. 2018; Moore et al. 2016). Stand-scale net precipitation is less than gross (above-canopy) precipitation, except during cloud or fog events (Bruijnzeel et al. 2011), due to water storage

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(Chap. 2) and evaporation (Chap. 3), but within-canopy transport processes can locally concentrate throughfall or stemflow. Thus, net precipitation patterns are spatiotemporally heterogeneous, creating highly localized relative wetter and drier spots—this chapter focuses on stand-scale throughfall and stemflow, see Chap. 6 regarding fine-scale variability. Net precipitation has demonstrable effects on broader hydrologic and biogeochemical processes across precipitation types and climates. During rainfall, throughfall and stemflow may induce preferential infiltration pathways (Bialkowski and Buttle 2015; Guswa and Spence 2012) or substantial runoff and erosion (Chap. 12). Snow and snowmelt-induced net precipitation affects the accumulation and structure of understory snowpacks (Shen and Anagnostou 2017; Veatch et al. 2009). Mixed snow-rain events with multiple freeze-melt cycles can significantly increase nutrient leaching losses from plant canopies (Levia and Herwitz 2000). Finally, fog deposition and routing by throughfall and stemflow in tropical montane headwater catchments, for example, supplies high-quality water resources to down-stream communities (Bruijnzeel et al. 2011).

Multiple reviews exist on stemflow (Johnson and Lehmann 2006; Levia and Frost 2003; Levia and Germer 2015; Van Stan and Gordon 2018) and throughfall (De Schrijver et al. 2007; Levia and Frost 2006; Levia et al. 2017), or both (Levia et al. 2011); but, none have performed a comprehensive global synthesis of hydrometeorological observations for both throughfall and stemflow across plant types. A synthesis like this is needed at this time, because the macroscale hydrologic and dynamic vegetation models that aid climate and water resource management decision-making currently consider all net precipitation as throughfall (Murray et al. 2013; Chap. 7), showing a coarse conceptual integration of throughfall processes and a nonexistent integration of stemflow into broader hydrologic and biogeochemical theory and models despite two major reviews on the topic (Levia and Frost 2003; Levia and Germer 2015). Bibliometric data from Chap. 1, in fact, show broad scientific interest in stemflow investigation has not kept pace with the growth rates observed for most scientific fields (Bornmann and Mutz 2015) or the hydrologic sciences overall (Fig. 4.1). Year-to-year publication output on stemflow has grown little over the past two decades, even decreasing compared to previous years for 9 of the past 20 years (Fig. 4.1a)—despite a steady positive year-to-year publication rate over the same period for "hydrology" overall (Fig. 4.1b). Note this is not a comparison of absolute numbers in publication output, but of year-to-year publication trends—and this comparison shows that growth in stemflow research has been limited compared to growth in hydrology research overall. Comparison of citation activity yields a starker contrast, where self-citations in stemflow research are 26% of total citations for articles published from 1997–2017 (5,816/22,325) compared to 2% for all hydrology over the same period (29,703/1,602,550).

Bibliometric results like these come with many caveats beyond the scope of this chapter, (see Harzing and Alakangas 2016; Mongeon and Paul-Hus 2016), but, in conjunction with stemflow's absence and throughfall's coarse integration into broader hydrologic research and models, it is clear that the impact of net precipitation research (especially for stemflow) has been limited. This chapter, thus, describes throughfall and stemflow (1) monitoring and analysis methods, (2) observations from vegetation types across the globe, (3) current knowledge on meteorological and plant structural influences, and (4) current knowledge gaps. Note that here throughfall and stemflow represent net precipitation flux to the litter layer.

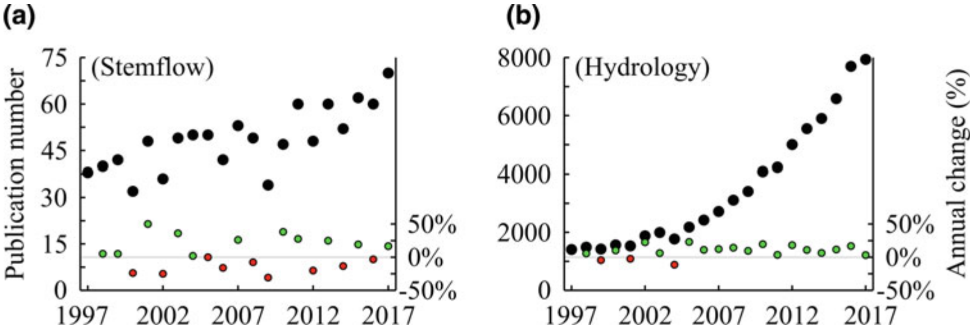


Fig. 4.1 Number of publications per year and the year-to-year changes in publication output for **a** stemflow research compared to **b** overall hydrologic research over the past two decades

4.1.1 The Many Names of Throughfall and Stemflow

Throughfall and stemflow observations are most commonly presented as depth equivalents (mm) over the projected canopy area (m^2), but terms used to describe throughfall and stemflow vary depending on the type of precipitation considered and the environmental setting. During rainfall, there are three throughfall types as defined by droplets' interaction with canopy surfaces (Fig. 4.2): (1) "free" throughfall, droplets that never contact canopy surfaces; (2) "splash" throughfall, droplets produced from impact against canopy surfaces or released from canopy surfaces due to momentum transfer; and (3) "drip" throughfall, droplets that were entrained on, and freely drained from, canopy surfaces (Levia et al. 2017). Under conditions where dew coalesces or fog/mist/cloudwater deposits onto vegetation, there is assumedly only drip and splash throughfall since, in these cases, there is no source of meteoric droplets independent of drip throughfall. When considering snow partitioning by vegetation (Fig. 4.2), throughfall is a term used solely to describe those ice crystals that reached the ground without contacting canopy surfaces (Lundberg and Halldin 2001). Any snowfall that reaches the surface after contact with vegetation is called "unloading" (Hedstrom and Pomeroy 1998). Finally, snow that contacts vegetation and drains to the surface as a liquid flux (due to thawing) is called "melt" throughfall (Hedstrom and Pomeroy 1998). Distinctions in the type of throughfall have physical meaning as they are linked to physical processes, like droplet-size distributions (for rain, occult deposition, and dew coalescence) which, in the absence of litter cover, can affect soil erosion and slope stability via the kinetic energy of precipitation reaching soils (see Chap. 12). For the cryosphere, estimates of gap, unloading and melt throughfall are necessary for understanding and predicting snowpack dynamics (Mahat and Tarboton 2014).

Stemflow also occurs as a result of liquid and solid precipitation; however, it has almost exclusively been investigated for rainfall (Van Stan and Gordon 2018) and occult deposition (Dawson 1998; Hildebrandt et al. 2007). Because stemflow generated during icy precipitation requires thawing to drain down the stem, it is often called "melt-induced" stemflow. There are two types of stemflow depth equivalents computed per hydrologic standards (*yield* per projected canopy area and *supply* per basal area, (mm)). For throughfall, the projected canopy area (including gaps) is the same as the input (or gauge collection) area, making throughfall yield and supply equivalent. On the other hand, yield and supply of stemflow differ substantially because, for most plants, canopy area is larger than basal area. Both are useful fluxes to report, but each has its hydrological context. Stemflow yields, for example, are often reported in the context of the canopy water balance (Van Stan and Gordon 2018). In the context of fine-scale spatial variability in soil processes, stemflow supply is often reported (Levia and Germer 2015). It has been stated that stemflow yield is a "flawed" metric because it "expresses stemflow asynchronous with its area of input" and essentially "masks its potential relevance for the generation of hot spots and hot moments" (Carlyle-Moses et al. 2018). However, this disagrees with long-standing hydrologic theory and norms of expressing hydrologic fluxes: i.e., does an estimate of watershed yield (per catchment area) express streamflow asynchronous with its area of input into another stream or, eventually, the ocean? Clearly not. Thus, stemflow yields are relevant metrics for net precipitation studies as they (i) link stemflow to its collection area and (ii) can easily be converted to supply with knowledge of basic stand structural traits (canopy area and basal area). Throughfall and stemflow, in addition to being expressed as depth equivalents, are commonly expressed as a percentage of incident precipitation over the plant canopy area—being called "relative" throughfall and stemflow. Care should be taken that the hydrologic terms of yield and supply not be confused with other units, like volume (L tree^{-1}), as has been done by Levia and Germer (2015).

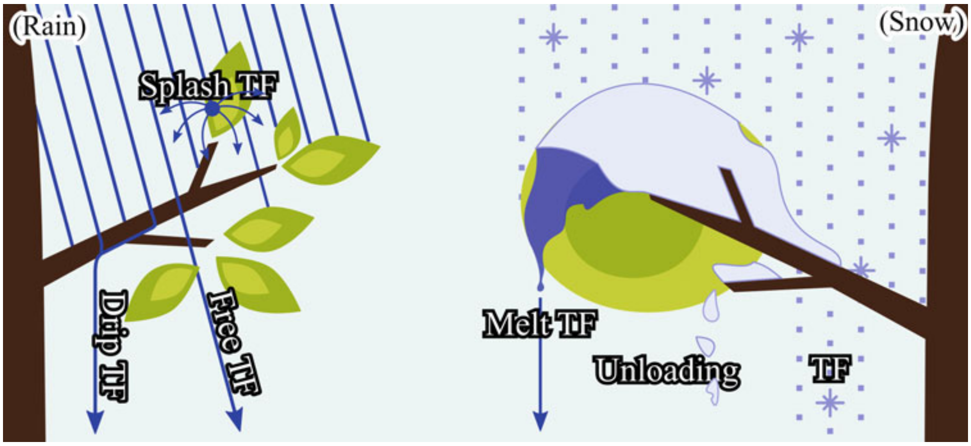


Fig. 4.2 The many names of throughfall (TF). (left) Rainfall passes through canopies as free, drip and splash TF; however (right) snow that falls directly through is simply called TF, but snow can drop to the surface in solid form, unloading, or drain as melt TF

4.2 Measuring Throughfall and Stemflow

Basic methods for observing throughfall or stemflow at any point during liquid and frozen storms generally rely on capture devices, like troughs, funnels or boards (in the case of snow), that divert precipitation to a measurement device, like tipping buckets (Iida et al. 2012), load cells (Lundberg et al. 1997) or manually measured bottles (as is most common).

Net precipitation measurement devices are still being developed, yet many of the newer devices have rarely been tested beyond a few isolated sites. As a result, this section provides an overview of the most common and often evaluated methods to date.

4.2.1 Throughfall Measurement Methods

Example throughfall measurement devices are shown in Fig. 4.3a, b. In addition to those described above, acoustic disdrometers have been tested for automated monitoring of liquid throughfall, but drip throughfall is unlikely to achieve terminal fall velocity before reaching the acoustic disdrometer (Friesen et al. 2010). Studies measuring liquid throughfall beneath short (crop) canopies have sealed and contoured areas at the surface to drain to a collection vessel (e.g., Butler and Huband 1985). Past studies have compared gauge designs for liquid throughfall, see Thimonier (1998) for an overview that is relevant to-date and culminates in the following gauge design recommendations:

- **Know collection area precisely**: opening area should be known within 0.5% and not deform under the range of expected environmental conditions;
- **The rim should be sharp**: gauge rim should be steeply beveled outside and vertical inside;
- **Depth and shape matter**: depth:diameter >1 and troughs should be v-shaped with walls >45° (also see Friesen and Köhler (2014) regarding trough designs);
- **Shield any collection vessel**: if the gauge stores precipitation until manually measured, it should have a narrow neck and be shielded from radiation.

Measurement of snow-related throughfall is typically done by manual surveys of snow depth and density in a forest and an adjacent clearing after snow storms or at times-of-interest throughout the snow season (Varhola et al. 2010). Automated

Fig. 4.3 Standard methods for measuring **a**, **b** throughfall and **c**, **d** stemflow in various plant types. **a** Throughfall can be measured at individual points using manual gauges connected to funnels or an automated network of tipping buckets. **b** Troughs may also be used to extend the sampling area. **c** Tree stems are wide enough to be wrapped with flexible tubing and connected to a monitor, like the tipping bucket in this photo. If a tipping bucket is used, a shield (not shown) is necessary to prevent measurement of throughfall. **d** Multiple collars of sealed aluminum foil connected to multiple vessels may be done for manual stemflow sampling of a smaller multi-stemmed plants or crops. All photos by John T. Van Stan, II

methods for snow-related throughfall involve acoustic snow depth sensors and modeled snow density (Bales et al. 2011). For mixed precipitation, heated sheets and gauges have been deployed beneath forest cover (Calder 1990; Lundberg et al. 1998). Although methods for observing liquid, ice, and mixed throughfall at any point are relatively simple, deploying enough gauge area, or number of gauges, is critical to attaining accurate estimates of stand-scale throughfall (Zimmermann and Zimmermann 2014) and even more important for evaluating sub-plot scale spatial structures in throughfall data (Voss et al. 2016). A detailed discussion of spatiotemporal variability in net precipitation is presented in Chap. 6 of this volume.

4.2.2 Stemflow Measurement Methods

Stemflow observations for individual plants are typically accomplished by installing a gutter around the stem that captures the water flowing down the bark surface and diverts it to a collection vessel or automated monitoring device (similar to those used for throughfall) (Fig. 4.3c, d). For modern studies, the gutter material most often consists of flexible tubing, when stems are large enough, i.e., for shrubs and trees (Levia and Germer 2015). Collars are installed on trees generally at breast height, ~1.30 m above the ground (Fig. 4.3c), which may alter stemflow volumes slightly due to the potential for ignored water losses resulting from storage and evaporation in bark or epiphytes at the stem base (Van Stan and Gordon 2018). Multi-stemmed shrubs or coppice stands may require multiple collars draining to a single vessel or to multiple vessels (Fig. 4.3d). In croplands where stems are quite thin, plastic bags have been wrapped around individual stems and sealed to serve as both collar and collection vessel (Paltineanu and Starr 2000). Other collar-like objects have been fixed to crop stems (small plastic cups) or tree saplings (rubber couplings) and drained to collection bins for stemflow measurement (Bui and Box 1992; Levia et al. 2015). A collar at the base of most grasses is impractical in the field, but stemflow production from grasses has been measured in the field by digging troughs that accept only rainfall from the base of grasses—where throughfall areas are sealed (Beard 1962). Another field study estimated stemflow production by comparing net precipitation collected in troughs with and without stemflow (Seastedt 1985). Individual grass' stemflow has also been measured via rain simulations with a plant model set in glass cylinders to collect the stemflow (De Ploey 1982). Stemflow generated from dew capture by herbaceous plants has been measured, initially by accident, using "stem wells" common in isotopic methods for studying food webs (Shure and Lewis 1973).

A common metric to evaluate stemflow production efficacy for individual plants is the dimensionless funneling ratio (Herwitz 1986), originally computed as stemflow volume (L) divided by rainfall depth (mm) over the basal area (m^2)—or, more simply expressed: the ratio of stemflow supply at the stem (mm) to rainfall depth in the open (mm). When the resulting dimensionless number exceeds 1, it suggests stemflow supply exceeds the amount of rainfall that would have been suspected if the plant were not present. Several funneling ratios now exist (e.g., Levia and Germer 2015; Carlyle-Moses et al. 2018), which compare observed stemflow volumes to many other notional hydrological circumstances, like (i) open rainfall depth or mean throughfall depth over stand-scale basal area (m^2 ha) or estimated/inferred stand-scale stemflow infiltration area (m^2 ha), or (ii) relative stemflow (%) to percent stand area represented by basal area or stemflow infiltration area (%). The result of having various ratios representing various notional hydrologic comparisons between other fluxes, stemflow, and its receiving area, is that it is extremely challenging to (i) disambiguate past results (which ratio was used?), (ii) perform cross-study comparisons, and (iii) develop a comprehensive conceptual model of stemflow hydrometeorological controls and processes. Thus, we briefly review standard funneling ratios from past work, then report past stemflow data per hydrologic norms (relative stemflow, yield, and supply). Reviews of standard funneling ratios (per basal area: Herwitz 1986) report the range of mean annual values being 3–37 for forests (Levia and Germer 2015)—but values exceeding 150 have been reported for individual trees (Herwitz 1986). This range may be biased toward efficient stemflow producers as a recent global synthesis found many forests stemflow production is simply reported as "negligible" and many other forest types may be unable to funnel enough precipitation to exceed unity (Van Stan and Gordon 2018). On the other hand, shrubs, grasses, and crops have very high funneling ratios that rarely fall below 20 because relative stemflow can range from 20 to 90% of rain (Beard 1962; Bui and Box 1992; Garcia-Estringana et al. 2010; González-Martínez et al. 2017; Jefferies and MacKerron 1985; Paltineanu and Starr 2000). Note that the low funneling efficiency for many trees should not preclude stemflow from being quantified and studied, as stemflow-induced resource scarcity may have as profound impacts as resource abundance (Van Stan and Gordon 2018).

When scaling stemflow observations from a group of individual plants, one should ensure that the individual plants being monitored represent the full range of species and canopy structural characteristics (stem diameter, branch configurations, proportion of epiphyte cover, etc.). Care should be taken to include in stemflow monitoring the range of species represented by all layers of the vegetated ecosystem, not just the dominant canopy. For example, understory saplings and shrubs

(González-Martínez et al. 2017), palms (Germer et al. 2010), grasses (Beard 1962; Gordon et al. 2018) and even ferns (Verry and Timmons 1977) can contribute significantly to stand-scale stemflow flux.

4.3 Where Has Net Precipitation Been Measured to Date?

This literature synthesis and analysis includes 644 net precipitation observations at the seasonal-to-annual scale around the globe and across climate zones (Fig. 4.4a). The greatest number of net precipitation observations have been reported in the temperate zone (*n* = 208), followed by sites in Mediterranean (*n* = 179), tropical (*n* = 133), subtropical (*n* = 81) and boreal climates (*n* = 43). Most throughfall observations are represented by forest sites (*n* = 503), followed by shrublands (*n* = 32), croplands (*n* = 22), and grasslands or short groundcover, like ferns and mosses (*n* = 7). Stemflow has also been most commonly measured in forests (*n* = 480), followed by shrublands (*n* = 58) and croplands (*n* = 20). Very little work has examined stemflow from grass canopies (*n* = 3), likely due to the difficulty of collecting stemflow at the point of grassblade

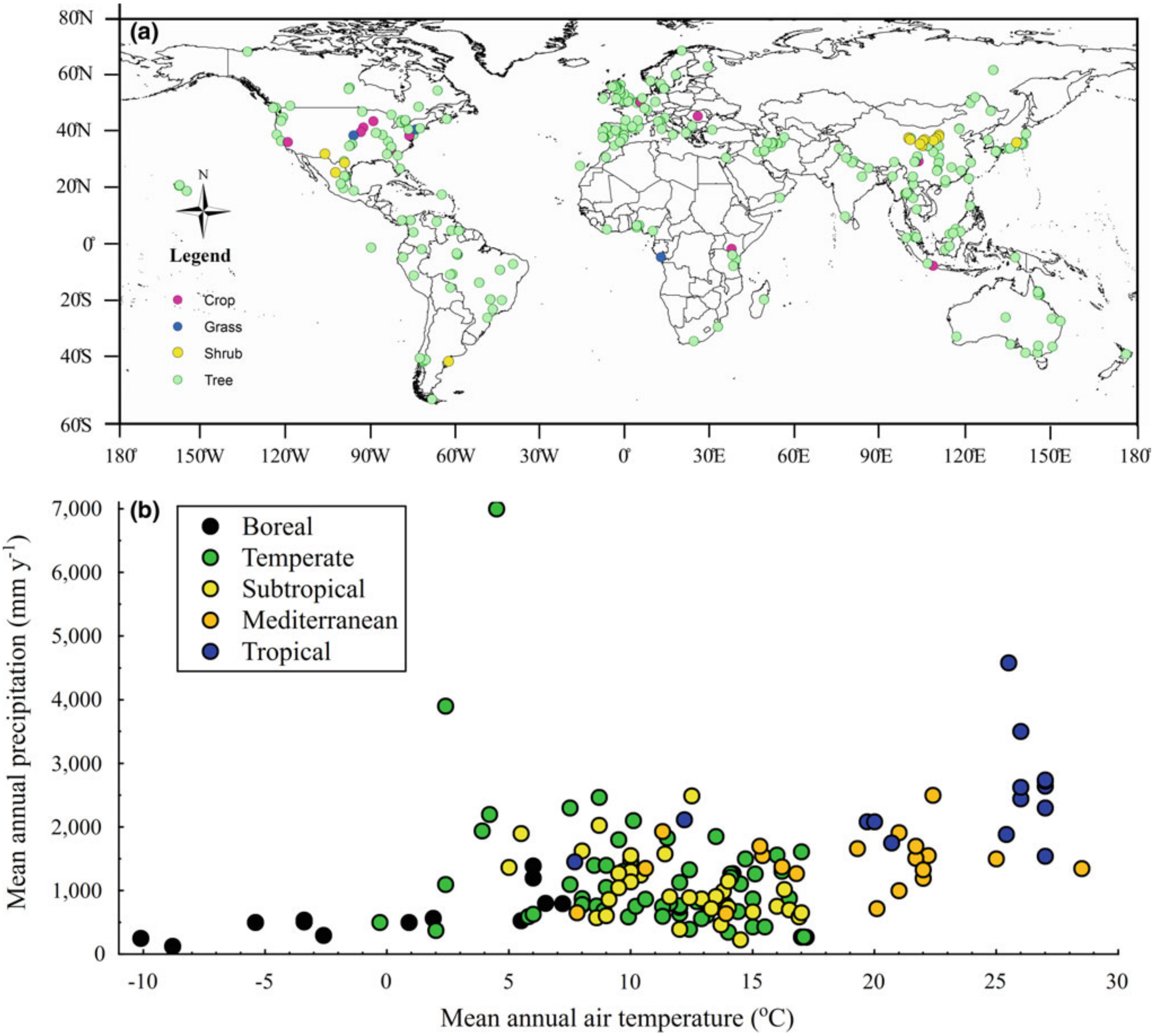


Fig. 4.4 **a** Global map of throughfall and stemflow studies in meta-analysis. **b** Plot of mean annual temperature and precipitation for each site where throughfall and stemflow have been measured

convergence, see De Ploey (1982). For both net precipitation fluxes across all vegetated ecosystems, there is a severe paucity of observations beneath short groundcover.

Net precipitation has been measured across a wide range of climates (Fig. 4.4b). Mean annual temperatures range nearly 40 °C across sites in this literature synthesis, where the minimum was −10.1 °C at a tundra site north of Inuvik in Canada's Northwest Territories (Gill 1975) and the maximum was 27.0 °C in a Bornean lowland tropical forest (Manfroi et al. 2006). The range in mean annual precipitation across sites from the selected literature was also large, approximately 6,800 mm year^{-1} (Fig. 4.4b). The greatest mean annual precipitation, 7,000 mm year^{-1}, was for a temperate rainforest site in southern Chile (Oyarzún et al. 2004), whereas the minimum, 165 mm year^{-1}, was for a desert site in central Iran (Sadeghaen et al. 2002). No throughfall or stemflow data were found for croplands in the boreal climate zone or for grasslands in subtropical and tropical climate zones. For stemflow, no data were found for Mediterranean and boreal grasslands, nor for boreal shrublands—the only study in our synthesis on net precipitation from a boreal shrubland assumed stemflow was negligible (Uehara et al. 2015).

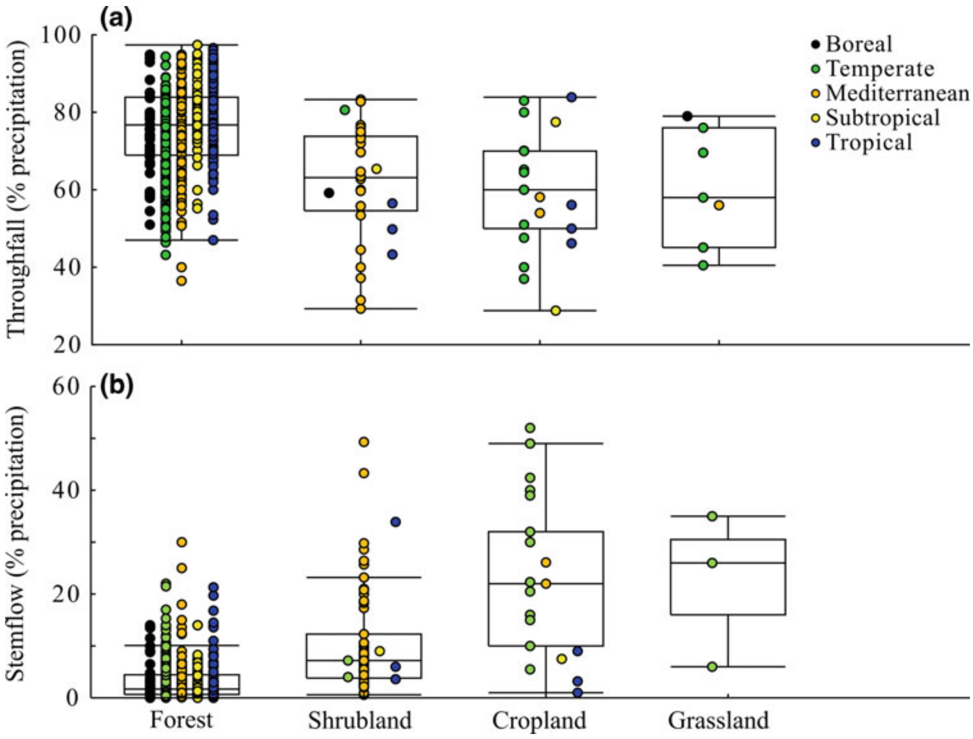
Observations are relatively well-distributed across the vegetated areas of the globe (Fig. 4.4a). The primary geographic gap in net precipitation observations, as has been previously noted by Van Stan and Gordon (2018), is in the African Congo rainforest (Fig. 4.4a). Otherwise, there are few studies in boreal ecosystems. Although there appears to be a large regional gap in Russia (Fig. 4.4a), a translated review of historical forest hydrologic research from this region (Molchanov 1963) indicates that multiple forest hydrological observatories have monitored throughfall and stemflow throughout the former Union of Soviet Socialist Republics. Other regions in Fig. 4.4a without net precipitation observations have little-to-no vegetation cover (i.e., Sahara desert). However, we note that net precipitation data do exist for plants in other desert environments (Martinez-Meza and Whitford 1996; Zhang et al. 2018). The authors were unable to find any throughfall or stemflow data for common coastal environments, like marshes, dunes, back-barrier islands (also called "hammocks"), or barrier islands, where freshwater inputs from precipitation may be important.

With regards to type of precipitation events, nearly all studies include observations during rainfall, even studies with a focus on snow or fog or cloud deposition (e.g., Brauman et al. 2010; García-Santos and Bruijnzeel 2011; Johnson 1990; Rowe and Hendrix 1951). More studies report net precipitation from fog deposition than from snowmelt. In fact, melt-induced stemflow has been generally ignored by cryosphere studies (Friesen et al. 2015; Lundberg and Halldin 2001) despite total winter stemflow being known since Miller (1966) and winter stemflow supply being up to 2–5 m at the stem base from canopy snowmelt (Herwitz and Levia Jr 1997) and a detailed discussion of its theoretical importance to snow and ice budgeting in vegetated ecosystems (Levia and Underwood 2004). It has been argued that the assumption of "no stemflow occurs during subzero temperatures" ignores the role that uncovered branch surfaces (with low albedo) can play in absorbing sunlight and causing localized melt which, in turn, generates stemflow (Herwitz and Levia Jr 1997; Levia and Underwood 2004). No studies have quantified stemflow generation from melting rime and only one forest site in Massachusetts (USA) has reported variability in stemflow during mixed (liquid-solid) precipitation events (Levia 2004). This indicates that stemflow processes during a large portion of the year in seasonal vegetated ecosystems that experience icy and mixed precipitation (particularly shrub-, crop- and grasslands) are generally unknown. Very few studies report any net precipitation fluxes under mixed-phase storms, and these are limited to stemflow (Levia 2004). Therefore, to fully scale and evaluate global hydrologic estimates of throughfall and stemflow, more observations are needed during solid and mixed-phase precipitation.

4.4 Relative Throughfall and Stemflow Across Climate and Plant Types

Overall, median relative throughfall and stemflow for all observations was 75.8% and 2.2%, with an interquartile range between 65.5–83.2% and 0.8–6.2%, respectively throughfall and stemflow as a proportion of precipitation varied markedly within plant and climates types, but larger differences appear to exist between plant types than climates (Fig. 4.5). Across climate types, median relative throughfall varied 10%, from ~70% in temperate and boreal sites to 80% in the tropics (Fig. 4.5a). When considering the 42 sites classified as arid or semi-arid that reported throughfall, a median relative throughfall of 69.7% was observed. Interestingly, this was not much lower than the median values observed for temperate and boreal sites. Lower relative throughfall in temperate, boreal, and (certainly) desert sites compared to tropical sites may be, in large part, due to wetter atmospheric conditions in the tropics reducing the evaporative demands that would otherwise consume throughfall (see discussions of sites across Mexico: (Návar 2017). Distributions of stemflow observations were significantly skewed across climates, making the median a poor representation of these datasets (Van Stan and Gordon 2018). Still, median relative stemflow varied little across climates (1.4–3.4%). The mode (perhaps a more appropriate

Fig. 4.5 Relative annual **a** throughfall and **b** stemflow observations for plants across climates. Median (line), interquartile range (box) and nonoutlier range (whiskers) provided for all observations in each plant type



statistic) had an even narrower range across climates (0.3–0.9%). Interestingly, for arid and semi-arid sites reporting stemflow (n = 67), relative stemflow was higher than in other more humid climates, with a mode of 2.7% compared to 0.4% for all non-dryland sites. This may be due to differences in the type of plant typically studied—shrubs representing nearly three-quarters (73%) of plants examined in dryland studies. This focus on shrubs at dryland sites appears to be linked to a long-standing theory that voluminous stemflow production in dryland shrubs is responsible for concentrating nutrients around plant roots (Whitford et al. 1997), but recent research found stemflow alone was insufficient for creating these “fertile islands” (Li et al. 2017). Additionally, plants in dryland ecosystems generally have waxy cuticles and outgrowths on the leaf surface, such as trichomes (Liu et al. 2015), that increase canopy hydrophobicity and facilitate the removal of water from the leaf surface (Rosado and Holder 2013).

Differences across plant type are particularly evident in the relative stemflow data (Fig. 4.5b). Both the medians and modes of relative stemflow increased dramatically with decreasing plant size (Fig. 4.5b), being greatest for grasses (26%), followed by crops (22%), then shrubs (7%) and being lowest for trees (<1%). Shorter plants, despite being little-researched, produced the top 10 highest relative stemflow values in our literature synthesis (Fig. 4.5b). The highest relative stemflow generating plants to-date appear to be potatoes (*Solanum tuberosum*), funneling up to 87% of rain to their stems in a single storm—and, impressively, this measurement did not even include stemflow from the largest plant stems (Jefferies and MacKerron 1985). Across plant types, median relative throughfall did not range as widely as for stemflow, being lowest (58%) beneath grass canopies and highest (77%) beneath tree canopies (Fig. 4.5a). Crops and shrubs produced a median relative throughfall of 60% and 63%, respectively (Fig. 4.5a). Diminished relative throughfall for shrubs, crops and grasses is, likely, a resulting trade-off from elevated stemflow generation (Fig. 4.5a vs. b).

4.5 Meteorological Controls Over Net Precipitation

Meteorological conditions appear to exert the greatest influence on throughfall and an individual tree’s stemflow by controlling the saturation state of contributing canopy and trunk surfaces (Carlyle-Moses et al. 2004; Levia et al. 2010; Zimmermann et al. 2009). Storm magnitude is directly related to both throughfall and stemflow across vegetation and climate types as it determines the amount of precipitation available for throughfall and stemflow in excess of water storage (and evaporation) (Table 4.1). Storm intensity can influence the time until saturation and, perhaps, saturate greater surface area (Carlyle-Moses 2004; Keim and Skaugset 2004; Levia et al. 2011; Price and Carlyle-Moses 2003). High wind speeds can cause entrained precipitation to detach or evaporate from vegetation surfaces, preventing them from being transported to the termination point of any throughfall or stemflow drainage pathway (Hörmann et al. 1996; Nanko et al. 2006; Van Stan et al. 2016a). Winds and atmospheric moisture demand (i.e., vapor pressure deficit) can further reduce net precipitation by increasing evaporative losses (Keim and Link 2018; Llorens et al. 1997; Staelens et al. 2008; Van Stan II et al. 2014). For individual plants, within-event intensity profiles and droplet impact energy have been linked to differential stemflow generation (Dunkerley 2014a, b). Precipitation type and temperature can also alter relative throughfall and stemflow amounts, as well as their timing. The temperature of meteoric ice crystals determines, in part, their morphology (Hallett and Mason 1958) and, therefore, the structure of the ice deposits on branches and leaves (see Chap. 2) and its resulting temporal throughfall and stemflow dynamics. For rainfall, droplet temperature may affect throughfall and stemflow, as it has been found to influence droplet retention on canopy surfaces (Klamerus-Iwan and Błońska 2018). The effect of mixed precipitation (i.e., storms with snow and rain) has only been examined for stemflow at a single site, where a rain and snow-to-rain event of otherwise similar storm conditions resulted in stemflow differing by 4 times for individual trees (Levia 2004).

Because of these various meteorological influences over small-scale, point throughfall and stemflow observations (i.e., individual gauges or trees), several decades of literature abound with assertions that drivers of variability in net precipitation are “complex” (Levia and Germer 2015) or even “unaccountable” (Law 1957) and even further complicated by canopy structural variables (see following section in this chapter). However, much explanatory power can be achieved solely from the relationship of stand-scale throughfall and stemflow to storm-scale precipitation amount for any type of vegetation cover (Table 4.1). The coefficients of determination (r^2) for sites selected to represent a comprehensive range of climates (from the tropics to the boreal) and canopy structures (from natural deciduous and coniferous forests to plantations and crops) indicate that, in most circumstance, over 95% of variability in stand-scale throughfall or stemflow can be predicted from the storm size alone. Certainly, there exists some nonlinearity in the net precipitation response to storm size for small storms (Krutzsch 1863; Leyton 1967); however, across vegetation types, regressions relating precipitation amounts to “dry” or “unsaturated” net precipitation fluxes also find strongly significant ($p < 0.01$) linear correlations ($r^2 > 0.9$) (e.g., Ford and Deans 1978; Link et al. 2004; Sadeghi et al. 2016). Additionally, the other aforementioned meteorological conditions (that act in concert with storm magnitude) tend to account for small proportions of throughfall and stemflow variability at the stand scale or across a larger sampling of plants. For example, r^2 values and effect weights derived from multiple regression analyses of storm intensity, wind speed and vapor pressure deficit on comprehensive stemflow or throughfall observations are typically <0.1 and, in some cases, all three of these meteorological variables have been insignificant or conflicting predictors of net precipitation (Bellot and Escarre 1998; Staelens et al. 2008; Van Stan II et al. 2014; Zheng et al. 2018).

4.6 Links Between Net Precipitation and Canopy Structure

Throughfall and stemflow amount and proportion of precipitation show distinct variations in relation to the structure of dominant and understory vegetation (Gerrits et al. 2010; Verry and Timmons 1977). Variability in canopy structures can result from a myriad of influences, including species-specific morphology (Sadeghi et al. 2016; Van Stan and Levia 2010), infestation (Michalzik 2011), fire (Onodera and Van Stan 2011), storm damage (Heartsill-Scalley et al. 2007; Neal et al. 1993), vegetation die-back (Frost and Levia 2014), pruning for agricultural and urban vegetation management (Hakimi et al. 2018; Van Stan II et al. 2018), thinning (Hakimi et al. 2018; Molina and del Campo 2012), epiphyte cover (Porada et al. 2018; Van Stan II and Pypker 2015), and, of course, phenology (Sadeghi et al. 2018; Šraj et al. 2008; Staelens et al. 2007). Several of these drivers—like infestation, fire, storm damage, die-back, and pruning—generally decrease canopy biomass, increase gap fraction, and thereby enhance relative throughfall at the expense of relative stemflow. Epiphyte cover tends to decrease both relative throughfall and stemflow due to increased water storage and evaporation and disruption of water draining down stems.

The largest non-disturbance related differences in relative throughfall typically occur between leafed and leafless states due to large changes in gap fraction. For example, throughfall diminished by 15–30% for various hardwood forests between leafed and leafless states (Dolman 1987; Sadeghi et al. 2015; Šraj et al. 2008), and by ∼40% as crops, like maize, develop their leaf canopies (Sun et al. 2017). For woody plants, it is generally assumed that relative stemflow is greater in the leafless season because of greater woody surface access to precipitation (Levia and Germer 2015). Certainly, greater woody surface access to precipitation can aid in saturating bark surfaces and generating stemflow; but satisfying bark water storage is not easily done because bark stores more water than most other canopy elements—representing 40–80% of the total water storage capacity of a fully leafed tree (Herwitz 1985; Levia and Herwitz 2005; Voigt and Zwolinski 1964). Thus, seasonal variability in storm size and its role in saturating stem surfaces may be as key as seasonal variability in leaf state. Climates

Table 4.1 Summary of regression statistics between storm amount (mm) and net precipitation yield (mm). Storm amount can typically predict >95% of the variance of throughfall or stemflow for different forest types across climates. *p*-values for regressions were at least $p < 0.01$

Flux, climate, vegetation	r^2	*a*	*b*	Form	References
Throughfall					
Sedimentary plain forest	0.99	0.93	−1.02	Linear	Tobón Marin et al. (2000)
Low terrace forest	0.99	0.92	1.02	Linear	Tobón Marin et al. (2000)
High terrace forest	0.99	0.91	−1.07	Linear	Tobón Marin et al. (2000)
Floodplain forest	0.99	0.89	−1.48	Linear	Tobón Marin et al. (2000)
Wetland forest	0.96	0.98	−0.58	Linear	Bryant et al. (2005)
Mature pine forest	0.88	0.75	−0.05	Linear	Bryant et al. (2005)
Pine plantation	0.97	1.02	0.16	Linear	Bryant et al. (2005)
Upland hardwood forest	0.93	1.00	−0.63	Linear	Bryant et al. (2005)
Mixed piedmont forest	0.92	0.82	0.01	Linear	Bryant et al. (2005)
Mediterranean holm-oak	0.99	0.82	−1.30	Linear	Bellot and Escarre (1998)
Temperate, spruce	0.99	0.83	−0.88	Linear	Nezamdoost et al. (2018)
Temperate, oriental beech	0.99	0.84	−0.46	Linear	Ahmadi et al. (2009)
Temperate, Japanese cypress	0.99	0.68	−1.25	Linear	Sun et al. (2014)
Temperate, maize (seedling)	>0.99	0.84	0.00	Linear	Zheng et al. (2018)
Temperate, maize (jointing)	>0.99	0.71	0.00	Linear	Zheng et al. (2018)
Temperate, maize (tasseling)	>0.99	0.54	0.00	Linear	Zheng et al. (2018)
Temperate, maize (mature)	>0.99	0.60	0.00	Linear	Zheng et al. (2018)
Semi-arid, 40 y/o Ailanthus	0.99	0.68	−0.12	Linear	Sadeghi et al. (2017)
Semi-arid, 30 y/o Ailanthus	0.99	0.75	−0.13	Linear	Sadeghi et al. (2017)
Semi-arid, 20 y/o Ailanthus	0.99	0.85	−0.25	Linear	Sadeghi et al. (2017)
Mixed pine-deciduous forest	0.99	0.76	−0.08	Linear	Mahendrappa (1990)
Spruce plantation	0.93	0.41	−1.36	Linear (dry)	Ford and Deans (1978)
Spruce plantation	0.95	1.01	−31.23	Linear (wet)	Ford and Deans (1978)
Montane hardwood forest	0.99	0.95	−0.09	Linear	Cappellato and Peters (1995)
Montane coniferous forest	0.99	0.82	−0.01	Linear	Cappellato and Peters (1995)
Stemflow					
Sedimentary plain forest	0.92	0.002	1.53	Power	Tobón Marin et al. (2000)
Low terrace forest	0.94	0.002	1.47	Power	Tobón Marin et al. (2000)
High terrace forest	0.95	0.003	1.42	Power	Tobón Marin et al. (2000)
Floodplain forest	0.91	0.003	1.33	Power	Tobón Marin et al. (2000)
Temperate, Japanese cypress	0.99	0.12	−0.39	Linear	Sun et al. (2014)
Temperate, maize (seedling)	0.96	0.13	0.00	Linear	Zheng et al. (2018)
Temperate, maize (jointing)	>0.99	0.20	0.00	Linear	Zheng et al. (2018)
Temperate, maize (tasseling)	>0.99	0.31	0.00	Linear	Zheng et al. (2018)
Temperate, maize (mature)	>0.99	0.25	0.00	Linear	Zheng et al. (2018)
Temperate, spruce	0.94	0.07	−0.19	Linear	Nezamdoost et al. (2018)
Temperate, oriental beech	0.95	0.13	−0.21	Linear	Ahmadi et al. (2009)
Mediterranean, holm-oak	0.99	0.13	−0.28	Linear	Bellot and Escarre (1998)
Semi-arid, 40 y/o Ailanthus	0.95	0.32	−0.47	Linear	Sadeghi et al. (2017)

(continued)

Table 4.1 (continued)

Flux, climate, vegetation	r^2	*a*	*b*	Form	References
Semi-arid, 30 y/o Ailanthus	0.95	0.25	−0.35	Linear	Sadeghi et al. (2017)
Semi-arid, 20 y/o Ailanthus	0.95	0.16	−0.20	Linear	Sadeghi et al. (2017)
Spruce plantation	0.94	0.32	−2.25	Linear	Ford and Deans (1978)
Net precipitation					
Tropical, Australian rainforest	0.99	1.14	3.58	Linear	McJannet et al. (2007)
Subtropical, Sierra Madre	0.97	–	–	Linear	Cantú Silva and González Rodríguez (2001)

where storm size decreases during the leafless season may not result in greater winter relative stemflow from woody vegetation.

Few studies exist comparing relative stemflow variability for sites of contrasting seasonal precipitation dynamics, but an example can be made for *Robinia pseudoacacia* as seasonal stemflow over 3 years has been reported for a wet-summer/dry-winter temperate site, Köppen *Dfb* (Tsakov and Alexandrov 2005), and a dry-summer/wet-winter Mediterranean site, Köppen *Csa* (Sadeghi et al. 2018). These sites have similar tree-size characteristics commonly identified as driving stemflow: 16 cm versus 19 cm DBH and 2.2 m versus 2.1 m crown diameter for Tsakov and Alexandrov (2005) and Sadeghi et al. (2018), respectively. Relative stemflow was actually less when leafless (6.5%) compared to leafed conditions (7.8%) for *R. pseudoacacia* in the temperate *Dfb* site, where monthly precipitation was 60% lower in winter, 15 mm month^{-1} (Nov–Feb mean), than in summer, 39 mm month^{-1} (Jun–Sep mean) (Tsakov and Alexandrov 2005). Conversely, similarly sized *R. pseudoacacia* trees at the Mediterranean *Csa* site produced higher relative stemflow when leafless (6%) and experiencing winter storms of larger mean magnitude, 4.8 mm event^{-1}, than during leafed conditions (1.6%) with smaller storms, 2 mm event^{-1} (Sadeghi et al. 2018). Despite the common emphasis on leaf versus leafless states, transitional leaf states (leaf-out and senescence) and their related shifts in storm conditions can also exert substantial influences over throughfall, by >10%, and stemflow, by ~5%—which is a large change for stemflow (Sadeghi et al. 2018). Transitional seasons, depending on the climate and vegetation type, can represent a substantial portion of the year: i.e., 4 months in Sadeghi et al. (2018).

Leaf area (specifically, LAI) currently plays a leading role in the way global land surface models predict net precipitation (Davies-Barnard et al. 2014; Murray 2014)—no global stemflow estimates are known to the authors. However, results from studies in our synthesis dataset indicate that LAI, alone, does not account for a significant portion of variability in throughfall from woody plants (Fig. 4.6). For herbaceous plants, on the other hand, LAI has been strongly correlated to throughfall and stemflow (Zheng et al. 2018). The strong correlation between LAI and stemflow for crops and grasses is likely because they rely on their leaves to capture precipitation for stemflow (De Ploey 1982). It has also been noted that leaf orientation/angle throughout phenological events can temporally impact stemflow and throughfall in herbaceous vegetation (Van Elewijck 1989; Zheng et al. 2018). For woody plants, differences in branch angle and bark thickness that arises from natural

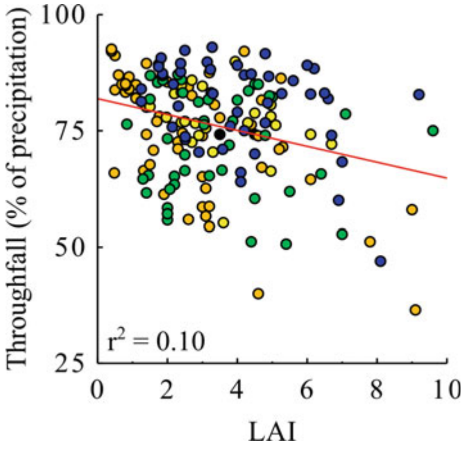


Fig. 4.6 Weak correlation between relative throughfall and LAI. Relative throughfall from sites across climates (color coded as in previous figures) plotted alongside reported LAI from studies in literature synthesis

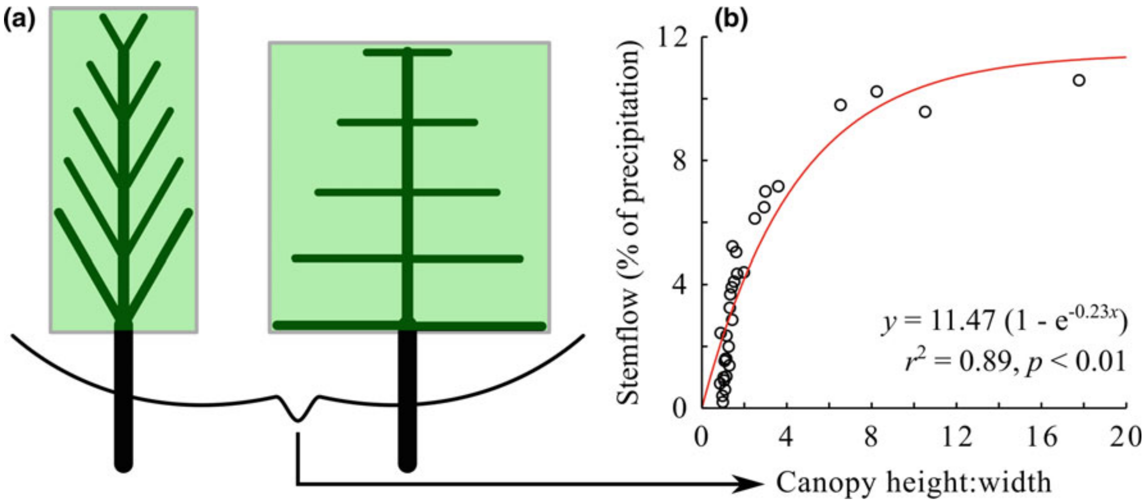


Fig. 4.7 **a** Schematic showing how increasing branch inclination angle can increase the ratio of canopy height:width (H:W). Note that decreasing branch angle below horizontal may also increase the H:W ratio; however, no data were found for this type of canopy morphology. **b** Scatterplot and correlation between H:W ratios for 31 genera from the US Forest Service i-Tree field data collection in several cities and relative stemflow collected from the literature (see Appendix A for underlying data)

interspecific variability or disturbance (pruning, planting, burning, etc.) may affect throughfall and stemflow. Throughfall can be reduced by lower branch angles increasing the projected canopy area occupied by biomass, or by thicker bark intercepting greater precipitation amounts (Pypker et al. 2011). The effect of branch angle and bark thickness on stemflow, however, is much stronger than observed for throughfall. Thicker barks tend to absorb more of the precipitation draining down stems (Ilek et al. 2017; Livesley et al. 2014; Van Stan and Levia Jr 2010; Van Stan et al. 2016b). The relationship between stemflow and branch angle has been difficult to estimate, having rarely been assessed quantitatively by, for example, hand-sampling of saplings (Levia et al. 2015) and terrestrial LiDAR-based structural modeling (Yankine et al. 2017). Neither study was able to shed broad quantitative insight into the relationship between branch angle and stemflow from woody plants. Perhaps canopy height-to-width ratios (H:W), which can geometrically abstract the stemflow drainage area, being generally larger for canopies of more steeply-inclined branches (Fig. 4.7a), can provide a broad quantitative insight? For a brief proof-of-concept, H:W values were compiled from the US Forest Service's i-Tree field data collection across several cities, averaged by genus, then plotted against relative stemflow values from across the literature for as many genera as possible. Data from 31 genera indicate a strong correlation ($r^2 = 0.89$, $p < 0.01$) between H:W and relative stemflow in the form of an exponential function that steadies at ~11% of precipitation (Fig. 4.7b). Note that:

- the H:W data is biased toward urban environments;
- there were few genera with stemflow data with average H:W > 2;
- a few studies report relative stemflow for forests ≫11%: e.g., for a *Pinus radiata* plantation in Chile, Uyttendaele and Iroumé (2002) reported 22% stemflow—although this exceeds relative stemflow from other *P. radiata* sites in the same region, 2–6% (Huber et al. 2008);
- There are other ways canopy structure may increase H:W without increasing branch angle (e.g., many stacked, flat, and short branches, or very droopy branches).

Finally, seasonal understory elements, when present, are highly relevant factors in determining the proportion of precipitation that reaches the surface of vegetated landscapes via throughfall and stemflow. One of the first examples of this was a study that included an annual understory fern, *Pteridium aquilinum*, which has a cosmopolitan distribution across ecosystems, barring hot and cold deserts (Page 1976). In the summer, *P. aquilinum* achieved significant stem densities of nearly 33,000 stems ha^{-1} and were able to drain 7.6% of growing season rainfall (4.2% of annual rainfall) to the soil as stemflow (Verry and Timmons 1977). The greater understory partitioning of precipitation as stemflow compared to the overstory is common in forests (Germer et al. 2010; González-Martínez et al. 2017; Price and Watters 1989). In fact, surprisingly little work has been done integrating net precipitation dynamics of the overstory and understory, despite long-standing calls rooted in solid observational data (Price et al. 1997; Price and Watters 1989; Yarie 1980).

4.7 Conclusions

Globally, throughfall and stemflow deliver significantly different amounts and patterns of water to the surface compared to bulk precipitation. However, there are challenges to estimating large-scale throughfall and stemflow fluxes and their variability, with the top three being: (1) too few throughfall and stemflow observations across too little collection area are made in most field studies to achieve an accurate estimate of net precipitation, see Zimmermann and Zimmermann (2014) discussion in their Sect. 5.5, for example; (2) too little data exists on throughfall and stemflow under solid and mixed precipitation events (see Levia and Underwood 2004); and (3) there is a severe dearth of observations for herbaceous vegetation compared to forests. Regarding this last point, it is surprising that we know the most about stemflow for the type of plants (i.e., woody) that generate the least relative stemflow. Clearly, work is needed on stemflow (and throughfall) generation from (1) the herbaceous crops that cover 11% of the land surface and form the foundation of our food supply (Alexandratos and Bruinsma 2012), (2) the understory vegetation that alters the abundantly researched throughfall and stemflow dynamics beneath forest canopies, and (3) the grasslands that cover ∼27% of the land surface (Suttie et al. 2005). This is quantitatively an obvious and significant knowledge gap in our understanding of net precipitation reaching the surface.

A fourth major challenge facing efforts to contextualize throughfall and stemflow in regional, continental and global scale hydrologic, ecological and climate processes is the field's current focus on small-scale, inherently complex (i.e., nonlinear) hydrometeorological processes (to which the chapter authors have contributed). We now suggest a shift in perspective is necessary. Over the past 15 years, throughfall and stemflow research has steadily increased the list of "important" variables driving fine-scale yields—i.e., a recent review describes dozens of biotic and abiotic factors driving individual tree stemflow yield, including fine-scale (∼5-min) intrastorm interactions between "evaporative processes, bark water storage and rainfall partitioning" (Levia and Germer 2015). Despite this, progress toward quantitatively integrating throughfall and stemflow into macroscale-to-global hydrologic, climate, and terrestrial ecosystem theory has been slow and limited for throughfall (Miralles et al. 2011; Murray 2014) and nonexistent for stemflow (see Chap. 7). Large-scale variability (e.g., watershed-to-watershed) in net precipitation has been estimated accurately by considering very few meteorological and structural drivers (Mitchell et al. 2012; Nieschulze et al. 2009; Schumacher and Christiansen 2015). Just as observed for watersheds (Loritz et al. 2018; Zehe et al. 2010, 2014), throughfall and stemflow observations across sites indicate that interactive nonlinear point-scale processes may "organize" into linear net precipitation responses to gross precipitation at larger scales (Table 4.1). We, thus, recommend future net precipitation research "catch-up" to broader hydrological monitoring/modeling efforts (Loritz et al. 2018) by seeking to improve our understanding of which system characteristics primarily drive larger-scale net precipitation responses and what level of detail is needed for representing these processes. Ultimately this may mean that scientists pursuing net precipitation field studies will have to take a step back, spatially, and put forth the rigorous effort necessary (i.e., the appropriate amount of gauges or gauge area) to accurately estimate stand-scale throughfall and stemflow to support integration of net precipitation into our understanding of global water and energy budgets.

Appendix A

Canopy height-to-width ratios (H:W) and mean stemflow values in Fig. 4.7b.

Genus/spp	H:W	Stemflow	Citations
(–)	(–)	(% rain)	(–)
Acer	1.3	2.0	Courchesne and Hendershot (1988), Mahendrappa (1974), Malone (2015), Schooling and Carlyle-Moses (2015), Schooling et al. (2017)
Big-leaf maple	3.0	7.0	Hamdan and Schmidt (2012)
Ailanthus	3.6	7.2	Sadeghi et al. (2017)
Betula	1.4	2.9	Abrahamsen et al. (1977), Courchesne and Hendershot (1988), Molchanov (1963), Wan and Chen (2000), Zabret and Šraj (2015)
Carya	1.1	0.9	Peterson and Rolfe (1982)
Catalpa	1.0	0.4	Schooling and Carlyle-Moses (2015)

(continued)

Genus/spp	H:W	Stemflow	Citations
(–)	(–)	(% rain)	(–)
Cercis	0.9	0.8	Peterson and Rolfe (1982)
Chamaecyparis	17.8	10.6	Sun et al. (2014)
Cupressus	10.5	9.6	Nasiri et al. (2012), Sadeghi et al. (2016), Suzuki et al. (1979)
Fagus	1.3	3.7	Chang and Matzner (2000), Ghorbani and Rahmani (2009), Krämer and Hölscher (2009), Mosello et al. (2002), Neal et al. (1993), Noirfalise (1958), Petit and Kalombo (1984), Schooling and Carlyle-Moses (2015), Schooling et al. (2017), Staelens et al. (2008), Van Stan II (2012)
Fraxinus	1.3	1.4	Malone (2015)
Gleditsia	1.1	0.6	Schooling and Carlyle-Moses (2015)
Ilex	1.4	5.2	Aboal et al. (2015), Masukata et al. (1990)
Juglans	1.0	1.0	Lazerjan (2012)
Juniperus	0.9	2.4	Badri and Gauquelin (1998), Van Stan et al. (2017), Young et al. (1984)
Liquidambar	1.5	4.1	Xiao and McPherson (2011)
Picea	1.7	4.4	Aussenac (1968), Bergkvist and Folkeson (1995), Cape et al. (1991), Johnson (1990), Mahendrappa (1974), Nihlgård (1970), Wheater et al. (1987)
Pinus	1.6	5.0	Bryant et al. (2005), Cape et al. (1991), Crockford and Richardson (2000), Foster (1974), Ibrahim et al. (1982), Lawson (1967), Lei et al. (1994a, b), Mahendrappa (1974), Majima and Tase (1982), Pryor and Barthelmie (2005), Sadeghi et al. (2016), Toba and Ohta (2005), Uyttendaele and Iroumé (2002)
Pinus (juvenile)	2.0	4.4	McKee and Carlyle-Moses (2016) *Assumed 1-m bole to bottom of H
Platanus	1.0	0.2	Peterson and Rolfe (1982)
Populus	1.4	3.9	Freedman and Prager (1986), Ma et al. (2014), Mahendrappa (1974), Molchanov (1963), Moore (2003), Verry and Timmons (1977)
Prunus	1.2	1.0	Schooling and Carlyle-Moses (2015)
Quercus	1.1	1.6	Pound (2017)
Robinia	1.1	1.6	Sadeghi et al. (2016), Schooling and Carlyle-Moses (2015)
Salix	1.3	3.3	Li et al. (2009), Schooling and Carlyle-Moses (2015), Yuan et al. (2016), Yue et al. (2014)
Thuja	2.5	6.1	Mathers and Taylor (1983)
Tilia	1.1	1.5	Schooling and Carlyle-Moses (2015)
Erica	2.9	6.5	Aboal et al. (1999)
Prestoea	6.5	9.8	Frangi and Lugo (1985) *W = 2.6 m from landscaping manual
Nothofagus	8.2	10.2	Godoy et al. (1999, 2001)

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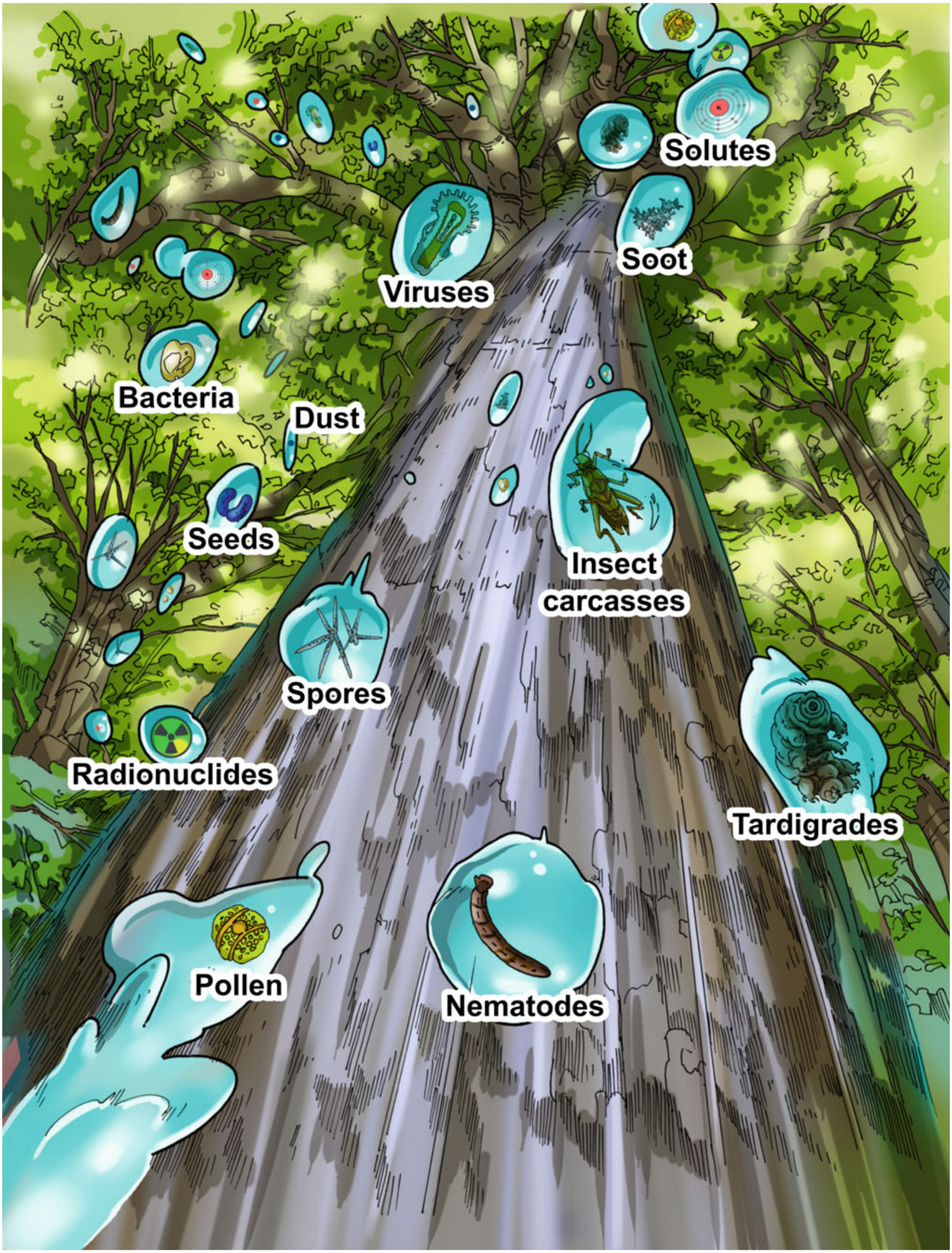
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Tardigrades
Pollen
Nematodes

5 Things Seen and Unseen in Throughfall and Stemflow

Alexandra G. Ponette-González, John T. Van Stan II,
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Abstract

For close to a century, scientists have recognized the important role of throughfall and stemflow (precipitation water that falls through plant canopies and runs down plant stems, respectively) in the cycling of materials. These “hydrologic highways” carry atmospherically deposited and canopy-derived materials from the top of the plant canopy to the ground below, thus integrating biological, physical, and chemical processes occurring at the top of and within the canopy and linking above and belowground components of ecosystems. Diverse in nature, abundance, composition, and effects, the materials that flow through plant canopies can be dissolved or particulate, living or nonliving, nutrients or pollutants, beneficial or pathogenic. Yet, despite decades of research, only a small fraction of the components within throughfall and stemflow have been “seen” in studies on material cycles. Thus, our goal in this chapter is to uncover and call attention to the plethora of “unseen” materials in throughfall and stemflow, for example, those that are discarded after filtration and those that remain hidden within precipitation waters. From a biogeochemical standpoint, their quantification is important. Recent research highlights the abundance of particulates, bacterial cells, fungi, and potentially even microplastics in throughfall and stemflow with broader social, economic, and ecological implications for nutrient cycling, soil formation and fertility, decomposition, aquatic ecosystems, climate change, air quality, decontamination, radiation hygiene, species distribution, and disease transmission.

Keywords

Dissolved solutes • Inorganic particles • Biological particles • Plant canopies • Material cycles • Biogeochemistry

5.1 Introduction

Countless living and nonliving materials are delivered in precipitation water from plant canopies to the ground, including pollutants from fossil fuel combustion (e.g., Weathers et al. 2000, 2001; Ponette-González et al. 2017), dust from arid land soils (e.g., Lequy et al. 2014), debris and excretions from herbivorous insect infestations (e.g., Arango et al. 2019; Michalzik and Stadler 2005), and microbes (Bittar et al. 2018; Teachey et al. 2018). These materials—in both dissolved and particulate form—move from the aboveground portion of the ecosystem to the ground below via throughfall, the water that drips from and passes through plant canopies, and stemflow, the water that flows down plant stems (Fig. 5.1). Regardless of the flow path taken, interactions between precipitation and canopy surfaces alter the *composition* of throughfall and stemflow water.

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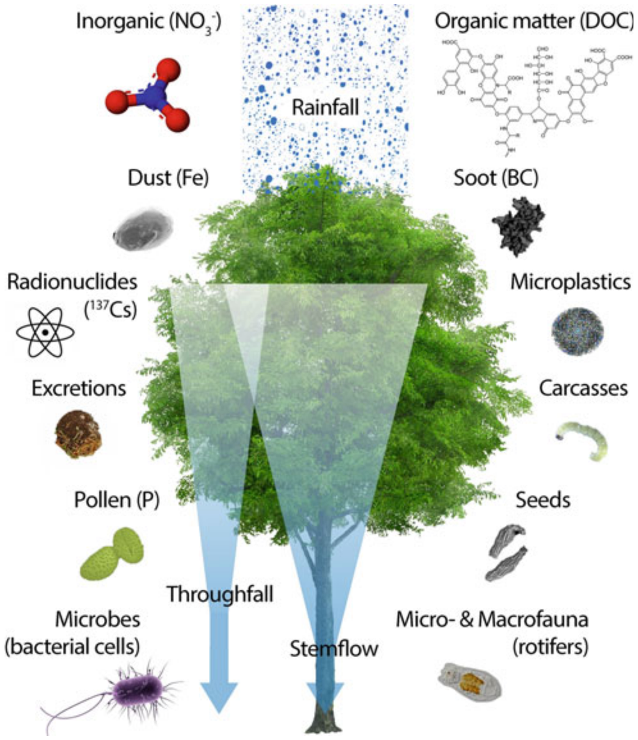

Fig. 5.1 Throughfall and stemflow are akin to "hydrologic highways". As these waters move through plant canopies, they transport and integrate diverse chemical, geological, biological materials deposited from the atmosphere to plant canopies and derived from the canopy itself to the ground below. Moving from top to bottom are examples of "seen" to "unseen" components of throughfall and stemflow (with examples in parentheses)

This change in composition is the result of three key processes: (1) "washing" of dry-deposited materials from the canopy; (2) uptake or retention of materials by the canopy; and (3) leaching of materials from canopy surfaces and from materials produced by canopy-dwelling organisms. While the significance of throughfall and stemflow in the cycling of materials has long been recognized (e.g., Eaton et al. 1973), we are only now gleaning the true potential for these "hydrologic highways" to affect a diverse suite of ecosystem processes, including primary productivity, decomposition, and nutrient cycling (e.g., Brando et al. 2008; Reynolds and Hunter 2001; Thomas et al. 2010).

In this chapter, we review recent advances and future frontiers in throughfall and stemflow research. In the first section, we highlight important findings from the large body of work on the dissolved components of throughfall and stemflow and direct the reader to myriad reviews on the subject. In the second section, we summarize the growing literature on the nonliving particulate fraction that also exists, but is often overlooked, in research on canopy to soil fluxes. We conclude by examining the current state of knowledge on the hidden life within throughfall and stemflow waters.

5.2 Dissolved Solutes: A Brief Summary of an Extensively Reviewed Literature

Routine measurements of throughfall and stemflow composition in studies of forest nutrient cycling date back to at least the 1950s (Eriksson 1952; Pozdnyakov 1956; Tamm 1951), and to the turn of the 20th century for agricultural systems (Le Clerc and Breazeale 1908). Motivated by a desire to better understand the contribution of throughfall and stemflow to plant nutrition and soil fertility (Parker 1983), research then (and now) has concentrated in large part on the concentrations and fluxes of essential plant nutrients (and in excess, pollutants), including nitrogen (N), potassium (K), sulfur (S), calcium (Ca), and magnesium (Mg). Moreover, the focus has been on the dissolved phase. Operationally defined as the fraction that can pass through a filter with a typical pore size of 0.45 microns (μm), these are the materials that are readily available for plant and microbial uptake and that represent an important addition to available soil nutrient pools (Kalbitz et al. 2000).

As research on throughfall and stemflow composition has expanded to include more and more locations around the world (Fig. 5.2) and more diverse ecosystem types (including tree-based and agricultural systems), so has the number of reviews on the subject. For further details, we refer the reader to reviews listed in Table 5.1. Briefly, we highlight a few key points

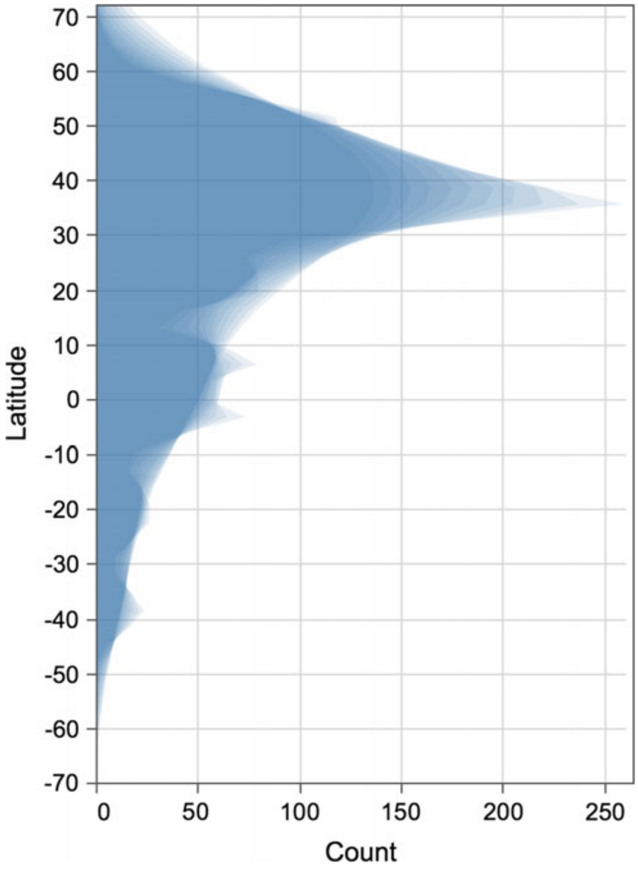

Fig. 5.2 Distribution of throughfall and stemflow composition observations by latitude. Observations (n = 777) were compiled from Chap. 4 of this volume, Ponette-González et al. (2014), and Ponette-González et al. (2016a). Although most observations (65%) are for midlatitudes, research on throughfall and stemflow composition in tropical ecosystems has increased considerably since the seminal review by Parker (1983)

from this literature. First, dissolved solute concentrations in throughfall and stemflow are often, but not always, higher than in rainfall (Ponette-González et al. 2014; Van Stan and Gordon 2018), with stemflow exhibiting higher and greater variability in concentrations than throughfall (Parker 1983; Van Stan and Stubbins 2018). However, interactions between elements and vegetation canopies take different forms (Ponette-González et al. 2016a). On the one hand, there are those elements, such as S, chloride (Cl), and sodium (Na), that behave conservatively within the canopy of many forest ecosystems (Lovett et al. 2005; Weathers et al. 2006). In other words, biological interactions within the canopy (uptake and leaching) are small relative to external inputs from wet and dry deposition. In contrast, there are elements, such as N, that undergo numerous biological and chemical transformations within the canopy (Umana and Wanek 2010; Woods et al. 2012). And, finally, there are elements that are readily leached from leaves, such as carbon (C) and K, and for whom internal leaching is greater than external inputs from wet and dry deposition (Tukey 1966; Tukey and Mecklenburg 1964). Second, throughfall and stemflow can be a quantitatively important component of the intrasystem nutrient cycle (Chapin et al. 2002; Van Stan and Stubbins 2018). It is not unusual for these processes to deliver 10s of kilograms of S, inorganic N, Ca, Na, and even 100s of kilograms of Cl to the ground surface (Du et al. 2014; Ponette-González et al. 2016a). Third, throughfall and stemflow fluxes exhibit high spatial and temporal variability due to a multitude of biotic and abiotic factors (Weathers et al. 2006; Zimmermann et al. 2008, 2015).

Concentrations and fluxes of dissolved organic matter (DOM) and phosphorus (P) are less frequently quantified in throughfall and stemflow water (Fig. 5.1). Phosphorus is a critical limiting nutrient in many terrestrial ecosystems (Vitousek et al. 2010), and recent work suggest that P fluxes via throughfall and stemflow can be significant in ecosystems affected by insect infestations (Arango et al. 2019; Seastedt et al. 1983), and downwind of deserts (Das et al. 2011), volcanic activity (Heartsill-Scalley et al. 2007), and biomass burning (Ponette-González et al. 2016b). In a tropical forested peatland in Borneo, Ponette-González et al. (2016b) documented inorganic P inputs on the order of ~8 kg ha^{-1} yr^{-1}, some of the highest P inputs recorded globally. More than 30% of the inorganic P in throughfall was deposited following major local and

Table 5.1 Publications that review the composition of throughfall, stemflow, or both. Note that TDS is Total Dissolved Solids

References	Vegetation	Scale	C	N	P	S	Ions	Metals	H	TDS
Throughfall and stemflow										
Parker (1983)	Forest	Global	x	x	x	x	x	x	x	
De Schrijver et al. (2007)	Forest, grass, heath	Europe, North America, Israel, Japan		x		x	x		x	
Van Stan and Pypker (2015)	Epiphytes	Global	x	x	x	x	x	x		
Van Stan and Stubbins (2018)	Forest	Global	x	x	x	x				
Decina et al. (in press)	Urban trees	USA	x	x	x		x			
Throughfall										
Levia and Frost (2006)	Forest	Global					x		x	
Ponette-González et al. (2014)	Forest, coffee, grass	Latin America, Hawaii		x						
Ponette-González et al. (2016b)	Forest	Global		x		x	x			
Stemflow										
Levia and Frost (2003)	Forest, crops	Global		x			x		x	
Levia and Germer (2015)	Forest, shrubs	Global	x	x	x	x	x	x	x	
Van Stan and Stubbins (2018)	Forest	Global								x

regional fire pulses. Pollen also represents a significant potential source of P as pollen P concentrations can be as much as three times greater, on average, as those in desert dust (Bigio and Angert 2018). For example, Decina et al. (2018) measured throughfall total P fluxes beneath urban trees that were sevenfold higher compared to rainfall P deposition; they suggested that high levels of P in spring throughfall could, in part, be due to pollen deposition. Direct quantification of the pollen contribution to throughfall P has not been conducted but may now be feasible. A recent study suggests that the oxygen isotope signature of phosphate coupled with elemental analysis may be used to identify dissolved P originating from pollen versus dust (Bigio and Angert 2018).

It is somewhat surprising that DOM inputs in throughfall and stemflow remain poorly quantified given that most DOM is derived from tree canopies including the associated biota (Van Stan and Stubbins 2018). In their review of tree-derived dissolved organic matter (tree-DOM) fluxes, Van Stan and Stubbins (2018) note that the amount of tree-dissolved organic carbon (DOC) yield per projected canopy "catchment" area (m^2) is comparable to normalized DOC exports from river systems. In forests, throughfall DOC fluxes range from 20 to 480 kg-C ha^{-1} yr^{-1}, while stemflow fluxes range from 0.1 to 8 kg-C ha^{-1} yr^{-1} (Van Stan and Stubbins 2018). Dissolved organic nitrogen (DON) fluxes are also often elevated beneath tree canopies: in temperate forests, DON fluxes range 1.2–11.5 kg-N ha^{-1} yr^{-1} (Michalzik et al. 2001), and in tropical forests can reach ~15 kg-N ha^{-1} yr^{-1} (de Souza et al. 2015). Additional measurements of tree-DOM and associated nutrients are warranted given the sheer magnitude of reported DOC and DON fluxes via these pathways, the large fraction of DOM that is thought to be biodegradable (Howard et al. 2018; Qualls and Haines 1992), and potential impacts on soil biogeochemical cycling and aquatic ecosystems (see Chap. 8 of this volume).

5.3 Particulates: An “Unseen” but Abundant Component in Throughfall and Stemflow

In contrast to most dissolved solutes, the flux of particulate matter from canopies to soils via throughfall and stemflow has, until recently, received relatively little attention in the literature (Levia and Germer 2015; Levia et al. 2013). This particulate matter (operationally defined as >0.45 µm) has two primary sources: the atmosphere and the canopy. Particles are delivered from the atmosphere to vegetation canopies in rain and snow (wet deposition) and directly to canopy surfaces through gravitation settling, impaction, and diffusion (dry deposition; Weathers and Ponette-González 2011).

The main components of atmospheric particles include inorganic species, organic species, black carbon (black C), mineral species, and primary biological aerosol particles (Boucher et al. 2013)—all have both natural and anthropogenic sources. Globally, mineral dust and sea salt are the most abundant aerosols in the atmosphere by mass (Boucher et al. 2013). Arid and semiarid regions are the major emitters of soil dust but land-use practices that reduce vegetation cover and degrade soil surfaces also promote wind-blown soil losses (Ginoux et al. 2012). Inorganic species are emitted to the atmosphere as a result of wave generation (e.g., Na, Cl), volcanic eruptions (e.g., sulfate), and biological activity (e.g., sulfate). For sulfate and nitrate, emissions from fossil fuel combustion dwarf these sources, while agriculture, animal husbandry, and biomass burning are the dominant sources of ammonia (Sutton et al. 2013). Atmospheric organic particles have multiple sources including terrestrial and marine ecosystems, sea spray, fossil fuel, biofuel, and biomass combustion. Globally, biomass burning is the dominant source of black C to the atmosphere, but in urban and industrial areas, the primary source is diesel exhaust from fuel combustion (Bond et al. 2013). Primary biological aerosol particles, including bacteria, archaea, fungi and fungal spores, pollen, viruses, algae, lichens, and plant and animal fragments, are also emitted from terrestrial ecosystems before being deposited (Després et al. 2012).

Given high rates of wet and dry dust deposition (Lawrence and Neff 2009; Ponette-González et al. 2018), especially near source regions, throughfall and stemflow may carry significant amounts of mineral dust and associated particulate elements to the below-canopy environment with implications for soil formation and fertility (e.g., Arvin et al. 2017). Yet, we know of only one study that has quantified particulate mineral dust in throughfall and stemflow (Lequy et al. 2014). These fluxes were up to three times higher in throughfall compared to rainfall, negligible in stemflow (Table 5.2), and represented an important addition of particulate Ca, K, and P (Lequy et al. 2014). In contrast to mineral dust, black C (or elemental carbon) represents only a small fraction of suspended fine particulate matter (US EPA 2012). Nonetheless, its delivery to the soil via throughfall and stemflow and subsequent storage could contribute to climate change and air quality mitigation (Grieshop et al. 2009; Grote et al. 2016). In an urban environment in Japan, up to 1 kg ha^{-1} yr^{-1} of black C was deposited in throughfall to a temperate forest soil, twofold more black C than that deposited via rainfall (Sase et al. 2012). Quantifying black C fluxes to soils is, therefore, crucial to assess the role of vegetation in the capture, cycling, and fate of black C Rindy et al. (2019).

Table 5.2 Examples of particulate fluxes measured in throughfall and stemflow in temperate forests, except where noted. Units are in kg ha^{-1} y^{-1} unless otherwise noted. “Neg” indicates that fluxes were reported as negligible. “N.M.” is used when the analyte or flux was not measured. “N.R.” indicates that the information was not reported by the study

Analyte	Throughfall	Stemflow	Size fraction	References
Total particulate matter[d]	123 ± 63	Neg.	>0.45 µm	Lequy et al. (2014)
Particulate organic matter	~51–103	Neg.	>0.45 µm	Lequy et al. (2014)
Mineral dust deposition	~24–47	Neg.	>0.45 µm	Lequy et al. (2014)
Microparticulates	5–150	N.M.	N.R.	Carroll (1979)[a]
Particulate organic carbon	16.9–17.1	N.M.	0.45–500 µm	le Mellec et al. (2010)
Particulate organic nitrogen	3.2–3.6	N.M.	0.45–500 µm	le Mellec et al. (2010)
Particulate hexose-C	17.5	N.M.	0.45 µm–2 mm	Michalzik and Stadler (2005)
Particulate amino-N	6.9	N.M.	0.45 µm–2 mm	Michalzik and Stadler (2005)
Elemental carbon	1.3	N.M.	<2.5 µm	Sase et al. (2012)[b]
Radiocesium (^{137}Cs)	~6.7–7.0[c]	~0.1–0.3[c]	N.R.	Kato et al. (2012)

[a] As cited by Sollins et al. (1980)
[b] Urban site
[c] Units in Bq m^{-2} yr^{-1} (scaled from 5-month sampling period to annual flux)
[d] Total particulate matter = particulate organic matter + mineral dust deposition

Particulate radionuclide transport from canopy to soil has been quantified following nuclear accidents, such as the one at Chernobyl and more recently at Fukushima (e.g., Endo et al. 2015; Kato et al. 2012). Immediately following the Fukushima disaster, measurements of radiocesium (^{137}Cs and ^{135}Cs) in throughfall and stemflow were conducted in Japanese cypress and cedar forests (Kato et al. 2012). Throughfall was the dominant mode of Cs transport to the forest floor (Table 5.2), while Cs in stemflow was often undetectable. However, while throughfall fluxes did not differ between forest types, radiocesium in cypress stemflow was ~three–fourfold higher than in cedar. Approximately 18 months after the accident, annual fluxes of ^{137}Cs in a mixed deciduous forest and cedar plantation (~3.0 kBq m^{-2}; Endo et al. 2015) were similar to those measured by Kato et al. (2012) during their 5-month campaign.

Microplastics are another particulate pollutant whose abundance in the environment has recently garnered considerable attention (Auta et al. 2017). In Paris (Dris et al. 2016) and China (Cai et al. 2017), microparticle concentrations >1 µm in wet and dry deposition ranged from 36 to 110 particles m^{-2} day^{-1}, with higher concentrations at an urban compared to a suburban site (Dris et al. 2016). Dris et al. (2016) estimated that 3–10 tons of synthetic fibers were deposited to the city of Paris annually. Similar to other atmospherically deposited materials, microplastics may move from vegetation canopies to soils via throughfall and stemflow, with unknown effects on ecosystems.

Just like atmospheric particulates, canopy-derived particulates originate from a suite of diverse physical, chemical, and biological processes. For example, leaf abrasion, leaf senescence, wax degradation, consumer activity, insect chewing, pollen and seed production, death of canopy-dwelling organisms, and animal excretions all generate particulate matter. Despite the abundance of canopy sources, data on throughfall and stemflow particulate organic matter (POM) fluxes remain scant (le Mellec et al. 2010; Levia et al. 2013; Michalzik and Stadler 2005). Of the few studies that have been conducted, it is clear that POM fluxes can be large. An early study by Carroll and Pike [cited in Sollins et al. (1980) as a personal communication which appears to be based on data from Carroll (1979)], and a more recent study by Lequy et al. (2014) both estimated throughfall particulate fluxes on the order of 150 kg ha^{-1} yr^{-1} (Table 5.2). Unfortunately, to the authors' knowledge, similar estimates are not yet available for stemflow. These throughfall fluxes have been found to represent a major contribution to C and N budgets. Particulate organic C fluxes in a German temperate forest were about 17 kg ha^{-1} yr^{-1} while particulate organic N fluxes were ~4 kg ha^{-1} yr^{-1} (le Mellec et al. 2010). Relative to the dissolved fraction, these particulate C and N inputs comprised up to 30% of total organic C and up to 20% of total N. In another study by Michalzik and Stadler (2005), particulate amino-N in throughfall, an indicator of epiphytic microbial biomass, was twofold higher than dissolved amino-N. Although some insect infestations are increasing in both frequency and magnitude (e.g., Senf et al. 2017), we still know little about the influence of insect excretions and carcasses on throughfall and stemflow composition (Fig. 5.1). The potential for throughfall and stemflow to transport pollen and seeds also has not been studied. In the case of seeds, there are implications for species distributions, especially in arid systems where this form dispersal is more prevalent, or for epiphytic vascular plants with easily transported seeds, like orchids.

5.4 Life: Frontiers in Throughfall and Stemflow Research

A multitude of lifeforms are suspended alongside, and riding atop, the inanimate particulates in throughfall and stemflow just described (Fig. 5.1). The presence and relative abundance of life in the atmosphere surrounding plants, canopies, and tree stems themselves, as well as in the litter and soil layers have been, and continue to be, researched extensively with regards to their microbial, protist, and metazoan communities and their biogeochemical functions. The same is true for most terrestrial waters: the life contained within incident precipitation, phytotelma (particularly in carnivorous plants), soil water, groundwater, runoff, wetlands, and streams have received at least a few decades of consistent research attention. Interestingly, quantitative investigation of the life carried by throughfall and stemflow from plant canopies to the litter, soil surface, roots, bulk soil and into connected aquatic ecosystems is rare, with most research limited to the past few years (Bittar et al. 2018; Magyar et al. 2017b; Ptatscheck et al. 2018; Teachey et al. 2018). This is a severe paucity of information that equates to a critical knowledge gap—for the life within every major terrestrial habitat and water flux examined to date has been found to play fundamental functions within those settings. We review this nascent literature, beginning with the most and ending with the least studied lifeforms.

5.4.1 Fungi

The most studied lifeforms in throughfall and stemflow are fungi, particularly fungal spores (Gönczöl and Révay 2004; Sridhar and Karamchand 2009). Fungal spores are deposited to vegetation from the atmosphere and are liberated from fungi living within and upon plant canopies. Plants, especially trees, provide a wide variety of niches for fungi, resulting in saprotrophic, lignicolous, phylloplane, endophytic and phytoparasitic fungi as well as mycoparasitic, predacious or entomophilous, and lichenicolous taxa being found on leaves, branches, bark, and roots (Lodge and Cantrell 1995; Shaw 2004; Stone et al. 1996). Throughfall and stemflow wash off fungal spores from plant surfaces (Gönczöl and Révay 2004). Some canopy fungi utilize these hydrologic fluxes as a vehicle to passively transport their spores to the ground below (Lodge and Cantrell 1995; Stone et al. 1996), with spores being produced, liberated, and dispersed synchronously with storms (MacKinnon 1982). Thus, a substantial quantity and diversity of fungal spores are available to throughfall and stemflow. Since precipitation drainage can follow various pathways through the canopy and across various substrates—resulting in varying residence times—concentrations of fungal spores range widely from 10–16,000 spores L^{-1} for throughfall and 10–13,800 spores L^{-1} for stemflow (Sridhar and Karamchand 2009).

Net precipitation (i.e., throughfall and stemflow) fluxes, particularly stemflow, contain spores of taxonomically, morphologically and ecologically heterogeneous groups of fungi. Example spores observed in stemflow clearly illustrate this high morphological heterogeneity (Fig. 5.3). Yet, many spores carried in net precipitation have not been identified even to the generic level (Gönczöl and Révay 2003, 2004, 2006). Fungal taxa that are commonly known to be transported by stemflow include molds (*Aspergillus, Mucor, Penicillium* and *Rhizopus*) and yeasts (*Leucosporidium scottii*)—although only one study examined their cultivation from stemflow (MacKinnon 1982). Insect-pathogenic fungi are known to inhabit bark fissures along which throughfall and stemflow drain (Doberski and Tribe 1980). A commonly extracted insect-pathogenic fungus, *Beauveria bassiana*, has been sprayed onto trees in a manner meant to mimic and form stemflow, with the treatment being as effective as the use of chemical insecticides (Jakus and Blazenec 2011). Microsporidia, spore-forming unicellular parasites that were once considered protists but are now recognized to be a form or relative of fungi (Corradi 2015; Corradi and Keeling 2009), have been found to successfully transmit (30–57% transmission rates) between moths within a tree canopy under light simulated rain (Neidel et al. 2017).

Although these fungal taxa are known to be transported in throughfall and stemflow, most mycological studies focus on stemflow and morphologically complex spores with star-like (staurosporous) or thread-like (scolecosporous) structures, or spores from plant pathogens. The complex “branched” shape of stemflow-specific spores likely aids in their liberation from colonies, being more easily torn from spore-bearing hypha or filaments by water tension than a spore with less surface area. This morphology may then aid in dispersal, where the branched spore occupies several planes that enhance its chance of resuspension into passing rainwater drainage after settling (MacKinnon 1982). Surprisingly, many stemflow-dispersed stauro- and scolecosporous fungi, called “Ingoldian fungi” after the first mycologist who described them, C. T. Ingold (Ingold 1942), are common stream-dwellers that support aquatic food webs. Ingold, himself, discussed the branched spore morphology, suggesting three selective pressures responsible for branched spore shapes: (a) delayed sedimentation for dispersal, (b) settlement on a suitable substrate and (c) prevention from ingestion by invertebrates (Ingold 1942, 1953). Such spores are also thought to hold water, increasing the possibility of quick germination (Sridhar and Karamchand 2009). The following sections will discuss these groups of stemflow-dispersed fungi, with information on throughfall where available.

5.4.1.1 Stauro- and Scolecosporous Fungi

Stauro- and scolecospores were initially defined by Saccardo in the 19th century, later redefined by Kendrick and Nag Raj (1979), and first observed in stemflow-generated samples of foam at the base of a beech tree (Gönczöl 1976). The systematic study of these fungi in throughfall and stemflow was pioneered soon after (Bandoni 1981). These investigations showed that the number of conidia transported is variable but can be enormous for individual storms: hundreds or even thousands of conidia were detected in some milliliters of throughfall or stemflow (Gönczöl and Révay 2004). An inverse correlation between spore production and temperature was observed in Vancouver, Canada (MacKinnon 1982), possibly because precipitation is greatest during the coldest months of the year at that site. The onset of the rainy season, in any environment, is probably the time when most of the specialized fungi begin to grow again after having remained dormant or grown vegetatively during the dry season (MacKinnon 1982). Two different subgroups of stauro- and solecospores are recognized in throughfall and stemflow: “true” aquatic (or Ingoldian) fungi and “canopy” fungi.

Ingoldian fungi are well-known from streams, so their discovery in throughfall and stemflow in temperate and tropical areas was surprising (e.g. Czeczuga and Orłowska 1999; Révay and Gönczöl 2011; Sridhar and Karamchand 2009).

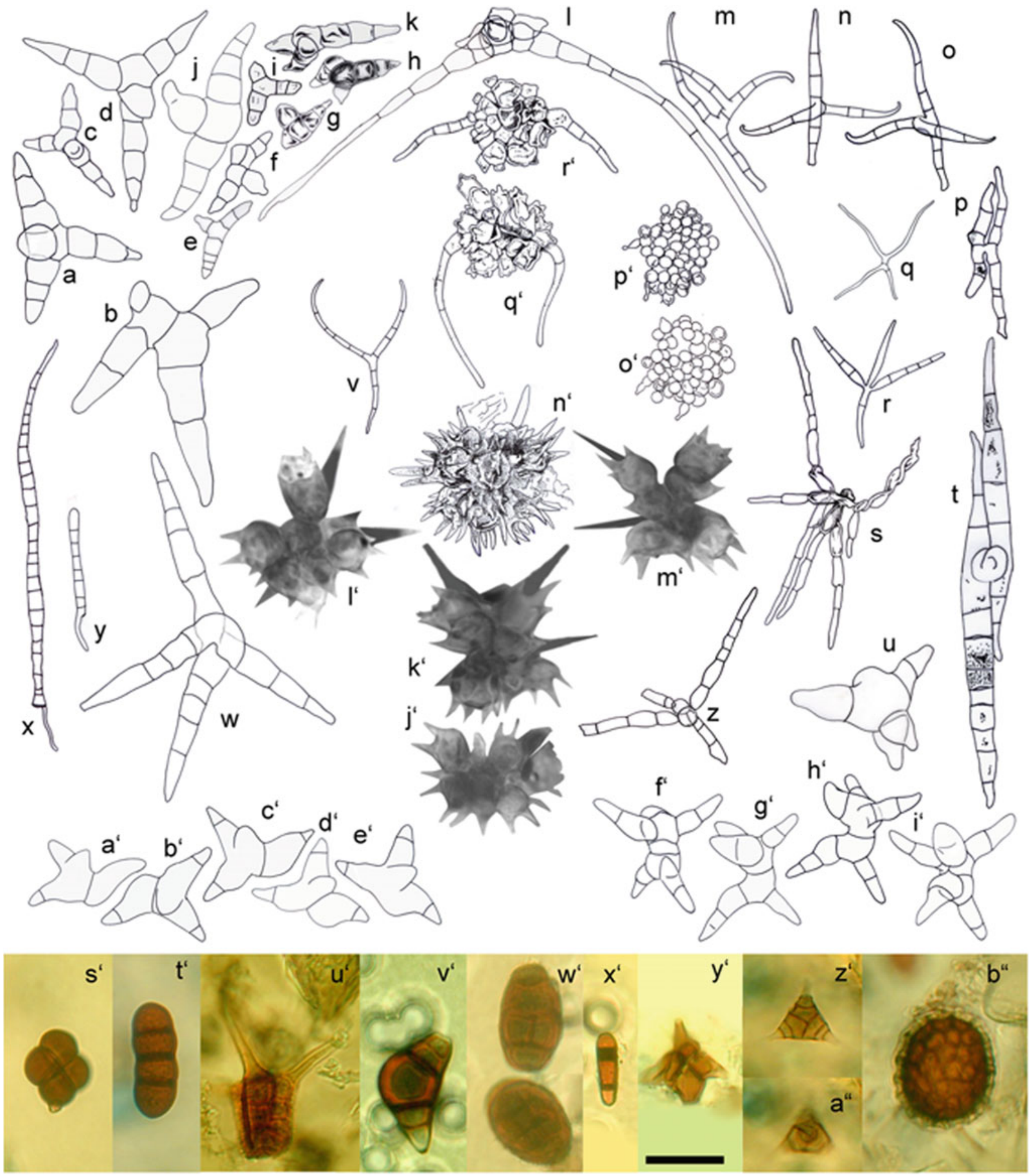

Fig. 5.3 Illustrations and photographs demonstrating the species and morphological diversity of fungal spores found in throughfall and stemflow. Although some of these spores are identifiable, many are unknown (l–p, s–u, z, a′–i′, q′–r′). Spores that have been identified include (a–k) *Tripospermum* spp., (q) *Curucispora ponapensis*, (r) *Isthmotricladia* spp., (v) *Retiarius* spp., (w) *Geniculospora* spp. (x–y) *Mycoentrospora* spp., (j′–n′) *Titea* spp., (o′–p′) *Atichia* spp., (s′) *Spegazzinia* spp., (t′) *Meliola* spp., (u′) *Tetraploa* spp., (v′) *Curvularia* spp., (w′) *Pithomyces chartarum*, (x′) *Triadelphia heterospora*, (y′) *Acrostaurus turneri*, (z′) *Diplocaldiella* spp., (b″) *Tilletia* spp. Scale bar = 20 µm. Collected by Kálmán Vánky. Photos and line drawings by Donát Magyar

After identification of these spores in net precipitation (Bandoni 1981), it was postulated that this fungal guild may “function in canopies much as classical Ingoldian aquatic hyphomycetes in streams” (Carroll 1981). Ingoldian fungal spores in throughfall and stemflow indirectly indicate their growth and sporulation in tree canopies, giving rise to fascinating mycological questions: Can Ingoldian fungi adapt to sporulation in free water in canopies? How can these fungi, well-known in-stream inhabitants, “go up” to colonize treetops? Sudheep and Sridhar (2010) suggest that the life cycle of Ingoldian fungi found in throughfall and stemflow alternates between aquatic and canopy habitats. Areas like the southwest coast of India that receive substantial monsoon rains may create long-lived, seasonal aquatic canopy habitats that enable Ingoldian fungi to inhabit tree canopies (Sridhar 2009). Some evidence suggests that these fungi can survive multiple environmental stressors, e.g., pollution or water intermittency (Vass et al. 2013) and that their teleomorph (i.e., sexually reproductive form) states enable them to survive under terrestrial conditions (Chauvet et al. 2016). There are many more speculations and hypotheses—most of which hinge on an improved understanding of interactions between Ingoldian spores and precipitation partitioning (Chauvet et al. 2016). Bandoni (1981) suspected that Ingoldian fungal spores formed in tree canopies could be directly broadcast to streams by stemflow, throughfall, or invertebrates. These fungi are also common in polluted urban canopies.

Throughfall and stemflow are also rich in other stauro- and scolecosporous spores unconnected to Ingoldian fungi. After their discovery, these fungi were labeled with tentative names like “arboreal aquatic hyphomycetes” (Carroll 1981) or “terrestrial aquatic hyphomycetes” (Ando 1992), but these names appear to be inadequate (see Gönczöl and Révay 2006). We now refer to these fungi as stauro- and scolecosporous canopy (SSC) fungi. Studies have since reported a diverse, global presence of SSC fungi in throughfall, stemflow, morning dew, snow, icicles and even honeydew (Ando 1984; Ando and Tubaki 1984; Czeczuga and Orłowska 1999; Gönczöl and Révay 2004; MacKinnon 1982; Magyar et al. 2005, 2016b; Sridhar et al. 2006). SSC fungi have apparently analogous or convergent evolution with the Ingoldian fungi of streams, as they face the same problem of running waters: spores are nonmotile, and passive transport is dominated by rainwater flowing through the canopy toward the soil (Chauvet et al. 2016). Perhaps colonization of stationary substrates in streams (litter, wood) and in stemflow (microlitter in accumulation areas) help some species overcome the risks of total removal and extinction due to unidirectional water flow. Intensive research for the source (i.e. sporulating colonies and habitats) of SSC fungi resulted in the description of new species (e.g., Magyar et al. 2017a, 2018; Magyar and Révay 2008, 2009a, b; Sokolski et al. 2006), but many SSC fungi in throughfall and stemflow remain unknown (Fig. 5.3) and their overall ecological role and source remain incompletely known (Révay and Gönczöl 2010).

Notwithstanding, the source and ecological role of known SSC fungi suspended in net precipitation fluxes are, so far, diverse and important. SSC fungi in net precipitation appear to live endophytically in plant tissues (Sokolski et al. 2006) while others may live in association with epiphytic ferns, bryophytes, and lichens (Sridhar et al. 2006). Most SSC species are likely saprotrophs, but predacious fungi of amoebae, nematodes, and rotifers may be transported by throughfall and stemflow. For example, *Dwayaangam heterospora* is known to parasitize eggs of rotifers and nematodes (Barron 1991) and *Lecophagus vermicola* hunts nematodes by capturing them on adhesive knobs that penetrate the victim’s cuticle. Clusters of colonized nematodes form a network to capture more prey (Magyar et al. 2016a). The branched spores of pollen-parasitizing fungi (like *Mycoceros* and *Retiarius*) are well-adapted not only for stemflow dispersal but also for trapping pollen grains deposited within bark fissures (Magyar et al. 2018). Protruding hyaline cells or horns on pigmented, multicelled spores (*Excipularia, Oncopodium,* and *Oncopodiella* spp., *Rebentischia unicaudata*) appear to be another adaptation for stemflow (Magyar and Révay 2009a, b). Clearly, within throughfall and stemflow there exists a rich community of SSC and Ingoldian fungi with myriad of potential sources and ecological interactions.

5.4.1.2 Plant Pathogenic (Phytopathogenic) Fungi

Many species of phytopathogenic fungi utilize throughfall (splash) and branch flow or stemflow to transport their spores or fruiting bodies, called “ascocarps.” For these fungi, accumulation areas (like water-filled tree holes or branch confluences) serve as reservoirs (or “spore banks”) that can be accessed and dispersed during precipitation. For powdery mildew, ascocarps are transported by stemflow. Their ascocarps (also called “chasmothecia”) are ~0.1 mm diameter fruiting bodies consisting of very tightly interwoven hyphae and many spores inside. These ascocarps are covered by elegant appendages with a terminal hook. Interactions between this fungus and precipitation partitioning are of major global economic importance, particularly for of grape powdery mildew (*Uncinula necator*) in cultivated grapevines (Pearson and Gadoury 1992). In this case, ascocarps are typically dispersed by late summer and transported by autumn rain from grape leaves to bark, where they overwinter (Pearson and Gadoury 1987). Hooked appendages seem to fasten water-dispersed ascocarps to bark fissures. Appendages of ascocarps may have similar functions than anchoring arms of staurosporous hyphomycetes. Anchorage hyphae bind the ascocarp to the mildew colony (Gadoury and Pearson 1988); stemflow dispersal occurs after necrosis and abscission of anchoring hyphae. A similar type of anchorage technique has been reported for *Microsphaera* species (Takamatsu et al. 1979) and similar detachment and dispersal mechanisms have been reported for *Pleochaeta* species (Kimbrough 1963). Potential population available for dispersal determines the incidence and severity of disease, but rain events determine the actual efficiency of transfer from infected organs to the bark of the vine (Emmett et al. 1992). Ascocarp dispersal is important in the epidemiology of grape powdery mildew because, although leaves, grapes and other organs where the powdery mildew feed are shed and destroyed in winter (Gadoury and Pearson 1988); stemflow transports inoculum to the bark, ensuring pathogen survival and placing spores immediately adjacent to emerging shoots in spring (Pearson and Gadoury 1987). Dispersal of *U. necator* ascocarps from parasitized organs to bark in vine plants via stemflow may, in fact, be a model of powdery mildews of other hosts, which are diverse, including apple, gooseberry, hawthorn, and oak (Gadoury and Pearson 1988).

Other spore types from phytopathogenic fungi, like the scolecosporous macrospores of *Fusarium* spp., are common in stemflow (MacKinnon 1982). It has been suggested that during the rainy season, stemflow plays a role in spreading the pathogenic *Fusaria* to unaffected cashew nut trees (Tibuhwa and Shomari 2016). A fungal species that causes peach scab, *Cladosporium carpophilum*, infects developing fruit during spring and early summer by long-distance airborne spores and short-distance dissemination via throughfall (splash) or stemflow (Lan and Scherm 2003). Waterborne spores have been observed to considerably contribute to disease development, primarily due to throughfall (splash) dispersal of conidia from twig lesions to the fruit—exclusion of throughfall splash with rain shields decreased disease severity by >90% (Lan and Scherm 2003). Stemflow from the twig to the fruit via the peduncle also contributed to scab development, as evidenced by the fact that exclusion of runoff by cotton wicks reduced disease severity by 32–45%; but this effect was not always statistically significant (Lan and Scherm 2003). Considering the vast biogeochemical and disease-related functions performed by fungi (Erwin and Ribeiro 1996; Gadd 2007), current knowledge on fungi in throughfall and stemflow is severely limited compared to other habitats and vectors.

5.4.2 Bacteria and Archaea

For decades, biogeochemists have speculated on the potential concentration and composition of bacteria and archaea in throughfall (Abee and Lavender 1972) and stemflow (Bollen et al. 1968; Ceccherini et al. 2008; Tarrant et al. 1968), and their role in N cycling. Increased N concentrations following precipitation–canopy interactions led some to hypothesize that N-fixing bacteria on leaves caused N-enrichment in throughfall (Abee and Lavender 1972) and that nitrifying (i.e., ammonia- and nitrite-oxidizing) bacteria on bark caused NO_3-enrichment in stemflow (Tarrant et al. 1968). Today, researchers continue to implicitly acknowledge the potential abundance of microbes in throughfall and stemflow by trying to inhibit their growth/metabolic activity between storm conclusion and sample collection. However, the sole study to assess throughfall for functional genes used by ammonia- and nitrite-oxidizing bacteria and archaea found only archaeal genes at concentrations <20 gene copies mL^{-1} (Watanabe et al. 2016). Phylogenetic analysis showed that throughfall contained taxa of ammonia-oxidizing archaea that were similar to archaea in phyllosphere communities which, in throughfall, may be free-floating or attached to canopy-derived particulates (Watanabe et al. 2016). A direct analysis of N-functional genes in bacteria or archaea suspended within stemflow has not been conducted, although it has been hypothesized that stemflow represents the link between similar ammonia-oxidizing bacteria communities in the bark and near stem soils of individual *Pinus nigra* trees (Ceccherini et al. 2008).

Only two studies report direct observations of bulk bacterial concentration and flux (Bittar et al. 2018) and community composition in throughfall and stemflow (Teachey et al. 2018), and both in one forest type in one location (Skidaway Islands, Georgia, USA). In these studies, bacterial concentrations in throughfall and stemflow, 10^4–10^6 cells mL^{-1}, were orders of magnitude greater than in bulk rainfall, 10^2 cells mL^{-1}, with mean concentrations significantly lower in throughfall than stemflow for both focal tree species (Bittar et al. 2018). In a single storm, bacterial stemflow fluxes from voluminous stemflow-generating trees—cedars partitioned up to 19% of rainfall as stemflow at this site (Howard et al. 2018)—were up to 200 times greater than any other net precipitation flux, reaching 28×10^9 cells m^{-2} h^{-1} (Bittar et al. 2018). At the stand scale, it was estimated that 1.5×10^{16} cells ha^{-1} y^{-1} were input to the forest floor by storms (Bittar et al. 2018). This number is an underestimate as it includes only "free" bacteria. Particle-attached bacteria could be $\sim 10^6$ cells cm^{-2} or 10^8 cells g^{-1} on leaf-derived particles (Bengtsson 1992; Remus-Emsermann et al. 2014). If just the free bacterial flux in throughfall and stemflow lysed and released their internal solutes, this could account for a quarter-to-half the net precipitation Na^+ and Cl^- fluxes from similar forests (Berger et al. 2008; Rodrigo et al. 2003) or, more modestly, 4–14% of particulate organic C flux (le Mellec et al. 2010). Still, total (free + particle-attached) bacterial flux may represent a substantial portion of nutrient flux to soils.

The first high-throughput bacterial community sequencing of throughfall and stemflow was recently conducted (Teachey et al. 2018) at the Bittar et al. (2018) study site. Although throughfall and stemflow interact with different phyllosphere bacterial communities (leaves versus bark), the bacterial taxa identified in these fluxes resembled those in rainfall, were not influenced by the presence or absence of arboreal epiphytic vegetation (specifically, *Tillandsia usneoides*), and varied significantly among storms. Thus, the Teachey et al. (2018) dataset suggests that throughfall may not disturb local phyllosphere communities—even at high rainfall intensities (31 mm h^{-1}). Many bacterial taxa found in throughfall have been linked to ecological functions at the surface and in the subsurface (see discussions by Teachey et al. 2018), indicating that there may be broad biogeochemical implications for forest floor ecosystems receiving this rapid microbial transfer from the phyllosphere. As these fundamental measurements and estimates have only just been published in the same year as this chapter is being written, the fate, transport and function of bacterial and archaeal communities in receiving systems remains elusive.

5.4.3 Protists

Protists are a diverse group of eukaryotes with cell structures similar to, but too simple to be classified as, plants, animals or fungi. Often protists are called plant-like (algae), animal-like (amoebas) and fungi-like (slime and water molds). All of these example protists reside within plant canopies as epiphytes or pathogens (Brooks et al. 2015; Garbelotto et al. 2003; Grandin 2011).

To the knowledge of the authors, no studies report concentration of protists in throughfall or stemflow for any plant. Yet, protists have multiple opportunities to interact with throughfall and stemflow across all plant types and climates. For example, in boreal forests, epiphytic algae can cover 13–24% of a single dominant tree species' leaf area (Grandin 2011), accumulating algal crusts over the years that then peel slowly and regrow (Søchting 1997). Throughfall and stemflow likely transport pieces of peeling algal crusts to the litter and soils below. Algal epiphytes can be abundant in woody and herbaceous crops (Brooks et al. 2015) and coastal vegetation (Fallon et al. 1985). For example, the standing dead leaves of a marsh grass with a native and invasive distribution along most coastlines throughout the globe, *Spartina alterniflora* (Zhu et al. 2013), can contain 1,500–440,000 cells m^{-2} of epiphytic algae (Fallon et al. 1985). Seeing as herbaceous plants are capable of generating substantial stemflow, 20–90% (Haynes 1940; Jefferies and MacKerron 1985), it is not unlikely that a portion of these algal epiphytes (which mostly reside on the stem) would be transported to the surface.

For amoebae, a throughfall exclusion experiment found that a type of amoeba which grow shells (i.e., "tests"), and are therefore called testate amoeba, decreased by 91% in the litter; this was attributed to shifts in litter moisture content and throughfall-associated nutrient supply (Krashevska et al. 2010). It is also possible that the substantial decline of testate amoebae with throughfall exclusion was simply due to the removal of its source. Thus far, every study of testate amoebas in vegetation canopies has revealed an abundant community: 10^2–10^4 shells cm^{-2} on trunk surfaces and nonvascular epiphytes in forests throughout Europe, Russia and Ecuador (Krashevska et al. 2010; Mazei et al. 2016; Payne et al. 2015); 1–35 individuals g^{-1} of *Sphagnum palustre* canopies in Polish peatlands (Mieczan 2007); and 10^2–10^3 individuals mL^{-1} of rainwater within vascular epiphytic "tank" plants (Carrias et al. 2012). The study on tank epiphytes found an abundant total protist community that could be mobilized by throughfall and stemflow: $10.1 \pm 29.4 \times 10^4$ algae mL^{-1}; $4.3 \pm 5.6 \times 10^2$ ciliates mL^{-1}; and $4.5 \pm 6.1 \times 10^4$ heterotrophic nanoflagellates mL^{-1} (Carrias et al. 2012).

Water molds can be significant plant pathogens (Garbelotto and Rizzo 2005), contributing multiple types of organic debris: Oogonia and antheridia for sexual reproduction, or asexual particles like sporangia, zoospores, and chlamydospores. Work on water molds within throughfall is limited, having only been "detected" in throughfall via qPCR in a single study (Benemann 2017). Slime molds, although present in crown humus (Stephenson and Landolt 2011) and the bark cortex (Everhart and Keller 2008) are also available for dispersal via throughfall and stemflow.

5.4.4 Multicellular Fauna

Precipitation can scour multicellular fauna from leaf, bark and epiphytic plant surfaces, including micro- and macrofauna. Microfauna suspended within throughfall and stemflow may include arthropods (like mites), crustaceans, tardigrades, rotifers, nematodes, among others. The only study known to measure microfauna focused on stemflow (Ptatscheck et al. 2018). The mean stemflow concentration of microfauna for three different trees was ~150 individuals L^{-1}; however, the maximum concentration exceeded 1,100 individuals L^{-1}. Microfauna composition in stemflow differed among the three tree species, with collembolans most abundant in *Quercus robur* stemflow (77%) and rotifers being most abundant in *Fagus sylvatica* (70%) and *Carpinus betulus* (69%) stemflow; tardigrades, nematodes and mites were observed in the stemflow of all study species (Ptatscheck et al. 2018). Stand scale estimates suggest 1.6 million microfauna can be transferred by a single tree's stemflow to soils each year—a number which compares favorably to mean annual abundance of soil microfauna (Ptatscheck et al. 2018). Many of the microfauna found in stemflow were soil colonizers and hyphal or bacterial feeders, highlighting their importance to soil biogeochemical cycling.

The size classification criteria for macrofauna is variable but is generally considered to be any animal that will not pass through 0.5–1 mm mesh. Although not directly measured, the presence of large macrofauna in throughfall and stemflow is often reported as a contributor to sample contamination. Future research should quantify the concentration, flux and/or composition of macrofauna transported in throughfall and stemflow. This includes the supply of arthropod carcasses to various habitats throughout vegetated ecosystems (e.g., tree holes, phytotelmata, litter, and soils) as they may supplement detrital resources.

5.4.5 Viruses

There are no data on the bulk virus concentration, flux or composition of throughfall and stemflow. However, dry deposition of viral particles has recently been estimated as $\sim 10^9$ viruses m^{-2} day^{-1} (Reche et al. 2018). Researchers have also found that within-canopy flowpaths during rainfall transport viruses and enable downstream infection. Viruses have a narrow window of opportunity for transmission and infection within-canopy ecosystems, since UV and water can breakdown the viruses' protective coatings within one day (Fuller et al. 2012). Host leaves or cadavers enable viruses to double their persistence time (Fuller et al. 2012), adding relevance to our call for attention to cadaverous macrofauna. An example highlighting the potential importance of throughfall and stemflow to viral transport, infection and even mortality can be found for the gypsy moth nuclear polyhedrosis virus (D'Amico and Elkinton 1995). Gypsy moths that are infected by this virus and die at the top of the canopy, putrefy there and contribute viruses to rainfall draining along throughfall and stemflow drainage paths. This can result in the infection and eventual death of gypsy moths throughout the canopy (D'Amico and Elkinton 1995).

5.5 Conclusions: Throughfall and Stemflow Response to Disturbance

Measurements of concentration and flux exist for many components suspended within throughfall and stemflow, albeit these measurements are sparse for DOM, and even rarer for particulates. Arguably, another major "unseen" component in throughfall and stemflow research relates to the natural and anthropogenic events and disturbances that affect their composition. Natural drivers at the top of this list include: phenology (Van Stan et al. 2012), synoptic meteorological conditions (Siegert et al. 2017), fire (Onodera and Van Stan 2011), seasonal dynamics of the phyllosphere microbial community (Copeland et al. 2015; Jumpponen and Jones 2010) and resident animals (Beard et al. 2002; Gilmore et al. 1984; le Mellec and Michalzik 2008).

Plant life events are visually obvious. They alter the amount of canopy surface available for dry deposition and leaching (Ponette-González et al. 2010) as well as the materials available for interaction with draining throughfall and stemflow, like bud break, leaf emergence (Van Stan et al. 2012) or secretion of glucose-rich nectar by extrafloral nectaries (Campbell et al. 2013). Phenology is linked to seasonal synoptic-scale weather conditions, which also influence the source and atmospheric path of aerosols and precipitation that eventually move to and through plant canopies (Siegert et al. 2017). In many vegetated ecosystems, synoptic conditions that create persistently dry regions lead to natural fire events even as anthropogenic activity affects fire and fire frequency. These fires have been shown to alter the flux of major plant limiting nutrients within throughfall and stemflow (Ponette-Gonzalez et al. 2016b; Wagner et al. 2018; White 2014). Many other discrete disturbance events remain relatively unstudied with regard to their impacts on throughfall and stemflow, including dust storms (Goudie 1978), hurricanes (Heartsill-Scalley et al. 2007), nuclear explosions (Endo et al. 2015), and insect infestations (Michalzik 2011).

Canopy fauna are rarely considered in estimates of precipitation–canopy interactions (Gilmore et al. 1984; Stadler and Michalzik 1998; Beard et al. 2002; le Mellec and Michalzik 2008), but plant canopies host abundant animal life, for example, 78–553 invertebrates m^{-2} in a tropical forest canopy (Ellwood and Foster 2004). These invertebrates as well as their amphibian, reptilian, and avian predators all excrete waste. When this waste is found in throughfall and stemflow samplers, the sample is often discarded as "contaminated." Perhaps throughfall and stemflow samples arrive to the sampler already rich in excrement? A few observations indicate this may be the case. Insect feces doubled total and dissolved organic C and N flux from throughfall during a lappet infestation (le Mellec and Michalzik 2008). The impact of feces and urine from just one species of tree frog in the Luquillo Experimental Forest (Puerto Rico) was estimated to alter throughfall concentrations of Ca, Fe, Mg, Mn, P, K, Zn, DOC, NH_4, and DON by 60–100% (Beard et al. 2002). Ant colonies actively engage with the canopy flowpaths that become throughfall and stemflow to prevent their colonies from being inundated: by spitting (Klein et al. 1993; Moog et al. 1997), carrying (Federle et al. 1998), and even communally urinating canopy water out of their nests (Maschwitz and Moog 2000). Bird roosting can coat entire tree canopies 1–2 cm thick with feces (Gilmore et al. 1984). Since canopy-dwellers each have their own distinct seasonal life cycles, could faunal excretion events represent a significant portion of the temporal variability left unexplained in precipitation–canopy dynamics?

We conclude with a two-pronged call for future research on throughfall and stemflow composition. First, there are numerous particulate and living elements that lack basic information with regard to their concentration and composition in throughfall and stemflow. Addressing even a portion of this knowledge gap is fundamental to our understanding of ecosystem functioning. Without a comprehensive understanding of ***what*** is in the precipitation reaching the soil or ground, we cannot know ***how much*** mass (of nutrients or metals or organisms) is available at the very start of terrestrial hydro-biogeochemical processes. Secondly, data on the dynamics of throughfall and stemflow composition is needed across temporal scales for various ecosystems. As throughfall and stemflow are the precipitation fluxes that initiate water-mediated biogeochemical processes in soils and downstream ecosystems, we suggest that future research aiming to evaluate hydrologic controls over ecosystem-scale elemental cycling help address these two objectives and monitor throughfall and stemflow composition.

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6 Spatial Variability and Temporal Stability of Local Net Precipitation Patterns

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Abstract

Redistribution of precipitation water by plant canopies increases the spatial variation of net precipitation at the surface, affecting soil moisture patterns, localized preferential flow, and soil biogeochemical processes. This chapter reviews methods for assessing and the current state of knowledge on spatial patterns of the two net precipitation components: throughfall and stemflow. Spatial variation in throughfall is caused by canopy morphology, including creation of rain shadows due to canopy topography and dripping points. Stand scale throughfall is less than above-canopy precipitation (in the absence of fog), however, localized throughfall receipt at the surface ranges widely—from negligible beneath dense canopy areas to 10 times greater than gross precipitation. Coefficients of variation of throughfall (CV_T) vary with canopy complexity, event size, and averaging period. In extreme cases, $CV_T > 1$ for single events in regions with complex canopies have been observed, but they decrease to <0.5 when considered over longer periods, and tend to be even lower in large events. Canopies of low complexity and small event sizes also tend to increase throughfall correlation lengths, which can be up to several meters in temperate regions and in leafed conditions. Arguably, the greatest variation in below-canopy precipitation is caused by the local input of stemflow. Local stemflow inputs at the base of individual trees on average exceed rainfall multifold (reaching 100 times), but local stemflow can also be less than rainfall. Stemflow from understory herbaceous plants, shrubs, and croplands can magnify rainfall by >2,500 times. Few studies select trees for stemflow measurement in a randomized fashion and in sufficient number; therefore, spatial CV_S between individuals are typically not reported. In the studies available $CV_T > 1$ are common and CVs of stemflow are typically much larger than those of throughfall. Differences between neighboring individuals are substantial, with tree species, tree size (e.g., canopy and stem size, number of branches) and crown architecture being reported as the most important drivers for observed variations. Both throughfall and stemflow contribute to comparatively stable net precipitation patterns over time, potentially much more so in stemflow compared to throughfall. For spatiotemporal patterns of solutes in net precipitation, little is known, and nothing is known about fine-scale patterns in particulates. Data collected to date are near-exclusively measured under overstory trees during rainfall, leaving the precipitation redistribution patterns that actually reach the surface beneath understory plants essentially unknown.

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Throughfall • Stemflow • Net precipitation • Spatial analysis • Coefficient of variation • Autocorrelation

6.1 Introduction

Plant canopies consist of spatiotemporally variable bark, leaf, and epiphyte elements, as well as other more ephemeral features, like flowers, seedpods, catkins, etc. The horizontal and vertical patterning of these elements creates a labyrinth through which hydrometeors must pass to reach the surface. Passage through the canopy reduces the total amount of precipitation available at the surface for infiltration and, just as importantly, introduces small-scale spatial variability (Hoppe 1896; Keim et al. 2005; Kimmins 1973; Metzger et al. 2017). Precipitation at the soil surface, below plant canopies, is called "net precipitation" and consists of two general hydrologic fluxes: throughfall and stemflow (Chap. 4). Throughfall is the portion of precipitation which drips (or, in the case of snow, mechanically unloads) from the canopy to the surface, after contacting canopy elements or by passing through gaps. It has been found to vary between windward and leeward sides of the canopy (Fan et al. 2015; Juvik and Nullet 1995; Scholl et al. 2007), canopy areas of leafy versus woody surfaces (Herwitz 1987; Nanko et al. 2011), and even between different leaf types (Brandt 1989; Crockford and Richardson 2000). Drip tips of different leaf structures differ in their capability to shed water, altering throughfall (Nanko et al. 2006, 2013). The most concentrated localized inputs of throughfall typically occur where water drains along branches and detaches prior to reaching the surface (Cavelier et al. 1997; Shuttleworth 1989; Zimmermann et al. 2009) as "drip points." Should precipitation drain completely down the plant's stem to the surface, it is considered stemflow. The result of precipitation through canopy gaps, drip points of throughfall from various leaf and woody structures, and stemflow is that precipitation can be magnified by >100 times at one microsite ("hot" spot, e.g., Herwitz 1986), while another nearby microsite receives much less water ("cold" spot, e.g., Lloyd and Marques 1988).

These markedly heterogeneous spatial net precipitation patterns have been invoked to explain several soil hydro-biogeochemical processes: variation of soil water content (Zehe et al. 2010) and soil water fluxes (Guswa and Spence 2012), including preferential flow (Klos et al. 2014), soil solution chemistry (Chang and Matzner 2000; Koch and Matzner 1993), soil formation and structure (Krutzsch 1855; Li et al. 2009), mineral weathering (Backnäs et al. 2012), soil microbial conductivity and community structure (Bundt et al. 2001; Moore et al. 2016; Rosier et al. 2015), soil micro-animal and metazoan community structure and function (Krashevska et al. 2012; Ptatscheck et al. 2018), and structuring the understory plant community (Andersson 1991; Barbier et al. 2008). Although the invocations are many, very limited experimental data support these myriad hypotheses as few studies have measured target soil properties in concert with fine-scale net precipitation patterns (e.g., Andersson 1991; Bouten et al. 1992; Metzger et al. 2017; Molina et al. 2019; Moore et al. 2016; Rosier et al. 2015). To fully assess these currently (often) hypothetical links between soils, throughfall, and stemflow, knowledge on the structure and causes of the input heterogeneity is commonly required. Moreover, determining an adequate sampling design should be based on information about the spatial variation (Zimmermann and Zimmermann 2014). This chapter, therefore, describes current methods for assessing throughfall and stemflow spatial patterns and their temporal persistence, and then discusses the state of knowledge regarding their principal drivers.

6.2 Assessing Spatial Patterns in Throughfall and Stemflow

6.2.1 Quantifying Spatial Variability of Net Precipitation

The most commonly reported distribution metrics of net precipitation, next to the arithmetic mean ($\bar{x}$) and standard deviation (s), is the coefficient of variation (CV):

$$CV = \frac{s}{\bar{x}} \tag{6.1}$$

Normalizing the sample standard variation by the arithmetic mean allows the comparison of variance between sites and events. It should be noted that the estimate of the sample variance requires considerable sampling effort. For example, without prior knowledge of the underlying variance, estimating the standard variation with 95% confidence within an error margin of 10% requires roughly 190 samples assuming an underlying Gaussian distribution (Greenwood and Sandomire 1950). Furthermore, suitability of those momentum-based metrics relies on the notion that the measurements are sampled from a Gaussian distribution and the sampling at different locations represents independent trials. The latter implies the absence of spatial autocorrelation. Both of those assumptions are often violated in net precipitation data. Most environmental variables are autocorrelated, that is, nearby values are more similar compared to those further away. Autocorrelation is well documented for throughfall, with correlation length ranging several meters (Zimmermann and Zimmermann 2014). To the best of our knowledge, autocorrelation for stemflow has not been evaluated, although there are some indications that stemflow may be affected by neighborhood and therefore might exhibit some degree of autocorrelation (Metzger et al. 2019). Furthermore, the underlying distribution of net precipitation data is rarely Gaussian. Both throughfall and stemflow spatial distributions are commonly skewed (Zimmermann and Zimmermann 2014) and typically include exceptionally high values like dripping points in throughfall (Keim et al. 2005; Lloyd and Marques 1988; Staelens et al. 2006; Voss et al. 2016) or extremely prolific stemflow on one tree (Metzger et al. 2019). At least that latter concern can be addressed by using quantile instead of momentum-based metrics for describing the distribution. The coefficient of quartile variation (CQV) is such an alternative metric describing the spread of the distribution:

$$CQV = \frac{Q_3 - Q_1}{Q_3 + Q_1} \tag{6.2}$$

based on quartiles (Q_1, Q_3 stand for the first, and third quartile) and has been reported alternatively to the coefficient of variation in net precipitation studies (e.g., Metzger et al. 2017). The coefficient of quartile variation (Eq. 6.2) is somewhat smaller than the classical coefficient of variation (Eq. 6.1) for normally distributed data.

Assessing the statistical properties of the underlying population requires both a dedicated sampling design and a sufficiently large sample size. A great deal of research has examined the appropriate spatial sampling for estimating the mean and the variance of the spatially distributed environmental variables (Strand 2017), including spatial averages of throughfall (Kimmins 1973; Thimonier 1998; Voss et al. 2016; Zimmermann and Zimmermann 2014; Zimmermann et al. 2010) and stemflow (Hanchi and Rapp 1997; Lewis 2003). The assessment of spatial variance structure of net precipitation components other than that of throughfall has received far less attention, and those that do exist are limited to throughfall (Voss et al. 2016). A reliable way to describe the spatial variation is by deriving a semivariogram (Fig. 6.1), which reveals at the same time the autocorrelation structure as well as the total variance (Oliver and Webster 2014). Voss et al. (2016) present a thorough modeling analysis of the influence of throughfall sampling and analysis decisions on the uncertainty of the variogram parameter estimates. They show that, in particular, for an appropriate estimate of the correlation length, very tight spacing of the measurements and large sample sizes (up to 500, but not smaller than 200 points) are required to ensure reasonable estimates for typical spatial throughfall patterns. Estimation of the sill (which corresponds to the variance) and nugget (Fig. 6.1) requires smaller but still considerable sample sizes ($\sim$200 points). Transect-based designs (as opposed to regular grid or complete random) using residual maximum likelihood (Oliver and Webster 2014) instead of the more

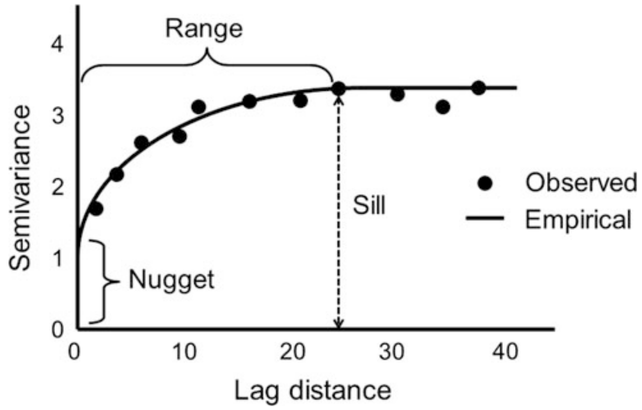

Fig. 6.1 An example semivariogram model that graphically illustrates estimation of the spatial structures in data. On the x-axis, the lag at which the change in semivariance steadies is the effective range. Two values on the y-axis are of interest: the semivariance at which the model's effective range is attained (sill), and the difference between the origin and the model y-intercept (nugget). As the origin of a semivariance model represents the case of sampling the same point (lag = 0), the nugget may represent error due to measurement or sources of spatial variation at lags less than the sampling interval (or both)

common methods of moments estimation decrease the required sample size and are therefore recommended for studies attempting to quantify throughfall variation. But in any case, for underlying distributions comparable to those of real throughfall spatial fields, sample sizes of 150–200 points are required for faithful estimates. Very few studies have performed this dense sampling regime (Voss et al. 2016; Zimmermann et al. 2016) and the required spatial arrangement and therefore in particular reported correlation length, but also estimates of variation need to be considered with caution.

Although stemflow reportedly has substantial influence on the spatial heterogeneity of biogeochemical fluxes and processes, there is strikingly little research explicitly describing subplot-scale spatial variability in stemflow (Holwerda et al. 2006; Metzger et al. 2017, 2019; Yankine et al. 2017; Zimmermann et al. 2015), and even fewer datasets based on a randomized or stratified selection of stemflow trees (Hanchi and Rapp 1997; Metzger et al. 2017, 2019; Zimmermann et al. 2015), which is, however, a prerequisite for evaluating spatial variation. Thus, only very few observations of spatial coefficients of variation for stemflow are available and we are not aware of any attempts for quantifying semivariograms of stemflow.

6.2.2 Temporal Stability of Patterns

Temporal stability refers to the similarity of spatial patterns of net precipitation between different rain events. A very common metric to investigating reoccurrence of spatial patterns is using normalized deviations ($\delta_{i,j}$) from the center of the observed sample (Vachaud et al. 1985). For example, when working with the arithmetic mean as the sample center:

$$\delta_{i,j} = \frac{x_{i,j} - \bar{x}_j}{\bar{x}_j} \tag{6.3}$$

where j stands for the event and $\bar{x}_j$ for the spatial mean of the event j. Some authors chose to use the median instead of the arithmetic mean for calculating $\delta_{i,j}$ in order to account for the often skewed distributions. $\delta_{i,j}$ has been used frequently for investigating temporal stability in distributed environmental variables, such as soil moisture (Vachaud et al. 1985), but has been used for throughfall (Keim et al. 2005; Staelens et al. 2006; Wullaert et al. 2009) and stemflow (Metzger et al. 2019) as well.

Another common method across disciplines for comparing temporal stability of spatial patterns is the correlation of the observations at one event with another event. More popular than the momentum-based methods (Pearson correlation coefficient) are quantile-based correlation measures, like the Spearman rank correlation (ρ) (Metzger et al. 2017; Staelens et al. 2006; Zimmermann et al. 2008), with the latter coefficient being less sensitive to outliers and the actual shape of the distribution:

$$\rho = \frac{Cov(rg_{X_j}, -rg_{X_l})}{s_{X_j} \cdot s_{X_l}} \tag{6.4}$$

where rg_{X_j} and rg_{X_l} refer to the ranks of the observations in events j and l, and s_{X_j} and s_{X_l} to the respective standard deviations.

Finally, one additional way of investigating temporal stability is by comparing the correlation length (Fig. 6.1) derived from the semivariogram across different precipitation events (Keim et al. 2005).

6.2.3 Quantifying Stemflow as a Point Source

Although stemflow supply [mm] (i.e., volume [L] over reference infiltration area [m^2]) is a measure of stemflow as a point source per hydrologic standards and is the most consistent measure to use alongside spatial plots of throughfall supply [mm], subplot-scale variability in stemflow generation has typically been discussed through the comparison of individual tree funneling ratios (F) or the ratio of stemflow supply [mm] to open or above-canopy precipitation [mm] or throughfall [mm] (Levia and Frost 2003; Levia and Germer 2015). F was first introduced by Herwitz (1986) as a metric describing the efficiency of trees to collect and generate stemflow:

$$F = \frac{V_{SF}}{P \cdot B} \tag{6.5}$$

where V_{SF} is the stemflow volume [L], P is the incident rainfall depth [mm], and B is the basal area [m^2], usually based on the diameter at breast height (DBH). $F > 1$ indicates that outward regions of the tree crown contribute to stemflow, and therefore precipitation is funneled toward the tree stem. However, there are now multiple F metrics that relate stemflow to different areas—individual tree basal area (Herwitz 1986), percent of stand area represented by basal area (Levia and Germer 2015), infiltration area (Carlyle-Moses et al. 2018), etc.—and to different notional hydrologic circumstances—e.g., rainfall or mean throughfall within the above-referenced areas in the absence of vegetation (see Chap. 4). Thus, it is recommended that stemflow supply [mm] and yield [mm] be reported alongside F and that the exact F applied to the stemflow data be carefully described in future stemflow research.

6.3 Spatial Structure in Net Precipitation Patterns

The first known assessment of fine-scale throughfall and stemflow spatial variability was conducted by Hoppe (1896). Three plots under spruce, pine, and beech were monitored during 2 consecutive years with 30 throughfall gauges and 6–9 stemflow gauges within 10 × 10 m plots (data recently digitized and presented in Friesen and Van Stan 2019). Per plot, 30 total throughfall gauges were deployed, 20 gauges aligned along a cross and the remaining 10 gauges were distributed at different distances from trees equipped with stemflow gauges. Hoppe (1896) noted high variability in relative throughfall (14–112% of open rainfall) and stemflow volume (0.1–200 L storm^{-1} tree^{-1}) across species and beneath the canopy of individual species, depending on multiple interacting factors, i.e., age, height, crown development, and storm characteristics. Influenced by Hoppe (1896), the first spatial fields of throughfall were monitored below single trees (apple, oak, maple, cedar, copper beech) under different phenological states (Linskens 1951, 1952). Based on 30 gauges per tree, isohyet-based throughfall

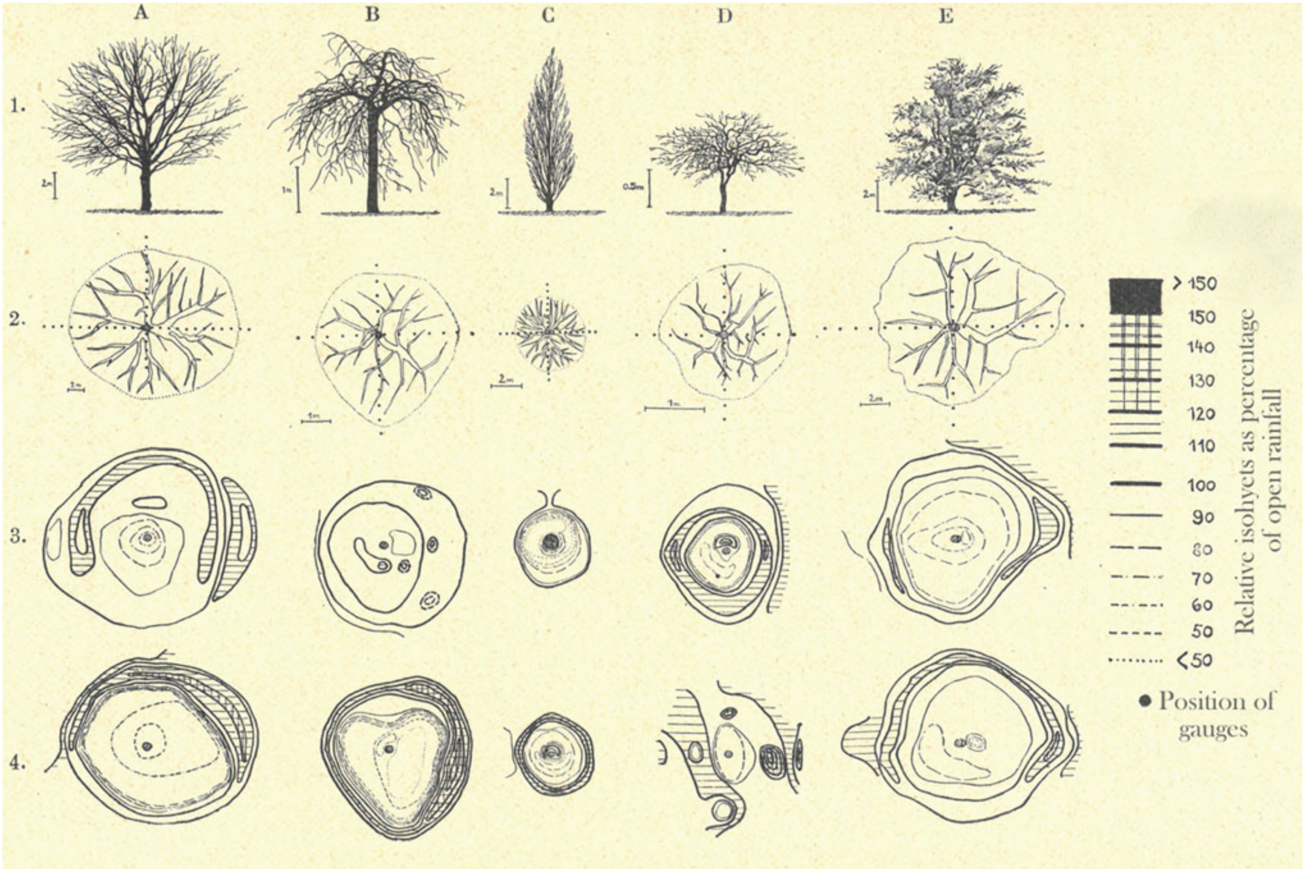

Fig. 6.2 Throughfall isohyets (percent of open rainfall) for leafless (row 3, winter) full-leaf (row 4, summer) states for five trees; **A** *Fagus silvatica* (L.) *forma artopurpurea,* **B** *Malus pumila forma pendula,* **C** *Quercus pedunculata* (Ehrh.) var. *fastigiata,* **D** *Acer palmatum* (Thbg.) var. *dissectum* (C. Koch) *forma viridis, and* **E** *Cedrus Libani*. Hatched regions show throughfall higher than open rainfall (translated from Linskens 1951)

maps were derived for full-leaf and leafless states (Fig. 6.2) and for 10 phenological states starting prior to budding and ending after leaf shedding (see Fig. 1 of Linskens 1952). With current knowledge of drip points, interpolation-based isohyets are probably not the most accurate; yet, these were the first studies to provide spatial fields of throughfall (Fig. 6.2). Results of these early studies found fine-scale throughfall patterns responded to the faster leaf growth on the south exposed sides as well as the effect of the predominant wind direction from the west—although measurements were limited to wind speeds <3 m s^{-1} (Hoppe 1896; Linskens 1951, 1952).

In the proceeding years, researchers continued looking at canopy structures to uncover drivers of throughfall spatial patterns (Helvey and Patric 1965; Keim et al. 2005; Kimmins 1973; Lin et al. 1997; Lloyd and Marques 1988; Voss et al. 2016; Wilm 1943; Zimmermann et al. 2009). These efforts identified a diversity of canopy structural traits that may be linked to throughfall variability (Levia and Frost 2006); however, the focus on deterministic relationships between throughfall and vegetation characteristics resulted in contradictory relationships across sites, for example:

- Is there more throughfall at the canopy edge or near the stem (Ford and Deans 1978; Herwitz 1987; Johnson 1990; Kittredge et al. 1941; Nanko et al. 2011)?
- Does this relationship depend on storm conditions, and if so, which storm conditions (amount, intensity, windiness, etc.) and to what extent (Kittredge et al. 1941)?
- Moreover, why does the presence of significant canopy biomass reduce throughfall in some cases (Hoppe 1896) but produce concentrated throughfall drip points in others (Cavelier et al. 1997; Keim et al. 2005)?

To answer these questions (and others), systematic research regarding major factors driving throughfall spatial patterns have turned to the development and application of statistical tools to decrease sampling errors (Hanchi and Rapp 1997; Lloyd and Marques 1988; Zimmermann et al. 2007; Zimmermann and Zimmermann 2014) and assess spatial heterogeneity to facilitate identifying broader drivers for those patterns (Cavelier et al. 1997; Keim et al. 2005; Voss et al. 2016; Zimmermann et al. 2007; Zimmermann and Zimmermann 2014).

Statistical measures of fine-scale throughfall and/or stemflow variability were not reported until Kimmins (1973); thereafter, coefficients of variation of throughfall have been found to vary with canopy complexity, event size, and averaging period (e.g., Table 6.1). In extreme cases, coefficients of variation in throughfall can be above 75% for single events in regions with complex canopies (Zimmermann and Zimmermann 2014) but decrease to values below 50% in cumulated events (Wullaert et al. 2009; Zimmermann et al. 2008, 2010; Table 6.1). Correlation lengths in throughfall increase with decreasing forest density (Zimmermann et al. 2016), ranging from roughly 1 m in tropical secondary forest with relatively high spatial throughfall variation (Zimmermann et al. 2016) to 6–10 m in natural temperate forests with comparatively low throughfall variation (Gerrits et al. 2010; Hsueh et al. 2016; Keim et al. 2005).

With there being a lack of studies reporting stemflow supply to the base of individual trees, we evaluate the heterogeneity of water input to the forest floor using the funneling ratio (see above). From the limited data available, stemflow patterns beneath all plant types are highly variable (Table 6.1). Funneling ratios >>1, implying substantial water subsidy near stems, have been reported from a wide range of ecosystems and tree species (Carlyle-Moses et al. 2018). However, also ecosystems with very low stemflow yield dominated by FR < 1, like mature pine forests (Yankine et al. 2017), have been reported (Van Stan and Gordon 2018). Those latter instances are difficult to identify in the literature, since many authors report “negligible stemflow” which does not allow discernment of whether stemflow funneling was present (or not) in those sites. Funneling may be substantial, even when average stemflow per plot area is very small, and, based on simulations during dry periods, may still affect deep percolation (Schwärzel et al. 2012; Spencer and van Meerveld 2016). Stemflow funneling can be substantial also in low vegetation such as in crops, like maize (Liu et al. 2015), or understory plants (Verry and Timmons 1977), which are rarely observed and reported. Thus, although potential importance of stemflow as a point input is widely recognized, there is comparatively little knowledge about the true variation of stemflow over a plot or different managed and unmanaged ecosystems, especially for crops and understory vegetation.

For those few studies that have assessed both coefficients of variation of throughfall and stemflow for different event sizes at the same site (Holwerda et al. 2006; Loustau et al. 1992; Metzger et al. 2017; Santos Terra et al. 2018), variation decreases with storm size for throughfall to $CV_T < 0.3$, while stemflow variation is generally elevated throughout all event size classes ($CV_S >> 1$) (Table 6.1). Thus, more prolific events, which contribute strongly to the annual sums, are characterized by rather homogenous canopy drip but very heterogenous stemflow yields.

Table 6.1 Studies reporting the coefficient of variation (CV, %) of throughfall and stemflow for multiple forest ecosystems. Information regarding each study's experimental sampling design ("design" and *n* storm^{-1}) is provided to contextualize the resulting CV. It is important to note that the proportion of throughfall and stemflow per storm is variable across storm size (as noted in the studies cited and Chap. 4 of this volume)

Study information	Throughfall			Stemflow		
Event type or size	Design	*n* storm^{-1}	CV %	Design	*n* storm^{-1}	CV %
Santos Terra et al. (2018)						
Semideciduous subtropical montane forest with summer precipitation (Minas Gerais, Brazil)						
All events, *n* = 52	–	–	–	Representative	32	103
Wet season events	–	–	–	Representative	32	58
Dry season events	–	–	–	Representative	32	196
Loustau et al. (1992)*						
Monoculture rows of Pinus pinaster in a temperate oceanic climate (Southwest France)						
0–5 mm, *n* = 13	Random	52	20–39	Representative	12	25–132
5–10 mm, *n* = 15	Random	52	16–30	Representative	12	30–143
10–30 mm, *n* = 41	Random	52	11–31	Representative	12	26–146
>30 mm, *n* = 17	Random	52	12–19	Representative	12	20–55
Metzger et al. (2017)**						
Natural humid continental forest, dominated by Fagus sylvatica (Central Germany)						
0–5 mm, *n* = 6	Stratified random	199	30–134	Total by subplots	65	87–800
5–10 mm, *n* = 5	Stratified random	200	21–42	Total by subplots	65	171–212
10–30 mm, *n* = 3	Stratified random	201	14–24	Total by subplots	65	157–203
Holwerda et al. (2006)***						
Lower montane tropical rain forest (Puerto Rico)						
Yearly sum	Stratified random	60	49	Representative	22	144

*Data digitalized from Tables 3 and 5 of the study

**Reported in study as coefficients of quartile variation, but here as coefficient of variation to allow comparison

***Stemflow was not measured through the entire study period on all trees, but sequentially for some events to establish a relation with gross precipitation, which was used subsequently to derive tree stemflow for the entire period

6.4 Potential Drivers of Spatial Variability

6.4.1 Throughfall

Broad canopy structural and meteorological conditions have been identified to influence throughfall patterns. For canopy structure, observations across forested sites find that variograms of throughfall volume can correspond to canopy size (e.g., radius) (Hsueh et al. 2016; Keim et al. 2005; Konishi et al. 2006), although this relationship weakens with increasing and decreasing canopy complexity. Indeed, uncorrelated throughfall patterns have been observed as canopy complexity increases with greater canopy overlap or interconnection by epiphytes/lianas (Zimmermann et al. 2007; Zimmermann and Zimmermann 2014) or when broadleaved canopies are leafless (or less structured, i.e., just branches) (Keim et al. 2005). Management of forest canopies, typically thinning, can reduce throughfall spatial variability through the introduction of greater gaps (Nanko et al. 2016; Sun et al. 2015). Storm conditions interact with canopy structural complexity to influence throughfall spatial variability. For low rainfall amounts, specifically those that do not saturate canopy storage, a higher spatial variability of throughfall quantity is reported (Bouten et al. 1992; Keim et al. 2005; Staelens et al. 2006; Zimmermann et al. 2008) and the coefficient of variation tends to diminish with increasing storm size (Carlyle-Moses et al. 2004; Holwerda et al. 2006; Lima et al. 2018; Llorens et al. 1997; Loustau et al. 1992; Metzger et al. 2017; Zimmermann et al. 2010). Few results have reported throughfall spatial variability or structure across other storm conditions beyond magnitude, like intensity (Loescher et al. 2002) and wind conditions (Nanko et al. 2011). Heavy winds and intensities may disrupt throughfall patterns by (1) mechanically shifting the location of canopy structures and (2) overwhelming established canopy drainage pathways. High wind speeds can cause entrained precipitation to detach from vegetation surfaces, preventing them from being transported to the termination point of any throughfall (or even eventual stemflow) drainage pathway (Hörmann et al. 1996; Nanko et al. 2006; Van Stan et al. 2016a). An interesting study in an evergreen montane rainforest (Ecuador) found no influence of meteorological conditions on throughfall patterns, ascribing all fine-scale variability to canopy structure alone (Wullaert et al. 2009).

6.4.2 Stemflow

Research comparing stemflow generation and F from individual trees indicate a hierarchy in potential drivers of stemflow spatial variability. The principal two overarching drivers include precipitation access and canopy structure. Stemflow generation requires precipitation; thus, access to precipitation is the major driver of stemflow volumes from individual trees of similar canopy structure—evidenced by the fact that stemflow volumes are typically strongly correlated with storm size ($r^2 > 0.9$; $p < 0.05$) across plant types (Aboal et al. 1999; Bellot and Escarre 1998; Ford and Deans 1978; Fowler 2015; Gordon et al. 2018; Horton 1919; Sadeghi et al. 2017; Sangster 1986; Sun et al. 2014; Tobón Marin et al. 2000; Zheng et al. 2018). The remaining variability around this direct relationship between storm size and stemflow volume has been explained by changes in rainfall intensity, intermittency, and wind conditions (Dunkerley 2014; Staelens et al. 2008; Van Stan et al. 2014; Zhang et al. 2017)—all of which likely alter stemflow due to enhancing or reducing access to precipitation. The degree of variability in any individual tree's stemflow generation left unexplained by rainfall amount is typically greater for trees with canopy structures that inefficiently funnel rain to the stem—e.g., *Quercus virginiana* v. *Juniperus virginiana* in (Van Stan et al. 2017)—highlighting the importance of canopy and forest structure. Indeed, stemflow responses to meteorological conditions are modulated by individual tree canopy structure and positioning in the forest, with studies having reported significant effects from tree size (Zimmermann et al. 2015), trunk lean and branch angle (Levia et al. 2015), bark roughness (Van Stan et al. 2016a), presence of epiphytic vegetation (Van Stan and Pypker 2015), and neighborhood conditions (Metzger et al. 2019).

The above understanding regarding stemflow variability from individual trees is primarily based on research from species with $F >> 1$ (Van Stan and Gordon 2018). Interestingly, for trees with $F < 1$, like some pine (Yankine et al. 2017), oak (Van Stan et al. 2017), and larch species (Toba and Ohta 2005), several differences may exist in their stemflow generation response to meteorological, canopy structural, and neighborhood conditions (Table 6.2). The stemflow response to rainfall amount among trees of similar size, or standardized by diameter (Aboal et al. 1999; Bellot and Escarre 1998; Ford and Deans 1978; Fowler 2015; Gordon et al. 2018; Horton 1919; Sadeghi et al. 2017; Sangster 1986; Sun et al. 2014; Tobón Marin et al. 2000), is often less variable than observed for species with $F < 1$, like *Pinus palustris* (Yankine et al. 2017) or epiphyte-laden *Quercus virginiana* (Van Stan et al. 2017). This difference may be a result of greater trunk or epiphyte water storage and surface roughness, which could increase in-canopy residence time and allow greater opportunity for dynamic intrastorm meteorological conditions to divert stemflow to storage, evaporation, or throughfall (Table 6.2), also see conceptual model in Fig. 4 of Van Stan et al. (2014). Another difference can be found in the stemflow response to greater woody canopy material (Table 6.2), which has been observed to increase individual tree stemflow generation for smooth-barked tree species, like *Fagus sylvatica* (Levia et al. 2015) or *Ailanthus altissima* (Sadeghi et al. 2017); however, for rough-barked

Table 6.2 General differences and commonalities in the stemflow response to independent storm, canopy, and stand variables between tree species with funneling ratios (F) > 1 and $F < 1$. Direct (+) and indirect (−) relationships are indicated with symbols

	Stemflow response from:	
Independent variable	$F > 1$	$F < 1$
Rainfall amount (mm)	+ ($r > 0.9$)	+ ($r > 0.8$)
Rainfall intensity (mm h^{-1})	+	+
Woody volume (m^3)	+	−
Trunk lean (degree)	−	−
Primary branch angle (degree)	+	+
Mean neighborhood height (m)	−	−

Pinus palustris, an increase in woody volume as derived from lidar point clouds decreased stemflow production (Yankine et al. 2017). This is likely due to the differing hydrological implications of extra woody biomass between tree species with $F > 1$ versus those with $F < 1$, where any added water storage incidental to an increase of woody volume is minimized for smooth-barked species due to the thin, unabsorbent bark covering (Van Stan et al. 2016b), ultimately promoting rainwater drainage. Alternatively, added branch or trunk volume in the canopy of rough-barked trees would be accompanied by large water storage demands (see Chap. 2) of a degree antithetical to stem drainage.

For understory vegetation, access to precipitation for stemflow production is not solely related to the relative neighborhood height and other structural factors (Metzger et al. 2019), but may be more likely related to overstory throughfall patterns (Gordon et al., in prep). Understory plants that receive throughfall drip points, for example, may be able to generate greater stemflow volumes and funneling ratios than those that are situated beneath gap throughfall or cold spots of throughfall (especially if canopy structure of the understory plants are similar). This is intuitive but in reality hypothetical, because no experimental results exist evaluating understory stemflow patterns and patterns of overstory throughfall due to the fact that sampling throughfall prevents stemflow from being generated. In the absence of significant understory hydrometeorological data, it is currently hypothesized that, similar to overstory variability in stemflow, the understory plant canopy structure is likely to play a dominant role in stemflow variability. In fact, calls to examine understory stemflow generation have been long-standing (Price et al. 1997; Price and Watters 1989; Verry and Timmons 1977; Yarie 1980).

6.5 Temporal Persistence of Throughfall and Stemflow Patterns

Most studies on the temporal autocorrelation of throughfall spatial patterns found that it can be strong—persisting for months, across seasons, and throughout years (Keim et al. 2005; Metzger et al. 2017; Raat et al. 2002; Staelens et al. 2006; Wullaert et al. 2009; Zimmermann et al. 2007, 2008, 2009). The time span over which throughfall spatial patterns persist can depend on the vegetation type. For deciduous forests (where studies are limited to the temperate climate zone) seasonal changes in leaf state (from leafed to leafless) alter throughfall spatial patterns and reduce their temporal persistence (Staelens et al. 2006). Temporal stability of throughfall patterns was also found to respond to season in a wet–dry tropical forest, gaining temporal stability as the rainy season progresses and new growth completes (Zimmermann et al. 2008). An evergreen coniferous forest canopy produced high temporal persistence of throughfall spatial patterns, assumedly as a result of greater temporal stability in leaf state (Raat et al. 2002; Zimmermann et al. 2009). Only one study known to the authors has reported temporal autocorrelation for stemflow patterns and found it to be considerably stronger than observed for throughfall patterns (Metzger et al. 2017), especially for large events, which contribute substantially to the water budget.

6.6 Spatiotemporal Patterns of Net Precipitation Chemistry

Variability in the fine-scale patterns of elements dissolved in throughfall and stemflow can be as high or higher than observed for net precipitation water fluxes (Kimmins 1973); yet, few studies have reported the spatial variability of throughfall chemistry (Beier et al. 1993; Duijsings et al. 1986; Lawrence and Fernandez 1993; Raat et al. 2002; Staelens et al. 2006; Whelan et al. 1998; Zimmermann et al. 2007, 2008), even fewer studies have examined the temporal persistence of throughfall chemistry or deposition (see discussion by Zimmermann et al. 2008), and no studies known to the authors have explicitly examined the fine-scale spatial variability of stemflow chemistry or its temporal persistence. Moreover, no studies have examined the spatial variability or temporal persistence of particulate matter (living or nonliving) fluxes in throughfall or stemflow.

Deposition data from throughfall chemistry studies show that spatial *CV* differs for each solute at all studied forests (Table 6.3). Forest types also differ in which solute varies most or least. For example, in a lower montane rainforest, throughfall NO_{3^-} deposition was extremely variable, $CV > 250\%$ (Zimmermann et al. 2007), yet spatial variability for this same solute was <10% in a temperate beech–oak forest (Duijsings et al. 1986). Spatial variability in throughfall (and stemflow) solute flux may be due to canopy structural variability. This is because canopy structure can alter (i) how much atmospheric dryfall is captured locally (i.e., is an area sheltered or exposed?) (Lindberg and Lovett 1985), (ii) what tissue surfaces, including epiphytes, are locally available to leach, take-up, or transform solutes in draining throughfall or stemflow

Table 6.3 Spatial variability of throughfall deposition (expressed as coefficient of variation [%]) for select solutes across a range of forest types

Forest type	NH_4^+	K^+	NO_3^-	SO_4^{2-}	Reference
Tropical rainforest	29	40	47	52	Zimmermann et al. (2008)
Tropical rainforest	60	68	252	48	Zimmermann et al. (2007)
Temperate oak–beech	15	21	9	13	Duijsings et al. (1986)
Temperate beech	23	13	14	16	Staelens et al. (2006)
Temperate spruce	44	32	39	41	Beier et al. (1993)
Temperate spruce–fir–pine	74	56	76	32	Lawrence and Fernandez (1993)
Temperate fir	26	18	19	26	Raat et al. (2002)
Temperate spruce	31–170	11–43	23–63	23–44	Whelan et al. (1998)

water (Olson et al. 1985; Van Stan and Pypker 2015), (iii) the extent of local canopy soil development (Gotsch et al. 2016) or accumulation of hyper-enriched detrital microenvironments, like water-filled tree holes (Schmidl et al. 2008), and (iv) the presence and abundance of epifaunal activity, like insect infestation (Michalzik 2011) or waste production from insectivores (Beard et al. 2002). These biogeochemical drivers of spatial variability in throughfall (and stemflow) chemistry are temporally variable—i.e., atmospheric chemistry, the configuration of canopy tissues, and the life cycle of epifaunal communities vary with season—thus, the temporal stability of throughfall solute deposition is weak (Raat et al. 2002; Staelens et al. 2006; Zimmermann et al. 2008). Since soil physicochemical and biological processes can significantly immobilize and transform solutes in net precipitation fluxes (Howard et al. 2018; Kirkham and Bartholomew 1954), this weak temporal stability indicates that throughfall solute deposition patterns may rarely induce unique biochemical microhabitats in soils, even if they are able to influence surficial soil solution chemistry. In fact, few studies have reported biochemical microhabitats in soils related to throughfall deposition, e.g., microsites of increased soil salinity alongside shifts in microbial community structure and N-functional genes have been identified on sandy soils beneath persistent epiphyte cover in a maritime setting (Moore et al. 2016; Rosier et al. 2015). It has been more common to observe soil microhabitats near stems, where stemflow infiltrates (Andersson 1991; Ceccherini et al. 2008; Chang and Matzner 2000; Gersper and Holowaychuk 1971; Rosier et al. 2016); however, no studies known to the authors have ruled out the myriad other near-stem processes at play in soils and the one study with long-term controls over abiotic factors found that stemflow is one of a suite of factors influencing near-stem soil microhabitats for dryland shrubs (Li et al. 2017).

6.7 Conclusions

Local spatial patterns of net precipitation supply (throughfall and stemflow) to the soil surface and their temporal persistence or variability are relevant to surface hydrological and ecological processes, yet few comprehensive direct observational connections have been made in this regard. Most studies report throughfall and/or stemflow means, fewer report variation, and very few report temporal persistence or spatial patterns like autocorrelation. For the solutes transported by net precipitation to the surface, studies reporting local spatiotemporal variability are scarcer than for the water itself. Few data exist that consider the entire field of net precipitation supply, i.e., both throughfall and stemflow. Extant data to date are almost exclusively measured beneath overstory forest trees during rainfall, leaving the actual precipitation redistribution patterns that reach the surface beneath the understory generally unknown across every precipitation type and during condensation events. In fact, fine-scale spatiotemporal variability of throughfall and stemflow in low vegetation (including grasslands, crops, urban gardens or bio-swales, etc.) is generally unknown. It is clear that, for the actual precipitation water (and related solute and particulate) fluxes that reach the Earth's surface beneath vegetation, our understanding is severely limited. The extensive knowledge gaps identified herein augment those identified in the preceding throughfall and stemflow chapters (Chaps. 4 and 5). Prioritizing an improved conceptualization of how net precipitation and its transported constituents vary across scales is clearly merited, as meteoric water and elemental supply are fundamental inputs at the start of any terrestrial ecohydrological process.

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$S^{t+1}=S^{t}+\int_{t}^{t+1}(P_r-E-D)\,dt$

7 Global Modeling of Precipitation Partitioning by Vegetation and Their Applications

Ethan D. Gutmann

Abstract

The partitioning of precipitation by vegetation canopies into throughfall and evaporation can have a large effect on water availability for both ecosystems and human consumption. Canopies are often the first point of contact between precipitation and the land surface, yet the complexity and inaccessibility of this interface make measurements extremely difficult, and as a result our attempts to understand and model the relevant processes are only weakly constrained. Here, we describe common approaches to modeling canopy interception processes, particularly in global models. These models use a wide variety of parameterization and parameters internally, suggesting that we do not have a good understanding of how to model canopy interception on a global scale. To begin to quantify how big a problem this may be, we present a few ideal model experiments exploring a range of modeling approaches and assumptions to document what effect these choices have on the projection of changes in inputs to the eco-hydrologic system. Perhaps unsurprisingly, these effects vary with vegetation type and density, as well as precipitation type, intensity, and changes in precipitation. In many cases, these effects are likely dwarfed by the uncertainties in predicted changes in regional climate, but not accounting for our lack of certainty in canopy processes can lead to an overconfident, and in some cases likely incorrect, projection of future changes in water availability. This should serve as a call to action for those studying canopy interception processes to better document and consider how theories can be put into a numerical framework.

Keywords

Model • Weather prediction • Vegetation • Interception • Evaporation • Climate hydrology • Streamflow

7.1 Introduction

Models provide a mechanism to test the combined effect and interrelationships between all our hypotheses of how a system works, and models provide a key application by allowing scientific discoveries to translate into better predictions for streamflow forecasting, climate assessments, weather prediction, and a host of other human endeavors. As such, the canopy interception and precipitation partitioning model behavior can be thought of as an emergent hypothesis of how one component of the larger earth system works. This book is filled with discussions ranging from detailed implications of vegetation precipitation partitioning on soils (Chap. 12) and biogeochemistry (Chap. 11), to the processes controlling evaporation (Chap. 3), stemflow and throughfall (Chap. 2), to microbiology (Chap. 14), and economic impacts (Chap. 15). Many of these processes are represented in land surface and hydrology models, though often in fairly simplistic ways (storage and drip), and many of these are absent from them (e.g., stemflow, microbiology, and throughfall heterogeneity). Here, we review the state of canopy interception modeling in widely used hydrology and land surface models.

A review of this sort is critical for this book because it puts the state of operational modeling in perspective of the amazing advances described elsewhere in this book and will perhaps allow the reader to see where new observations could

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be used to improve models, where models can (or cannot) be used to inform our study, and where existing theory and observations can be better integrated into these models.

Our ability to model precipitation partitioning by vegetation is important for a wide variety of applications. One of the primary effects of canopy interception on the water cycle occurs through its impact on evaporation (Porada et al. 2018). Intercepted canopy water is stored on a widely distributed surface (leaves, needles, stems, and epiphytic vegetation) often high off the ground where the wind is stronger, and thus evaporative fluxes can be much greater. Our ability to model this evaporation is important for water resources because evaporated water is lost as supply to local soil water recharge and streamflow. In addition, this evaporation has multiple important effects on the weather; evaporated water is added back to the atmosphere thus influencing downwind humidity and precipitation (van der Ent et al. 2014), and that evaporation has a local cooling effect thus decreasing the local air temperature (Davies-Barnard et al. 2014). Both evaporation and the simple mechanism of storing water in the canopy affect streamflow (Swank and Douglass 1974). The evaporative losses mean that water is not added to the soil where it is slowly released into the stream channel, and the temporary storage in the tree canopy provides an additional buffer that can modulate flooding (Trabucco et al. 2008). Particularly when one considers snow in the vegetation canopy, there is a major additional effect on the surface energy budget through the change in the albedo of the land surface; this affects the weather, and integrated over time this can affect the climate system as a whole (Lundberg and Halldin 2001; Sturm et al. 2017). Warming air temperatures will set off a positive feedback, known as the snow albedo feedback, wherein warmer temperatures cause snow to fall as rain (or to melt earlier), which in turn results in less sunlight reflected and that leads to warmer air temperatures (Letcher and Minder 2015).

7.2 Precipitation Partitioning Models

A computer model is little more than a collection of equations integrated forward in time numerically. These equations relate state variables, e.g., the amount of water stored in the canopy, with input forcing, e.g., the precipitation rate and air temperature, to calculate the fluxes, e.g., throughfall, stemflow, and evaporation. The most common such equation is the simple mass balance for the canopy (Eq. 7.1)

$$\frac{\mathrm{d}W_\mathrm{c}}{\mathrm{d}t} = f_\mathrm{veg}(P - E - S - D) \tag{7.1}$$

where W_c is the intercepted water in the canopy [kg m^{-2}], t is the time [s], P is the precipitation rate [kg m^{-2} s^{-1}], f_veg is the fraction of land covered by the vegetation canopy, E is the canopy evaporation rate [kg m^{-2} s^{-1}], S is the stemflow flux [kg m^{-2} s^{-1}], and D is the drip throughfall from the canopy [kg m^{-2} s^{-1}]. For the fraction of land beneath canopy gaps, this "gap throughfall" is equivalent to P. This seemingly simple equation is at the heart of precipitation partitioning, how much water falls to the surface as drip, throughfall, and stemflow, and how much is "lost" to evaporation. Note that each one of those parameters and fluxes has one, or in some cases many, equation associated with them. For example, the evaporation rate is often computed based on a Penman–Monteith (Penman 1948; Monteith 1965) combination equation which couples the moisture and energy budget after making some simplifying assumptions (Eq. 7.2), though simpler methods exist based on radiation (Priestley and Taylor 1972), or temperature (Thornthwaite 1948). However, evaporation can also be computed through numerical integration over the separate energy and moisture components.

$$E_\mathrm{p} = \frac{\Delta(R_\mathrm{n} - G) + \rho_\mathrm{a} c_\mathrm{p}(e_\mathrm{s} - e_\mathrm{a})/r_\mathrm{a}}{\Delta + \gamma} \tag{7.2}$$

E_p is the potential evaporation, Δ is the slope of the saturation vapor pressure curve, R_n is the net radiation, G is the ground (or stem or leaf) heat flux, ρ_a is the density of air, c_p is the specific heat of air, e_s is the saturated vapor pressure of air, e_a is the actual vapor pressure of the air, r_a is the aerodynamic resistance to turbulent fluxes, and γ is the psychrometric constant (66 Pa K^{-1}).

This deceptively simple mass balance equation can be solved by a variety of approaches. In field-based studies, it is not uncommon to combine the measurement of some of these components to derive the others; indeed, evaporation is often simply calculated from observed precipitation and interception loss (Friesen et al. 2015). In more theoretical approaches, an estimate of average evaporation rates over a storm can be combined in an analytical solution for total evaporative losses (Gash 1979). For more predictive, applied models, a numerical solution is typically used as in the pioneering work of Rutter et al. (1971). These are the types of models explored here; however, many developments in analytical model frameworks, such as variable storage capacity (Bulcock and Jewitt 2012), or the impact of epiphytes (Van Stan et al. 2016) are important and their inclusion in predictive models needs to be better explored.

Here, we present an overview of the canopy interception component of common models of the land surface and provide some examples showing how the canopy interception model affects our estimate of precipitation partitioning, including changes in that partitioning in a future climate.

7.3 Model Overviews

There are a very large number of modeling systems in various states of operational usage around the world. Here, we focus primarily on widely used hydrology, snow, and land surface models. The hydrology models are often used in water resource planning and streamflow prediction, the snow models are commonly integrated into another land surface model, or they are used for specific snow-related applications (e.g., avalanche prediction or ecosystem studies), while the land surface models often provide the lower boundary condition in atmospheric models, both for the climate system and for weather prediction. There are a few cases of overlap, e.g., the National Water Model (Cosgrove 2017) uses the Noah-MP land surface model (Niu et al. 2011) and as such it is not discussed under hydrology models, though it used for hydrologic applications.

One thing that most if not all models have in common is the value they gain from remotely sensed vegetation properties. To apply any model globally, or even regionally anywhere in the globe, one must have a way of describing what is unique about that location for the model. The most commonly prescribed parameters are soil classifications to describe soil hydrology, which is very poorly constrained (Gutmann and Small 2005), topography, which is relatively well known, and vegetation (Gutman and Ignatov 1998). Vegetation is typically described based on very broad classifications of plant functional types, e.g., evergreen needleleaf, broadleaf deciduous, or grassland, and such broad classifications are available globally (Fig. 7.1), typically derived from the seasonal time series of a remotely sensed vegetation index such as the Normalized Difference Vegetation Index (NDVI; Tucker 1979) (Fig. 7.2), or more recently, the Enhanced Vegetation Index (EVI; Huete et al. 2002). While such broad classifications may seem like a poor representation of the world to a researcher focused on evaluating the difference between an Aspen (*Populus tremuloides*), an Oak (*Quercus*), and a Maple (*Acer*), these are the classifications currently supported by available datasets, and arguably the classifications for which models can presently be parameterized. Along with the plant functional type maps they enable, these vegetation indices are also used to

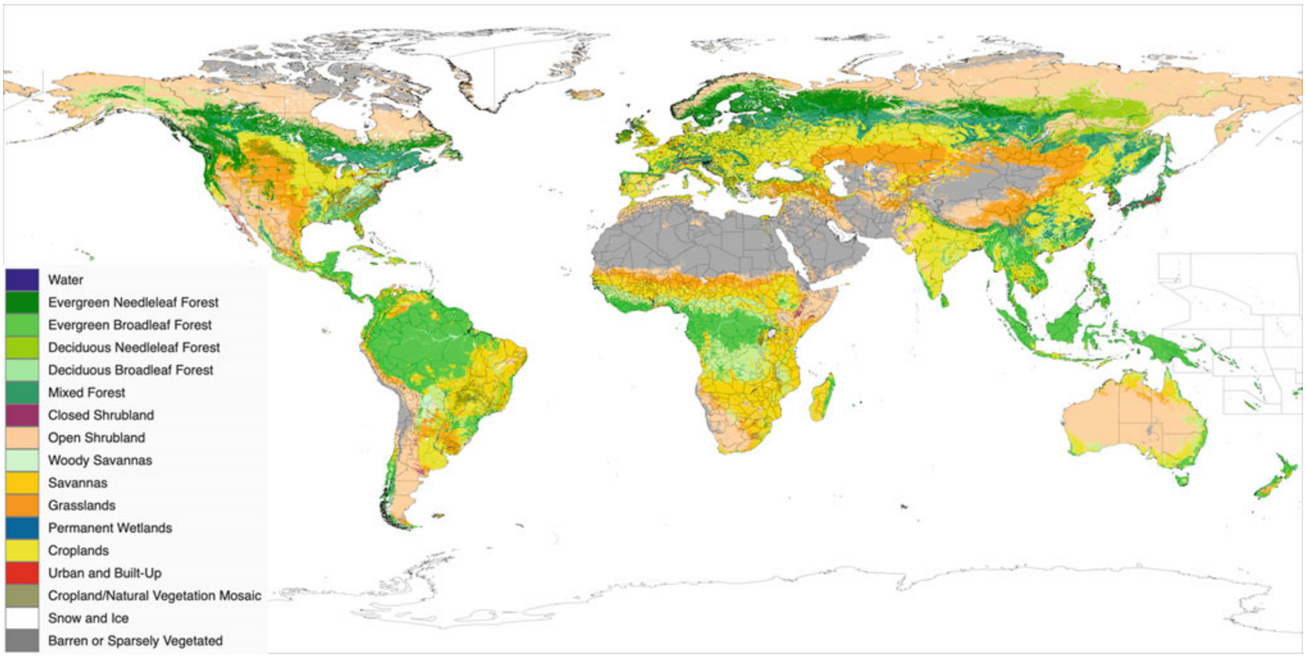

Fig. 7.1 Global land cover map derived from the NASA MODIS sensor in the International Geosphere-Biosphere Programme (IGBP) class definitions, such classes are widely used in land surface models as the primary method of distinguishing different vegetation types. Creative Commons License: https://commons.wikimedia.org/wiki/File:Land_cover_IGBP.png

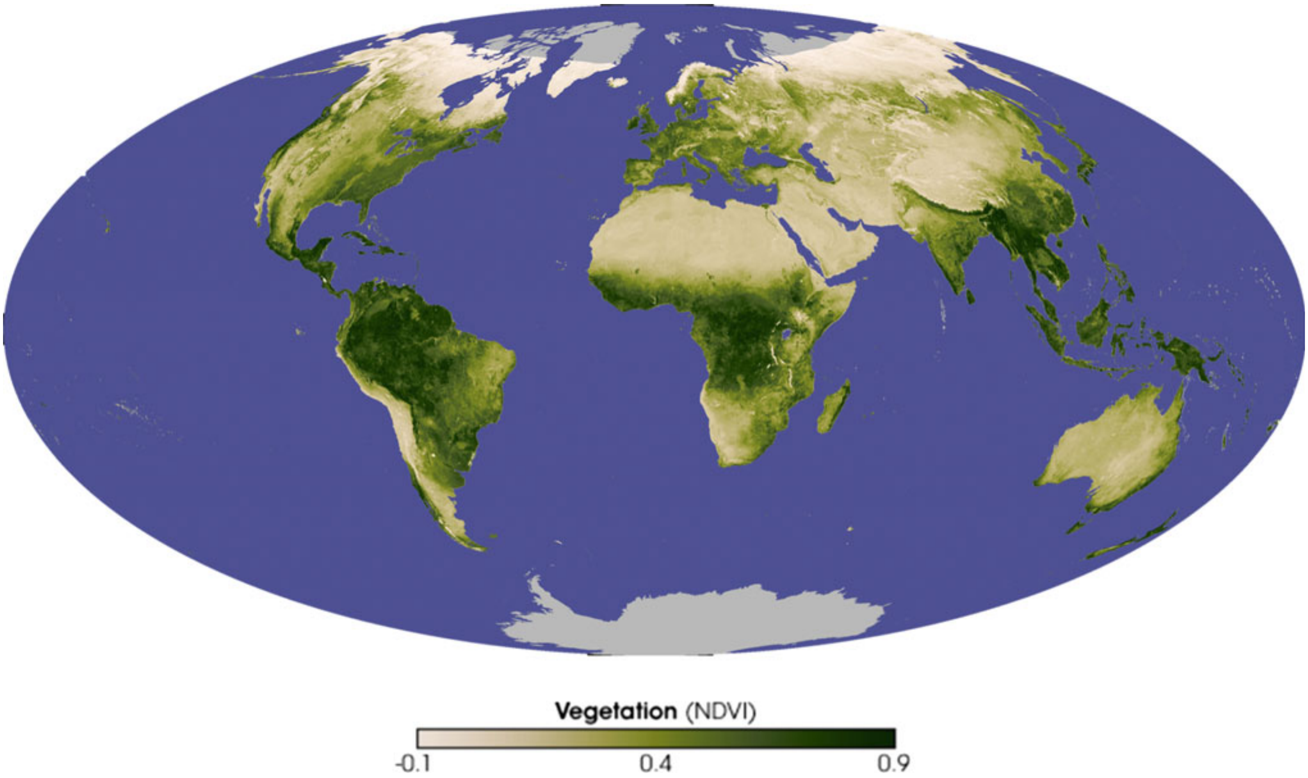

Fig. 7.2 Global map of the normalized difference vegetation index widely used to measure vegetation abundance, e.g., leaf area index or vegetation fractional cover for parameters in global land surface models. Creative Commons License: https://commons.wikimedia.org/wiki/File:Globalndvi_tmo_200711_lrg.jpg

estimate the abundance of different plant types through a simple time mean, a climatological annual cycle, or as a transient evolution of the surface. While these vegetation index datasets and plant functional types are widely used, little consideration is given to understanding the uncertainty in these datasets themselves (Hartley et al. 2017).

In reviewing the section headings and list of models below, one may note that modelers have an affinity for acronyms; one has to admire the ingenuity and creativity that has gone into such a large collection of names. Although the following sections cannot document all details of all canopy models, these sections attempt to highlight many of the key features of a variety of models.

7.3.1 Hydrology Models

Hydrology models typically focus on the prediction of streamflow for either streamflow forecasting and flood applications or water resource management. These models can be global in nature, as is the case for the Global Flood Alert System (GFAS; http://gfas.internationalfloodnetwork.org/gfas-web/), continental such as the US National Water Model (NWM; Cosgrove 2017) (https://water.noaa.gov/about/nwm), regional, as many applications of the Variable Infiltration Capacity (VIC) model that is often used for regional water resource management applications, or local as many implementations of the Sacramento Soil Moisture Accounting model (Sac-SMA) used by the River Forecast Centers (RFCs) in the US National Weather Service.

7.3.1.1 Variable Infiltration Capacity (VIC) Model

The Variable Infiltration Capacity (VIC) model (Liang et al. 1994) is widely used in water resource and hydrologic applications, including climate change impact studies (Brekke et al. 2009), and long-term surface monitoring in continental domain models (Mitchell 2004) for, e.g., drought monitoring (Shukla and Wood 2008). VIC represents vegetation heterogeneity within a grid cell using multiple independent land cover tiles. VIC uses the Penman–Monteith combination equation to estimate potential evaporation rate. This potential evaporation is then modified by the amount of water in the canopy (Eq. 7.3). This formulation permits evaporation to occur at the maximum potential rate limited only by atmospheric demand when the canopy is saturated, and this rate decreases as the amount of water in the canopy, and thus the exposed surface area of water, decreases.

$$E_c = \left(\frac{W_i}{W_{im}}\right)^{\frac{2}{3}} * E_p * \frac{r_w}{r_w + r_o} \tag{7.3}$$

where E_c is the canopy evaporation, W_i is the intercepted canopy water, W_{im} is the maximum intercepted canopy water content for the given vegetation type, E_p is the potential evaporation rate, r_w is the aerodynamic resistance to evaporation between leaves in a canopy and the air above the canopy, and r_o is the architectural resistance specific to each vegetation type. W_{im} for rain is 0.2 * the Leaf Area Index (LAI) after (Dickinson 1984). In some models, the stem area index (SAI) can be included in this relationship.

Canopy snow in VIC is treated explicitly, with the canopy interception rate of snow being equal to the precipitation rate scaled by a vegetation efficiency parameter of 0.6 (Storck et al. 2002) up to a maximum interception capacity given by the product of the LAI, the ratio of observed interception capacity and LAI, and a leaf area ratio as a function of temperature. Snowmelt in the canopy is calculated directly from a modified energy balance, and rain on snow in the canopy is also intercepted according to the water holding capacity of the snow in the canopy. Unloading of snow from the canopy is computed relative to drip of excess meltwater using a ratio of 0.4 (Storck et al. 2002). For a recent comprehensive review of canopy snow processes in VIC, see Andreadis et al. (2009).

7.3.1.2 Precipitation Runoff Modeling System (PRMS)

The Precipitation Runoff Modeling System (PRMS; Leavesley et al. 1983) is a popular hydrology model developed by the United States Geological Survey (USGS). It is used to produce streamflow forecasts and has been used to evaluate climate impacts on hydrology (Markstrom et al. 2012). For rain, PRMS computes available canopy storage as the difference between the maximum storage capacity and the currently stored water. Any precipitation in excess of this available storage is partitioned into throughfall (Markstrom et al. 2015). The spatial discretization of PRMS permits divisions of the area to be modeled into Hydrologic Representative Units (HRUs), with no expectation that HRUs follow a grid, and the precipitation partitioning calculation is tracked for each HRU independently based on the vegetation cover density and type in each HRU. Like VIC, evaporation from the canopy is based on a background potential evaporation rate; however, PRMS provides multiple methods to estimate that background evaporation rate or potential evaporation can be provided as an input forcing dataset. Snow interception and rain interception are treated discretely in PRMS, but only one can be present in the canopy at a time, and the maximum interception capacity is simply defined for each. Snow sublimation from the canopy is treated as a fraction of the potential evaporation rate.

7.3.1.3 Regional Hydro-Ecologic Simulation System (RHESSys)

The Regional Hydro-Ecologic Simulation System (RHESSys; Tague and Band 2009) is an eco-hydrology model, primarily used in research applications, and is often applied for the hydrologic implications of land cover change studies. RHESSys also maintains a detailed biogeochemical state and can be used to dynamically change the vegetation as it runs. RHESSys can include multiple canopy layers in each horizontal patch, and, like PRMS, horizontal patches are not constrained to be on a grid. As a result, RHESSys can simulate the extinction of incoming radiation, precipitation, and wind through multiple canopy layers and different layers can have different properties, thus permitting the explicit simulation of a vegetation overstory and understory. As with PRMS, RHESSys follows a simple relationship that permits the canopy to collect any additional rain up to the maximum storage capacity. RHESSys differs in that it permits throughfall from one canopy layer to be intercepted by lower layers, with the effect cascading down through as many layers as are specified. Snow is treated in the same way, but with a different maximum interception capacity. Evaporation from the canopy is assumed to occur at the potential rate; however, RHESSys computes a new potential rate for each layer in the canopy based on changes in radiation extinction through the canopy (following Beer's Law), and reductions in wind speed through the canopy, in addition, sunlit and shaded portions of the canopy are treated independently.

7.3.2 Land Surface Models

Land surface models are primarily used in atmospheric models to provide the lower boundary condition for both weather and climate simulations. As such, these models often focus much more heavily on processes that affect land–atmosphere interactions. So, while hydrology models such as RHESSys and PRMS often use a daily time step, most land surface models use an hourly or sub-hourly time step to explicitly resolve the diurnal cycle. When run coupled to an atmospheric model, they may even be integrated into sub-minute intervals.

7.3.2.1 Community Land Model (CLM)

The Community Land Model (CLM; Lawrence et al. 2019) provides the lower boundary condition for the Community Earth System Model (CESM; Hurrell et al. 2013). CLM has a long history focusing on biogeochemical fluxes, e.g., carbon, as well as the hydrologic cycle. This focus is evident in that a paper describing improvements to the canopy model in CLM does not mention interception, focusing instead on gross primary production and transpiration (Bonan et al. 2011). That is not to say that CLM has a simplistic canopy representation, merely to illustrate that the development focus of most models is not on canopy interception. The treatment of canopy effects on net evaporation is discussed in detail in other publications (Lawrence et al. 2007), and version 5 includes significant advances in the canopy hydrology representation, in particular, version 5 now tracks canopy snow and liquid water independently and incorporates a canopy snow unloading term as a function of wind speed. The interception of rain and snow occurs at the precipitation rate scaled by a function of leaf and stem area. "Drip" of both snow and liquid from the canopy occurs to remove any canopy water stores in excess of the maximum interception capacity, with different capacity factors for rain and snow. One of the more interesting additions in CLM's treatment of snow in the canopy is the ability to unload snow as a function of wind speed (Eq. 7.4) and temperature (Eq. 7.5).

$$q_{\mathrm{u,w}} = \frac{uW_{\mathrm{cs}}}{1.56 * 10^5\,\mathrm{m}} \tag{7.4}$$

$$q_{\mathrm{u,t}} = \max(0, \frac{W_{\mathrm{cs}}(T - 270\,\mathrm{K})}{1.87 * 10^5\,\mathrm{K\,s}}) \tag{7.5}$$

where $q_{\mathrm{u,w}}$ is the unloading due to wind, u is the wind speed, W_{cs} is the canopy snow, $q_{\mathrm{u,t}}$ is the unloading due to temperature, T is the air temperature, and all other values are constants with units. All subject to the constraint that the unloading flux may not exceed the canopy snow content. In addition, the wetted fractions of the canopy (including rain and snow separately) are used when estimating canopy albedo and evapotranspiration fluxes.

7.3.2.2 Noah Multi-physics (Noah-MP)

The Noah Multi-Physics (Noah-MP; Niu et al. 2011) model is an important LSM to consider because it currently forms the basis of the United States National Water Model (NWM) and it provides the lower boundary condition for the Weather Research and Forecasting model (WRF; Skamarock and Klemp 2008). The National Water Model provides real-time forecasts of streamflow and other hydrologic variables for the United States National Oceanic and Atmospheric Administration (NOAA). WRF is perhaps the most widely used weather and regional climate model in the world.

The canopy interception model in Noah-MP treats liquid and frozen water separately, and permits both to be present simultaneously with conversions handled explicitly. Noah-MP also tracks unloading of snow from the canopy, though now explicit representation of drip from liquid water is mentioned in the canonical reference (Niu and Yang 2004). The interception of snow in Noah-MP is calculated as a function of the remaining storage capacity of the canopy, and the snowfall rate (Eq. 7.6), and the maximum interception capacity is itself calculated as function of both the combined Leaf and Stem Area (LSAI) as well as the density of fresh snow (Eqs. 7.7 and 7.8). The interception capacity for rain is simply ten percent of SLAI.

$$R_{\mathrm{load}} = (M_{\mathrm{ice,max}} - M_{\mathrm{ice}})\left(1 - e^{\frac{-\rho_{\mathrm{s}}\Delta t}{M_{\mathrm{ice,max}}}}\right)/\Delta t \tag{7.6}$$

$$M_{\mathrm{ice,max}} = \alpha(0.27 + \frac{46}{\rho_{\mathrm{s}}})\mathrm{LSAI} \tag{7.7}$$

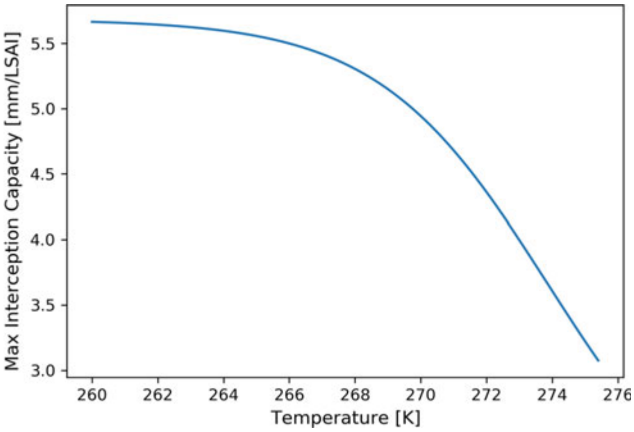

Fig. 7.3 Maximum canopy snow interception per unit of leaf and stem area in the Noah-MP land surface model as a function of air temperature

$$\rho_s = 67.92 + 51.25e^{(T_{\text{air}}-273.16)/2.59} \tag{7.8}$$

where R_{load} is the total snow interception rate, $M_{\text{ice,max}}$ is the maximum canopy snow interception capacity, M_{ice} is the current intercepted snow mass, P_s is the snowfall rate, ρ_s is the density of fresh snow, ρ is a constant (approximately 6), LSAI is the combined leaf and stem area index, and T_{air} is the air temperature. The combination of these equations means that new snow density increases with increases in air temperature near freezing; however, the maximum interception capacity actually decreases with increases in air temperature (Fig. 7.3). This has important implications for any climate change analysis as increases in temperature will be expected to decrease canopy snow interception, and thus associated evaporation and sublimation. Noah-MP also includes a wind and temperature modification to snow unloading from the tree canopy as in CLM, though it also includes no effect of wind on the interception of snow or rain.

7.3.3 Other Models

We have necessarily described just a few of the many hydrology and land surface models that exist. The reader is referred to the literature for a description of, for example, the Hydrology Tiled ECMWF Scheme for Surface Exchanges over Land (H-TESSEL; Balsamo et al. 2009), Interaction Soil–Biosphere–Atmosphere (ISBA; Noilhan and Mahfouf 1996), ORganizing Carbon and Hydrology in Dynamic EcosystEms (ORCHIDEE; Krinner et al. 2005), Simple Biosphere model (SiB; Sellers et al. 1986), Joint UK Land Environment Simulator (JULES; Best et al. 2011), the Community Atmosphere Biosphere Land Exchange (CABLE; Wang et al. 2011), and the Structure for Unifying Multiple Modeling Alternatives (SUMMA; Clark et al. 2015a, b) models.

7.4 Future Model Improvements

Perhaps, the most important needs in developing better models of interception are centered on the parameters used in these models. While there are many different approaches to representing the fraction of water that is concentrated in stemflow, the volume of water intercepted, the canopy drip rate, etc., all of these approaches have parameters within them that vary dramatically in field studies, often by an order of magnitude (see Chaps. 2–4). While the experimentalist can simply document these variations, the modeler is required to put something into their model. In most cases, this results in a simple average value from whatever field studies the modeler is able to find in the literature. In reality, it is likely that a stochastic approach to modifying parameters in space and time might represent a more realistic spatiotemporal variability. However, when judging a model based on its predictions, it is very often the average values that will do the best by the common mean squared error metric. This does not make these values correct. Importantly, many different modeling groups have used data from the same, relatively small, set of field experiments (e.g., FIFE and BOREAS), as such these semi-independent models are in reality being constrained to match the same limited set of data, and as such cannot be used to represent independent samples for, e.g., uncertainty quantification (Clark et al. 2016; Abramowitz et al. 2019). There is an important need in the community for a much larger sample of observational studies to be collated for future model development and testing of canopy interception processes. There will also be a substantial benefit in a wider review of the literature to incorporate additional processes such as stemflow (Zhang et al. 2015). For example, functions exist relating rainwater unloading as a function of wind speed (Hormann et al. 1996) that could be added to models in the future. Because some of these land surface models are developed in an open environment, it is possible for the canopy interception community to coordinate with the developers and add such improved formulations and parameters directly to the source code and parameter files.

In streamflow modeling, often the individual parameters of interest are intrinsically impossible to measure (e.g., related to widely distributed transfers of water deep in the soil); as a result, many model parameters are instead calibrated based on a goodness of fit metric to some holistic behavior of the system, e.g., observed streamflow. A similar approach might be taken to improving estimates of landscape-scale effects of canopy interception on water resources, land surface albedo, and evaporative processes, though such macroscale calibration runs into significant problems due to the compensating effects of multiple parameters, as such it must be heavily guided by theoretical understanding and, when possible, distributed measurement as from satellite-based sensors.

Improving parameters can focus on several aspects. Experimentalists and theorists can work to explain the source of the variability such that a model can incorporate additional processes to predict the correct parameter. Modeling efforts also benefit from better spatial measurements of the parameters more directly, e.g., through better remotely sensed products. For example, past work (Gutmann and Small 2010) has attempted to use Earth's surface skin temperature measurements over time, in comparison to model predictions, to modify the soil parameters and thus improve evapotranspiration estimates in a model. This worked reasonably well in areas without dense vegetation cover; however, in areas with dense canopies, the thermal properties of the surface might be better related to the canopy structure and water status, including intercepted rainwater and vegetation drought stress. Indeed, the NASA ECOSTRESS sensor is designed to exploit precisely this relationship by using very high-resolution and high radiometric precision to better monitor vegetation water stress characteristics. Similarly, remotely sensed snow-covered area can be used to estimate when snow is present in the forest canopy, and this could be used to improve canopy snow interception characteristics including interception efficiency and melt rates or mechanical unloading parameters. Novel remote sensing products such a vegetation optical depth (Rodríguez-Fernández et al. 2018) may provide additional useful canopy structure information on global scales.

While more direct measures of properties via remote sensing estimates may have the best chance of improving models in the short term, without a reliable understanding of these parameters and the causes for their variations, it becomes impossible to predict how they will change in the future. This is important for studies that attempt to predict the effect of, e.g., forest thinning, wildfires, changing forest species distributions, or global climate changes that can both alter the forest and the weather conditions in which the forest is operating. Such understanding and capability require a quantifiable mechanistic model of the forest canopy behavior, most likely beyond what the current state of the art in dynamic vegetation models (see: Fisher et al. 2017) are capable of.

7.5 Example Macroscale Applications

In this section, we step away from the details of model parameterizations and instead examine the results of these models. We illustrate how one model (VIC) portrays the partitioning of evapotranspiration into the transpiration, bare soil evaporation, and canopy evaporation components across the Contiguous United States (CONUS). We then compare the estimates of canopy evaporation in VIC with those in CLM, and finally we examine the changes in the canopy water storage term in a climate change scenario using the Noah-MP land surface model within the Weather Research and Forecasting (WRF) regional climate model.

7.5.1 Modeled Evapotranspiration Partitioning

When looking at standard output of the VIC hydrology model (Liang et al. 1994), it is clear that canopy evaporation will only be important in some seasons and regions. Figure 7.4 shows the partitioning of total evapotranspiration predicted by VIC over the CONUS domain. In this example, VIC was run using a gridded daily observation dataset (Maurer et al. 2002)

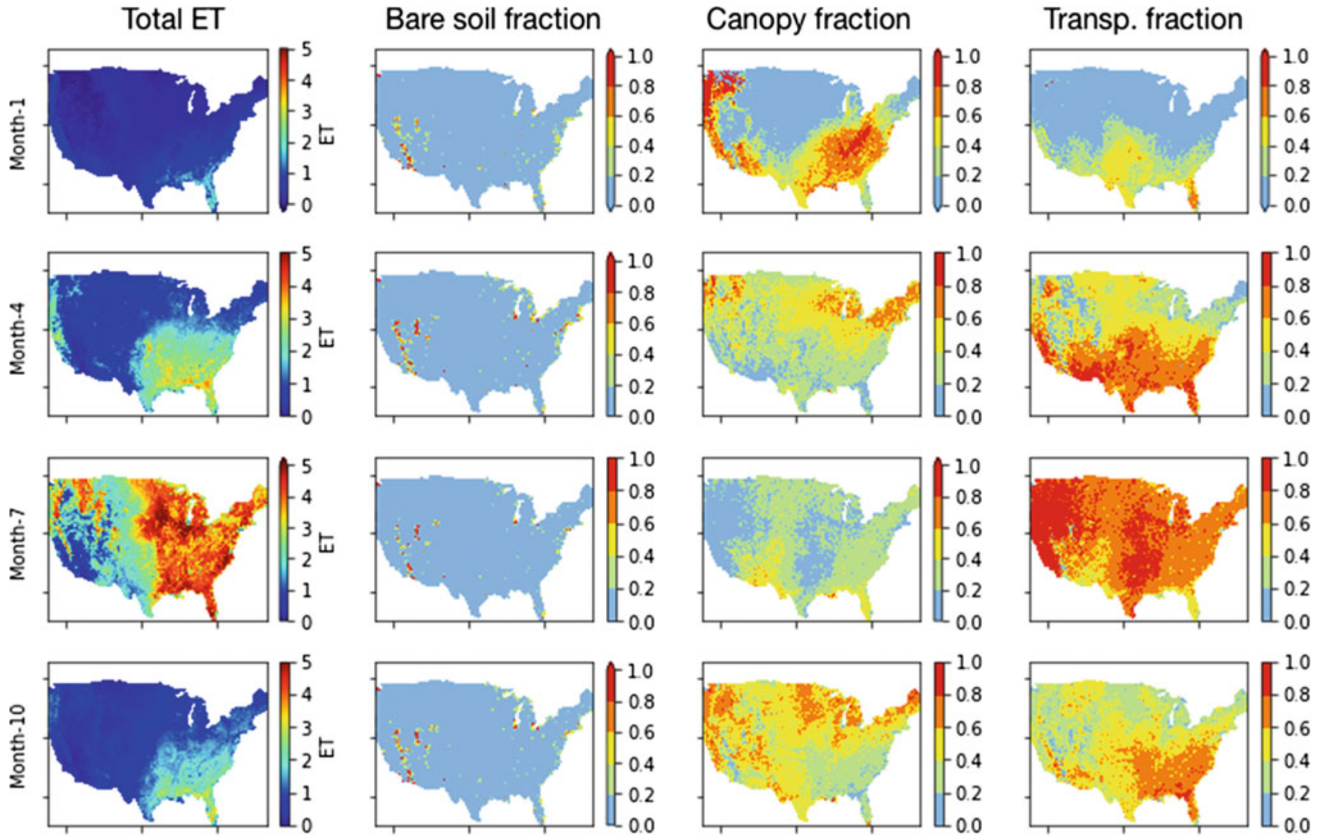

Fig. 7.4 The seasonal evolution of evapotranspiration (ET) in mm/day in the VIC model (left) and the fractional contribution of bare soil evaporation (center left), intercepted canopy evaporation and sublimation (center right), and vegetation transpiration (right)

of precipitation and temperature as input to the model. Many months and regions are dominated by transpiration and some by bare soil evaporation in isolated cases. Evaporation from the canopy is relatively more important in winter, at least where vegetation is abundant and substantial precipitation is present. Transpiration is dominant in summer when more energy is available, and plants are considered more active. While it is likely that evaporation from the canopy in the summer is a larger total flux, it is worth emphasizing that sublimation of snow from the canopy in the winter is a much larger fraction of ET at the time, and measurements of snow interception are much less common, this is almost certainly a topical area ripe for future work. However, it should go without saying that these are simply model results, and a focused evaluation of this partitioning through, e.g., eddy covariance and isotopic measurements would yield exciting comparison points for any model.

7.5.2 Model-to-Model Variability

It is useful to look across models to get some sense of how confident any single model's representation of total canopy evaporation may be. Here, we present a brief discussion of the canopy evaporation predicted by two widely used models, VIC and CLM, over a region with a lot of evapotranspiration, the Tennessee River Basin in the Southeast United States. In this region, canopy interception is clearly an important process throughout the year (Fig. 7.4). When looking at the regional climatology of annual total canopy evaporation predicted by these models (Fig. 7.5), we see very large differences in mean annual canopy evaporation (by a factor of 2) in just the average canopy evaporation [mm year^{-1}]. Over this river basin, VIC estimates canopy evaporation totals in excess of 400 mm year^{-1}, while CLM typically estimates less than 200 mm year^{-1}. A few of the key differences in these models are described in the sections above, but these differences alone do not immediately point to an obvious reason for the differences in total canopy evaporation. It is likely that it is not so much the model structure that is controlling this difference, but the model parameters, in particular, the assumed total canopy water holding capacity. This

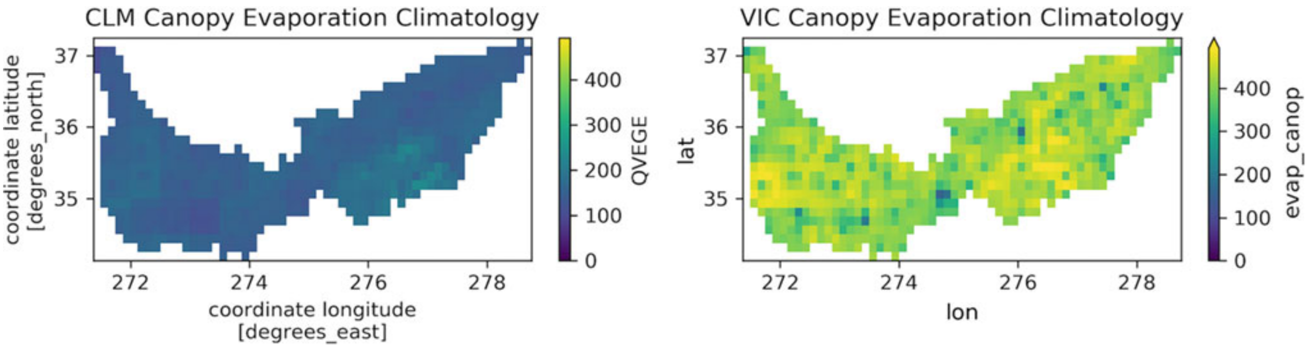

Fig. 7.5 Mean annual canopy evaporation in two different models, CLM (left) and VIC (right) over the Tennessee River Basin. Note that axis and colorbar labels are in the native nomenclature of the two modeling systems and both represent latitude, longitude, and canopy evaporation in mm per year

is a key variable in both models, has a wide range of estimated values in the literature, and exerts a strong control on the total evaporation because it controls the point at which precipitation ceases to be intercepted and it is permitted to pass to the land surface below. Better estimates of how this parameter, canopy water holding capacity, can be included in models likely to significantly improve models that are used in a wide variety of applications and should be a focus of future work.

7.5.3 Climate Change

Stepping back to the full CONUS domain once more, we next look at the role of models in climate change applications through an example projection using the Noah-MP model embedded in the WRF regional climate model. Noah-MP was used to simulate the land surface in a 13-year simulation of the WRF model for the period 2001–2013. In this simulation, the ERA-interim reanalysis (Dee et al. 2011) dataset was used as the observed atmospheric state on the boundaries of the model, and WRF simulated the weather internal to the domain throughout this time period in a convection-permitting mode (Liu

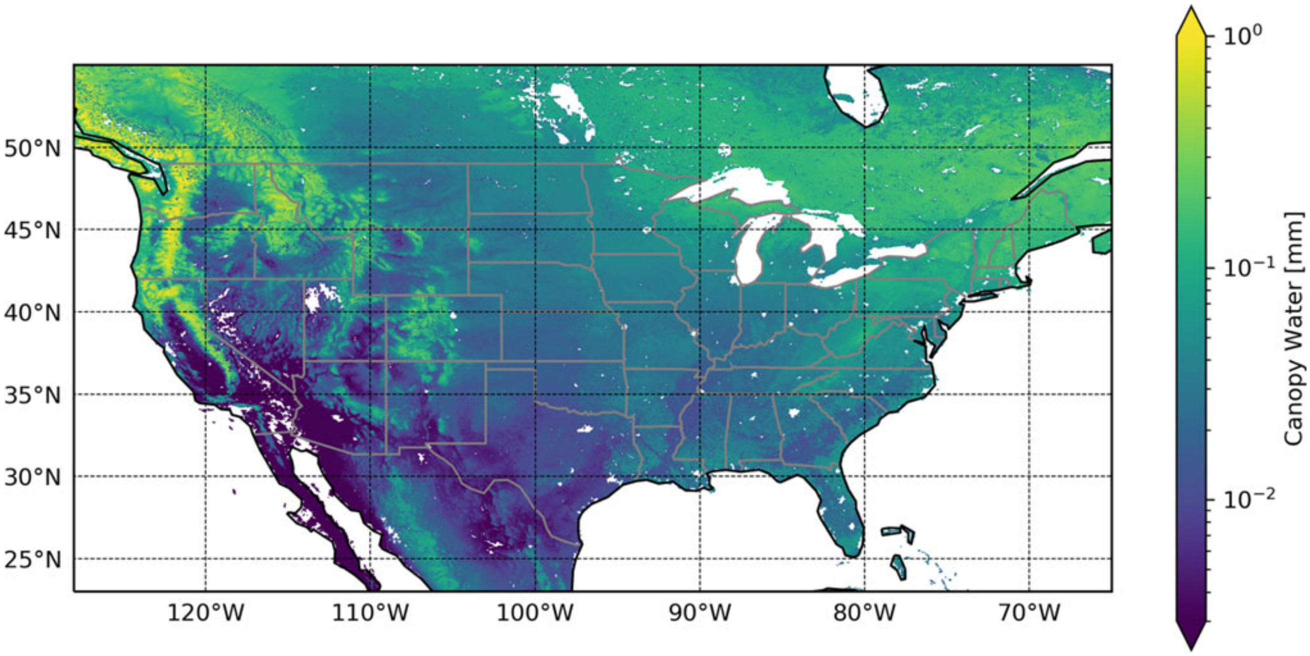

Fig. 7.6 Mean annual canopy water content in the Noah-MP land surface model over much of North America, focused on the United States. Note that white areas correspond to regions that the model treats as lacking any vegetation, e.g., oceans, lakes, bare soil, and dense urban areas

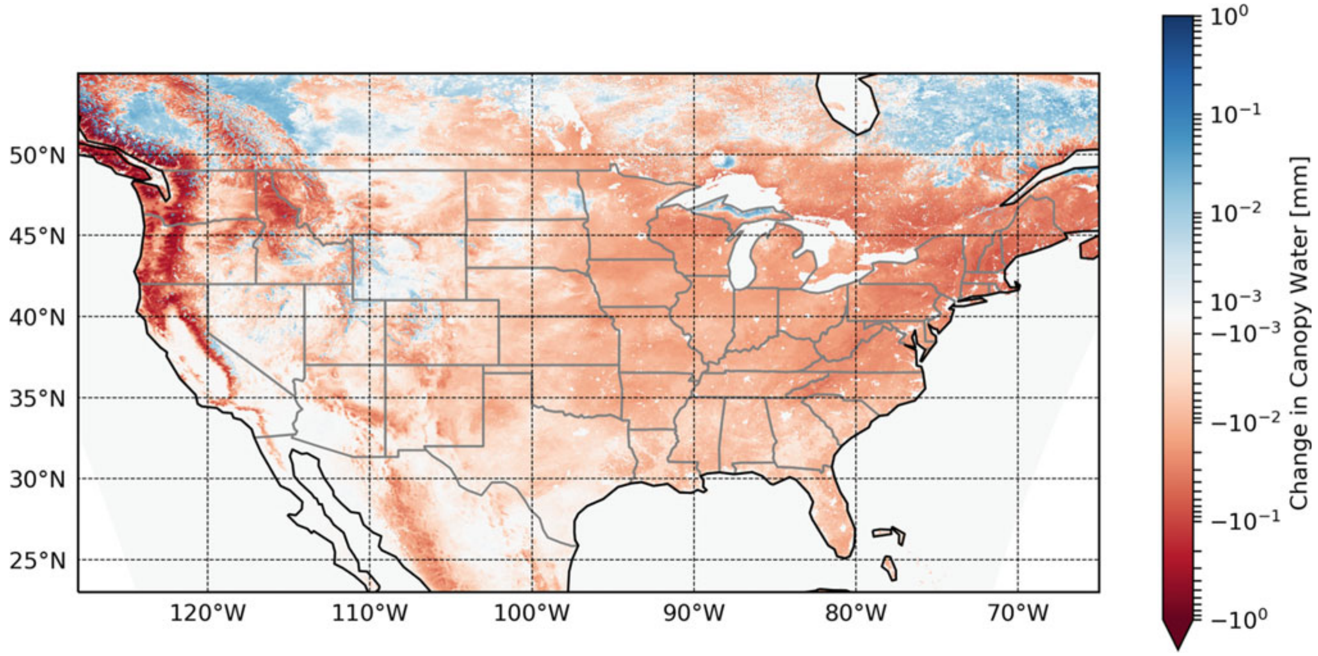

Fig. 7.7 Fractional change in canopy water content in a future warmer climate simulation. Note the positive and negative log scale, blue indicates increases in the average amount of water stored in the vegetation canopy, and red indicates decreases

et al. 2016). As such, WRF provided the precipitation, temperature, humidity, radiation, and other input variables to Noah-MP as a coupled system (e.g., Noah-MP's evapotranspiration was provided back to WRF to provide humidity flux from the surface). To provide a baseline for the reader, the average canopy water content [mm] over the course of the year in the current climate is presented in Fig. 7.6. The absolute values are small in part because this includes many times with no water in the canopy at all. There are relatively substantial spatial variations in the water stored in the canopy (climatologically) in the current climate, with differences tied both to land cover type (forest, grass, or crop, see, e.g., patterns in the Southeastern US) and climate (see, e.g., the Pacific Northwest compared to the desert Southwest, though there also are not a lot of trees where it does not rain much).

Because this baseline is derived from a regional climate model, it is possible to compare it to a future warmer climate by running that regional climate model with a warmer atmosphere. In this case, the same weather events are used to minimize problems due to chaotic variability, and the WRF boundary conditions are simply perturbed using the mean climate change signal for temperature, moisture, pressure, and wind fields in what is termed a Pseudo-Global Warming (PGW) experiment for the same 13 years. The predicted change in water stored in the canopy in the PGW future climate reveals striking patterns of increases and decreases in canopy water content (Fig. 7.7). The decreases in canopy water content may cause decreases in evaporative losses or may be caused by increases in evaporative losses. Even without changes in evaporation, these changes are consistent with the general expectation that precipitation events will increase in intensity, but may decrease in frequency. However, this is only a useful evaluation in almost entirely rain-dominated settings.

There appear to be large regions with increases in average canopy water content, particularly across much of Canada, and to a lesser extent in parts of the mountainous western United States. This could correspond to warmer temperatures causing what were light snow events to have more moisture, and thus more total snowfall available for the interception in these regions. However, the relationship between air temperature and snow interception capacity noted for Noah-MP (Fig. 7.3) suggests that, in this model, it is not warmer, stickier snow causing the increase. The strong decrease in canopy water content in the coastal ranges of the west coast likely correspond to significant shifts from snow to rain, and smaller maximum canopy water holding capacities for liquid water compared to snow, as well as possible shifts in the maximum intercepted snow capacity associated with warmer temperatures.

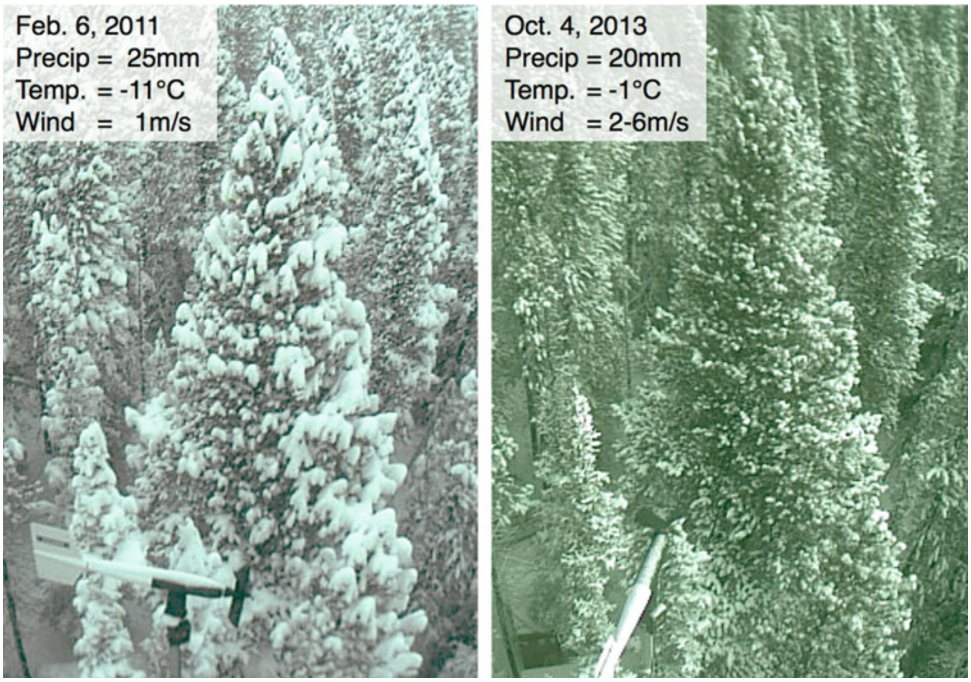

Fig. 7.8 Observed canopy interception of snow during two snowstorms with modest differences in total precipitation as photographed from by the Phenocam on the Niwot Ridge Ameriflux tower

Given the variability noted earlier between different model depictions of canopy water processes (e.g., Fig. 7.5), we might question how confident we can be in these predicted changes. Clearly, significant work is also warranted on the sensitivity of vegetation partitioning of precipitation to climatological factors such as temperature, precipitation phase, and intensity, and, though not discussed here, even wind, radiation, and humidity. As an example, Fig. 7.8 illustrates how different environmental conditions can change the amount of intercepted snow in a tree canopy. This figure shows that two different events with similar magnitude snowfall (25 and 20 mm) can have substantially different amounts of intercepted snow in the canopy. In this case, the low temperature on the left might be expected to decrease the amount of snow intercepted as warmer snow typically sticks to branches, but the higher wind speeds on the right may have dominated this effect by blowing snow out of the tree canopy. It is also possible that some rain was mixed in the snowstorm on the right, although temperatures rarely exceeded 0 °C throughout this event, and snow will not transition to rain until well above 0 °C because it is the cooler temperature at higher elevations in the atmosphere that control precipitation phase. The effect of wind on snowfall interception is not parameterized in most models in part because there are very few observations to quantify the relationship.

7.6 Concluding Thoughts

While much progress remains to be made in the modeling of precipitation partitioning, there are many reasons to be optimistic. The state of the science has advanced dramatically in recent years, as evident from the other chapters in this book, and measurement advances both in the field and from space promise to fill in the gaps in the state of knowledge. For example, recent studies have developed methods to estimate leaf traits in more detail from remotely sensed data (Moreno-Martínez et al. 2018). Measurements in a wide variety of vegetation canopies and climates are critical to advancing what are often global modeling endeavors (e.g., for climate and weather applications), and perhaps more importantly, documenting and cataloging these measurements to make them accessible for integration into models, or as the big data building blocks for new ways of looking at the field. In addition, a review of the parameters used in those models by the observational community can help either guide future observations to provide the information needed in models, or begin a conversation with the modeling community to fundamentally change the way those models work in the first place.

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8

Throughfall and Stemflow: The Crowning Headwaters of the Aquatic Carbon Cycle

Aron Stubbins, François Guillemette, and John T. Van Stan, II

Abstract

Dissolved organic matter (DOM) is a master variable that modulates the form and function of many ecosystems. Approximately, half of the mass of DOM is carbon. Fluxes of DOM transfer carbon and other vital elements between ecosystems and between organisms (e.g., trees to bacteria) and components (e.g., vegetation to soil) within ecosystems. The DOM flux out of trees and understory plants to the forest floor is a poorly studied component of the carbon and nutrient budgets of forest ecosystems. In freshwater systems, studies of DOM transport through terrestrial systems usually start at the stream. However, the interception of rainwater by vegetation marks the beginning of the terrestrial hydrological cycle making plant canopies the crowning headwaters of terrestrial aquatic carbon cycling. Rainwater interacts with canopies picking up DOM, which is then exported from the plant in stemflow and throughfall, where stemflow denotes water flowing down the plant stem and throughfall is the water that drips from and through the leaves, branches, and epiphytes of the canopy. As nearly all studies of vegetation-derived DOM to date report DOM derived from tree canopies (tree-DOM), in this chapter we discuss the quality, potential sources, and potential fates of tree-DOM. We then describe and discuss the drivers of variation of quantitative fluxes of tree-DOM and place these quantitative fluxes in biogeochemical and ecological contexts at scales ranging from the individual tree, forest, and watershed to global trends.

Keywords

Carbon • Dissolved organic matter (DOM) • CDOM • FDOM • Stemflow • Throughfall

8.1 Introduction

Dissolved organic matter (DOM) is a master variable in ecosystems. In soils, DOM affects the stabilization and distribution of soil carbon, soil microbial activity and function, and soil development processes (Jansen et al. 2014). In natural waters, DOM fuels microbial production and influences pollutant transport and bioavailability, and the colored fraction of DOM is the primary absorber of visible and ultraviolet sunlight and initiator of photoreactions (Mopper et al. 2015; Moran et al. 2016). Approximately half of the dry mass of DOM is carbon (DOC), the rest being comprised of hydrogen, oxygen, and other heteroatoms such as nitrogen and phosphorous (Dittmar and Stubbins 2014). From these few elements, a vast diversity

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of chemical form and function are manifest within the DOM pool. Ultrahigh-resolution mass spectrometry (UHR-MS, e.g., Fourier transform ion cyclotron MS) has resolved thousands of molecular formulas within DOM (Mopper et al. 2007), including tree-DOM (Stubbins et al. 2017). Each of these molecular formulas represents the ratio of elemental building blocks (e.g., C, H, O, N, S, and P) that give rise to a certain mass observed by the mass spectrometer. However, for many of these molecular formulas, the theoretical number of ways in which the elements can be arranged (i.e., the number of potential isomers per formula) exceeds many millions (Hertkorn et al. 2007). Consequently, the DOM pool may contain billions of different molecules. Within this plethora of molecules are compounds of diverse source, chemistry, and reactivity. Aromatic compounds absorb light, making them the main component of the colored DOM (CDOM; Weishaar et al. 2003) that is the main initiator of photoreactions in natural waters (Mopper et al. 2015). In terrestrial systems, these aromatics are derived primarily from the structural compounds within vascular plants (Hedges 2002). Due to its color, CDOM can be easily quantified and characterized by absorbance and fluorescence spectrophotometry, while more advanced analytical approaches including nuclear magnetic resonance spectroscopy (NMR) and UHR-MS are required to characterize the entirety of DOM (Mopper et al. 2007).

In freshwater systems, DOM studies usually start at the stream, with some studies focusing on organic fluxes from leaf litter and soils (see Table 8.1). However, on vegetated landscapes, plants are the first interceptors of precipitation and the first potential source of DOM to the forest floor and the downstream aquatic carbon cycle (Fig. 8.1). Although vegetated ecosystems consist of a diverse array of plant types, few studies report DOM in net precipitation beneath the canopies of any

Table 8.1 Summary of annual areal carbon fluxes in tropical and subtropical, temperate, and boreal ecosystems

		Carbon Flux (g-C m^{-2} yr^{-1})	Combined TF+SF %	References
Tropical/Subtropical	Stemflow DOC	0.1–8.0	–	Van Stan and Stubbins (2018)
	Throughfall DOC	10–30	–	Van Stan and Stubbins (2018)
	NPP	1600–2200	0.5–2.4%	Stiling (1996)
	Soil respiration (SR)	1092	0.9–3.5%	Raich and Schlesinger (1992)
	Heterotrophic SR	764.4	1.3–5.0%	Raich and Schlesinger (1992)
	Litter leachate	47–56	18–81%	Fujii et al. (2009)
	Organic soil horizons	9	110–420%	McDowell et al. (1998)
	Mineral soil horizons	4	250–950%	McDowell et al. (1998)
	Streams (1st order)	3	330–1280%	McDowell et al. (1998)
Temperate	Stemflow DOC	0.1–5.6	–	Van Stan and Stubbins (2018)
	Throughfall DOC	7–34	–	Van Stan and Stubbins (2018)
	NPP	1200–1300	0.5–3.3%	Stiling (1996)
	Soil respiration (SR)	662	1.1–6.0%	Raich and Schlesinger (1992)
	Heterotrophic SR	463.4	1.5–8.6%	Raich and Schlesinger (1992)
	Litter leachate	5–20	36–800%	Park and Matzner (2003)
	Organic soil horizons	7–40	18–570%	Michalzik et al. (2001)
	Mineral soil horizons	2–19	37–2000%	Michalzik et al. (2001)
	Streams (first order)	2	360–2000%	McDowell and Likens (1988)
Boreal	Stemflow DOC	0.01–0.7	–	Van Stan and Stubbins (2018)
	Throughfall DOC	1.9–4.1	–	Van Stan and Stubbins (2018)
	NPP	800	0.3–0.6%	Stiling (1996)
	Soil respiration (SR)	322	0.6–1.5%	Raich and Schlesinger (1992)
	Heterotrophic SR	225.4	0.8–2.1%	Raich and Schlesinger (1992)
	Litter leachate	20–48	4–24%	Koprivnjak and Moore (1992)
	Organic soil horizons	22–60	3–22%	Koprivnjak and Moore (1992)
	Mineral soil horizons	12–22	9–40%	Koprivnjak and Moore (1992)
	Streams (first order)	3–7	27–160%	Eckhardt and Moore (1990)

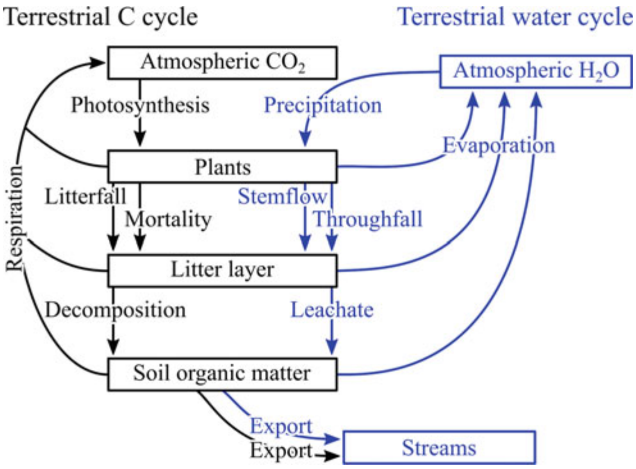


Fig. 8.1 Conceptual overview of the terrestrial carbon cycle and its interactions with the terrestrial water cycle. These carbon–water interactions along the precipitation-to-runoff pathway contribute, remove, and modify dissolved organic matter (DOM) in terrestrial waters

other plant besides trees (Gray 1997; Koprivnjak and Moore 1992). The earliest trees appear in the fossil record approximately 385 million years ago (Stein et al. 2007), since when they have fundamentally altered terrestrial (Algeo et al. 2001; Gensel and Edwards 2001) and wetland ecosystems (Greb et al. 2006). Forests are estimated to have covered close to 50 million km^2 of the planet 5000 years ago (Food and Agriculture Organization 2016) equivalent to approximately one-third of the earth's land surface. Just as forests transformed the global ecosystem, humans now have a similarly profound influence upon global ecology and biogeochemistry. Deforestation during the Anthropocene (Crutzen 2002) or noösphere (Vernadsky 1945) has seen forest land cover reduced by approximately 50% to 31.7 million km^2 as of 2005 (Hansen et al. 2010) and deforestation was continuing at a rate of approximately 1.5 million km^2 yr^{-1} between 2000 and 2012 (Hansen et al. 2013). Despite the vast and rapidly changing expanse of land covered by trees, forests still intercept most of the rainwater falling over land and account for 22% of global evapotranspiration (Porada et al. 2018). Once intercepted, ~90% of annual rainfall takes one of two hydrological flow paths to the forest floor: throughfall (water that drips from the canopy or falls directly through canopy gaps; 66–83% of precipitation) and stemflow (water funneled by the canopy to the stem; generally <3% of precipitation) (see Chap. 4 of this volume by Sadeghi et al. for a global review of throughfall and stemflow hydrology in forests and other vegetated ecosystems). Both stemflow (5–200 mg-C L^{-1}; Levia et al. 2011; Moore 2003; Tobón et al. 2004) and throughfall (1–100 mg-C L^{-1}; Inamdar et al. 2012; Le Mellec et al. 2010; Michalzik et al. 2001; Neff and Asner 2001) are enriched in DOM relative to rainwater (0.3–2 mg-C L^{-1}; Willey et al. 2000). Enrichment of throughfall and stemflow with tree-DOM is often enough to create visible changes in precipitation by absorbing light and "browning" the water (Fig. 8.2). In a recent manuscript, we reviewed much of the current literature on tree-DOM chemistry, concentrations, and fluxes (Van Stan and Stubbins 2018). In the current chapter, we summarize these topics and update or supplement them where appropriate. In particular, we have incorporated additional studies of tree-DOM fluxes and sought to further contextualize these fluxes at scales from the single tree to global trends.

8.2 Chemistry and Likely Sources of Tree-DOM

As noted above, stemflow and throughfall are enriched in DOC compared to the rainfall that is intercepted by trees. Thus, when rain falls on to trees it is picking up organics. However, it remains unclear if the organics in stemflow and throughfall are produced by trees, deposited upon trees, or generated by epiflora and epifauna. In all likelihood, each of these potential sources contributes a portion of the DOM washing from trees. The chemistry of tree-DOM can provide some insight as to its source.

Tree-DOM varies in its elemental stoichiometry both with flow path (stemflow versus throughfall) and species (Van Stan and Stubbins 2018). On average DOM C:N varies from 9:1 to 44:1 in throughfall (Goller et al. 2006; Michalzik et al. 2001; Schrumpf et al. 2006) and was 19:1 in the one study of stemflow we could find (Goller et al. 2006). These values are similar to those of vascular plant-derived sedimentary organic matter (C:N typically >20; Prahl et al. 1994), within the range of C:N values reported for river waters (33±16:1; Sipler and Bronk 2015) and toward the lower end of values for plant leaf

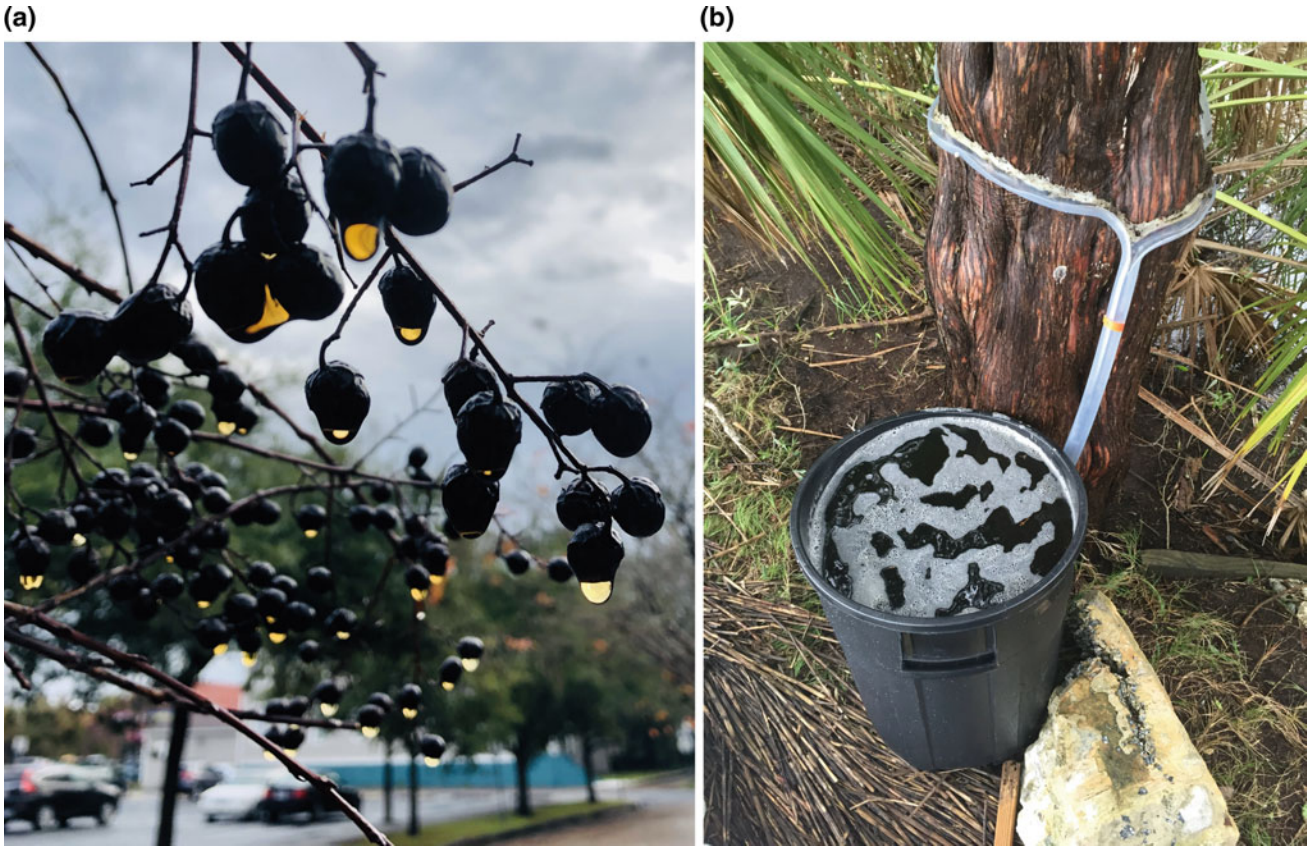


Fig. 8.2 Photographs showing **a** throughfall droplets enriched in CDOM prior to dropping to the surface and **b** stemflow being sampled during a large storm. *Credit* John T. Van Stan II

leachates (19 to 108:1; Fellman et al. 2013). Another ratio, between DOM color (i.e., absorbance at 254 nm) and DOC concentration, referred to as SUVA$_{254}$ (L mg-C^{-1} m^{-1}), provides an assessment of the relative aromatic content of DOM (Weishaar et al. 2003). SUVA$_{254}$ values for throughfall-DOM (2.0–2.9 L mg-C^{-1} m^{-1}; Stubbins et al. 2017; Van Stan et al. 2017) and stemflow-DOM (2.5–6.2 L mg-C^{-1} m^{-1}; Levia et al. 2012; Stubbins et al. 2017; Van Stan et al. 2017) are at the higher end or exceed the range in mean SUVA$_{254}$ values reported for US rivers (1.3–4.6 L mg-C^{-1} m^{-1}; Spencer et al. 2012) indicating that throughfall and stemflow, in particular, are enriched in highly colored, aromatic-rich DOM compared to river DOM. Tree-DOM SUVA$_{254}$ values are similar to those for DOM leachates from freshly collected leaves (2.7–3.4 L mg-C^{-1} m^{-1}; Fellman et al. 2013) and water-soluble organic carbon from atmospheric aerosols (1.3–2.9 L mg-C^{-1} m^{-1}; Fan et al. 2016), but exceed the SUVA$_{254}$ values observed for rainwater when measured at the same site as tree-DOM SUVA$_{254}$ (e.g., 0.4–1.0 L mg-C^{-1} m^{-1} for rainwater and >2 L mg-C^{-1} m^{-1} for all tree-DOM flow paths in Stubbins et al. (2017) and Van Stan et al. (2017)).

Few studies have used fluorescence spectroscopy to characterize tree-DOM. For throughfall fluorescent DOM (FDOM), 80–90% and 90–96% of total fluorescence in epiphyte-laden oak–cedar and broadleaved forests was humic-like in character (Inamdar et al. 2012; Van Stan et al. 2017). The only stemflow-DOM fluorescence study known to the authors reported a higher humic-like character (90–100% of total fluorescence) in stemflow compared to throughfall (80–90%; Van Stan et al. 2017). Protein-like fluorescence values for throughfall (4–20%) and stemflow (0–10%) are at the lower end of the range reported for leachates from fresh plant material (4–70%; Beggs and Summers 2011; Cuss and Guéguen 2013; Inamdar et al. 2012; Ohno and Bro 2006; Van Stan et al. 2015, 2017; Wickland et al. 2007), but exceed the concentrations found in streams (<10% although values up to ~30% have been reported at high discharge; Fellman et al. 2009) and in rainwater by more than four times on average (Van Stan et al. 2017). This suggests that, although tree-DOM is generally rich in humic-like fluorescence, throughfall and stemflow can contain relatively high levels of protein-like fluorescence (Howard et al. 2018; Qualls and Haines 1992), which can be exported to soils and streams.

Although it is unclear how features in fluorescence spectra for complex mixtures such as DOM relate to specific dissolved organic molecules, optical signatures similar to those observed in tree-DOM have been related to various moieties within DOM. For instance, the short-wavelength excitation:emission features have been related to aromatic amino acid structures (Tryptophan/Tyrosine; Fellman et al. 2010) and pools of more biolabile, and freshly produced or autochthonous DOM. Meanwhile, longer wavelength excitation:emission features are generally related to humic-like fluorescence of quinones (Cory and McKnight 2005), tannins (Maie et al. 2008), lignins (Hernes et al. 2009), and other polyphenolic structures consistent with tree-derived sources (Beggs and Summers 2011). The fluorescence signature of tree-DOM varies by tree species across a range of rainfall volumes and storm intensities (Cuss and Guéguen 2013; Van Stan et al. 2017). This suggests that trees and their associated biota impart species-specific and flow path-specific chemical and optical signatures to tree-DOM and that these signatures may be used to track tree-DOM from different flow paths and species into receiving ecosystems.

NMR data are scarce for tree-DOM. The data that exist indicate that aromatics (16–34%), carbohydrates (24–31%), and aliphatic carbon (14–25%) are the main structural components within tree-DOM (Bischoff et al. 2015). Trees and their epiphytes are direct sources of soluble carbohydrates (Coxson et al. 1992; Mahendrappa 1974), leaf waxes are readily eroded when leaf surfaces are abraded by rainfall (Baker and Hunt 1986), and aromatic lignin is a major structural component of vascular plants, the degradation products of which are washed from tree surfaces (Guggenberger and Zech 1994). Therefore, the enrichment of tree-DOM in carbohydrate, aliphatic, and aromatic carbon is consistent with tree-DOM being derived directly from modified foliar leachates and wash off (Guggenberger and Zech 1994; Kalbitz et al. 2007; Michalzik et al. 2001).

UHR-MS studies of tree-DOM are also rare. As of writing, a literature search turned up two studies (Ide et al. 2019; Stubbins et al. 2017). The molecular signatures of tree-DOM in throughfall and stemflow are broadly consistent with those of DOM in other aquatic ecosystems. Tree-DOM contained thousands of molecular formulas spanning the range of potential structural classes normally observed for DOM in natural waters via UHR-MS and included condensed aromatic, aromatic or alicyclic, and aliphatic compounds (Stubbins et al. 2017). Although tree-DOM was enriched in CHO-only formulas, nitrogen-, sulfur-, and phosphorous-containing formulas were also assigned. The molecular properties of tree-DOM are consistent with an autochthonous aromatic-rich source associated with the trees, their epiphytes, and the microhabitats they support. Elemental formulas enriched in oak stemflow were more diverse, enriched in aromatic formulas, and of higher molecular mass than for other tree-DOM classes, suggesting greater contributions from fresh and partially modified plant-derived organics (Stubbins et al. 2017). Oak throughfall was enriched in lower molecular weight, aliphatic and sugar formulas, suggesting greater contributions from foliar surfaces. While the optical properties and the majority of the elemental formulas within tree-DOM were consistent with vascular plant-derived organics, condensed aromatic formulas were also identified (Stubbins et al. 2017). As condensed aromatics are generally interpreted as deriving from partially combusted organics (Wagner et al. 2018), some of the tree-DOM may have derived from the atmospheric deposition of thermogenic and other windblown organics.

The above concentration and DOM quality data can inform, but not resolve questions about the source of organics in stemflow and throughfall. The high concentrations of DOC in stemflow and throughfall relative to rainfall clearly indicate that precipitation becomes enriched in organics as it interacts with vegetation. Furthermore, the C:N, optical and chemical character of tree-DOM is consistent with organic matter that is derived directly from the tree and its inhabitants. However, the tree-DOM quality data are also consistent with a depositional source that could accumulate on tree surfaces during dry spells and become mobilized during rainfall. In summary, the data suggest that trees are the predominant source of the DOM they export, but further studies are required to quantify the relevant contributions of trees, epibiota, and deposition to tree-DOM fluxes.

8.3 Tree-DOM Carbon Fluxes in Context

Fluxes of DOC from trees to the forest floor are a significant term compared to other forest and freshwater carbon fluxes. To allow comparisons between tree-DOM fluxes and other carbon fluxes, we report tree-DOM yields which have the units g-C m^{-2} yr^{-1} and are calculated as the DOC load exported to the forest floor per projected canopy area (m^2) and, for a completely forested catchment, is directly comparable to classical DOC yields for fluvial systems that are normalized to the whole catchment area. These yields are also directly comparable to forest carbon cycle terms that are reported per area of forest.

An in-depth review of literature values and discussion of these calculations are provided in Van Stan and Stubbins (2018). In summary, stemflow DOC yields ranged from 0.01 to 8 g-C m^{-2} yr^{-1} for tropical and subtropical forests, from 0.1 to

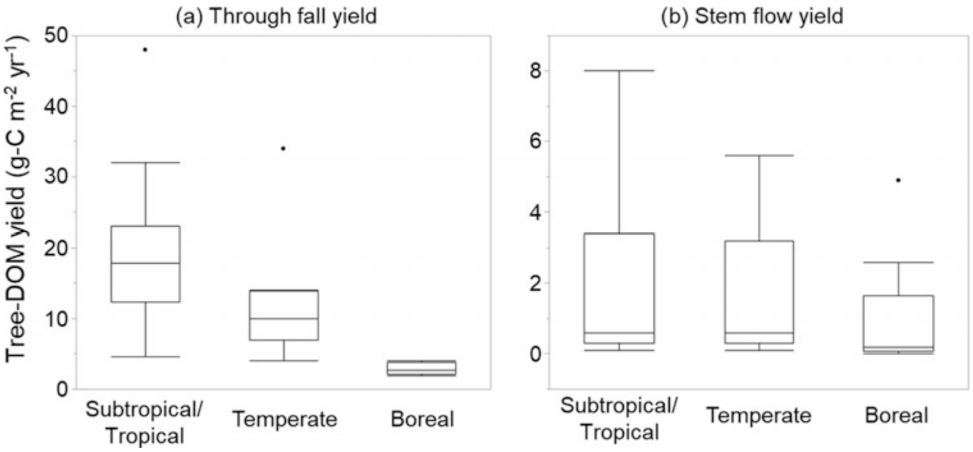


Fig. 8.3 Trends in tree-derived dissolved organic matter (tree-DOM) yield with latitude for **a** throughfall and **b** stemflow

5.6 g-C m^{-2} yr^{-1} for temperate forests and from 0.01 to 0.7 g-C m^{-2} yr^{-1} for boreal forests (Table 8.1 and Fig. 8.3). Throughfall DOC yields ranged from 4.6 to 48 g-C m^{-2} yr^{-1} for tropical and subtropical forests, 7 to 34 g-C m^{-2} yr^{-1} for temperate forests, and 1.9 to 4.1 g-C m^{-2} yr^{-1} for boreal forests (Table 8.1; Fig. 8.3). Although throughfall contains lower concentrations of DOC than stemflow, throughfall DOC yields are higher than for stemflow due to the throughfall having far greater water yields (see Chap. 4).

Also apparent from these data is the trend in decreasing tree-DOM yield from the tropics toward the poles with yields of both stemflow and throughfall DOC being an order of magnitude lower in boreal systems than in the tropical, subtropical, and temperate forests (Table 8.1 and Fig. 8.3). This trend is consistent with, but stronger than, the latitudinal trend in forest net primary production (NPP) which falls by a factor of approximately 4 from tropical to boreal forests (Table 8.1; Stiling 1996). Consequently, combined tree-DOM yields (i.e., stemflow plus throughfall yields) constitute approximately 0.5–3% of total NPP in tropical, subtropical, and temperate forests, but only 0.3–0.6% of NPP in boreal forests (Table 8.1). Thus, the flux of carbon from trees to forest floor in stemflow and throughfall is a modest but significant fraction of forest carbon production.

Table 8.1 also compares combined tree-DOM yields to other fluxes of DOM in terrestrial flow paths from the litter on the forest floor to the streams draining forested catchments. Tree-DOM yields are similar in magnitude to the DOC fluxes from litter leachates into soils with litter-derived DOC fluxes usually exceeding tree-DOM yields. In the tropics and subtropics, tree-DOM yields exceed rates of DOC generated as water passes through organic and mineral soil horizons possibly by up to 9.5 times (Table 8.1). Tropical and subtropical tree-DOM yields also exceed DOC yields in streams draining forested catchments by 3–13 times. Moving to temperate systems, tree-DOM and soil leachate yields are similar in magnitude, but as in lower latitude systems, tree-DOM yields exceed stream DOC yields this time by a factor of 3.6–20 (Table 8.1). Finally, in boreal systems, tree-DOM yields are lower than DOC yields from soils but still remain similar to DOC yields in first-order streams. Though including significant uncertainty, this coarse comparison demonstrates that tree-DOM fluxes are of similar quantitative importance to other commonly studied aquatic carbon fluxes in forested catchments. Further, the broad latitudinal trends in tree-DOM and other yields suggest that the influence of tree-DOM in soil and stream organic matter biogeochemistry may be greatest in the tropics and diminish toward the poles. Comparing global distributions of soil and biomass organic carbon density reveals that the contribution of vegetation (i.e., biomass) to areal carbon stocks is greatest in tropical and subtropical forests, declining through temperate systems, and reaching global minima in boreal systems where soil organic carbon stores are generally greatly in excess of above-ground biomass carbon (Scharlemann et al. 2014). The influence of these global trends in the above- and below-ground distribution of organic carbon stocks likely drives the relative importance of soil- versus tree-derived fluxes of DOC at the global scale with tree-DOM dominating vegetation carbon-rich tropical and subtropical forests and soil-DOM dominating in soil carbon-rich boreal systems. That said, even in forested boreal systems, tree-DOM yields may still exceed DOC yields measured in the streams draining forested catchments.

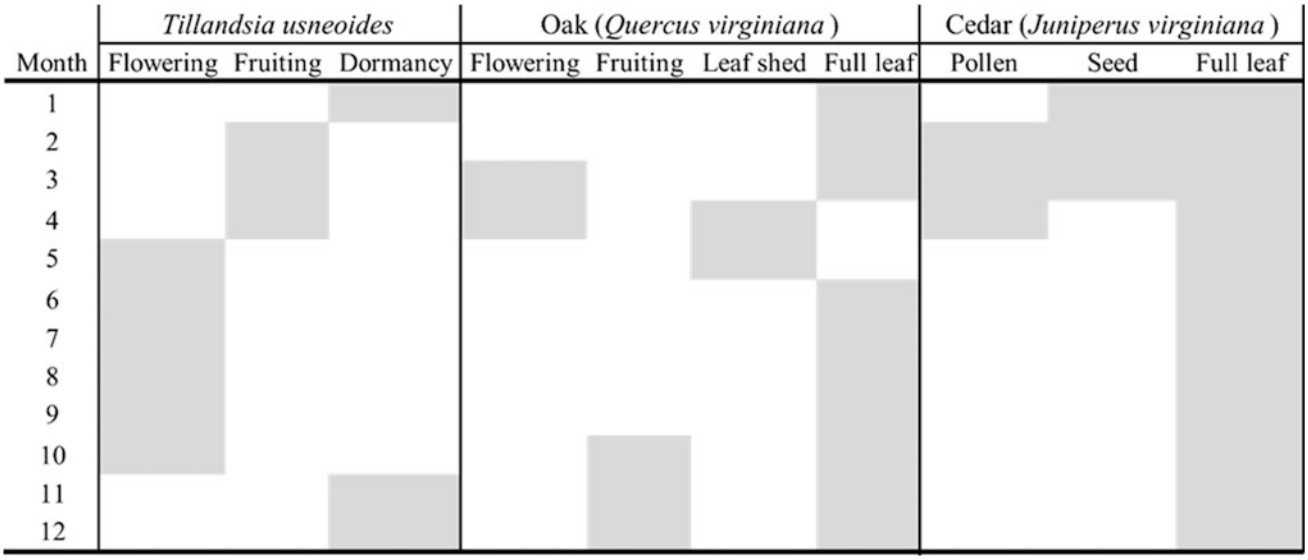
As a major flux to the forest floor, tree-DOM may also contribute to carbon storage in soils. In mature temperate soils, carbon accumulation is relatively slow (1 to 12 g-C m^{-2} yr^{-1}), whereas rates in recently disturbed temperate soils can range from ~5 to 40 g-C m^{-2} yr^{-1} (Schlesinger and Bernhardt 2013). Comparing these accumulation rates to the total amount of tree-DOC (stemflow + throughfall) delivered to temperate forest soils (~7 to 40 g-C m^{-2} yr^{-1}; Table 8.1), it is apparent that tree-DOC could provide a significant fraction of the carbon that accumulates in soils. Soil carbon is one of the largest organic carbon pools on Earth (Schlesinger and Bernhardt 2013). Thus, understanding how soil carbon will respond to land use, climate, and other environmental change is critical to predicting the future carbon budget and climate of the planet. The role of tree-DOM in soil carbon accumulation has been overlooked in both natural and urban settings to date. Future research is required to remedy this critical knowledge gap.

8.4 Biological Activity and Potential Impact and Fate of Tree-DOM

The above compared the quantitative fluxes of tree-DOM to other forest and aquatic carbon fluxes. Now we will consider the potential impact and fate of tree-DOM. There are a limited number of studies of tree-DOM biolability. Biolabile DOM is commonly defined as the fraction of DOM that can be readily consumed by microbes during relatively short-term bottle incubations (typically less than 1 month, e.g., Howard et al. 2018). These experiments are typically conducted under nutrient-replete conditions to try and ensure that DOC quality is the factor-limiting microbial activity and the percentage of DOC lost. These experiments are designed not to assess the rate of DOM loss in a natural system, but to assess a quality of the DOM—its biolability—quantified as the percentage of DOM lost during the incubation. The limited studies that have quantified tree-DOM biolability to date reveal that 30–73% of tree-DOM is biolabile (Howard et al. 2018; Qualls and Haines 1992). These results place tree-DOM among the most biolabile forms of DOM encountered in natural systems (e.g., DOM from phytoplankton cultures: 40–75% biolabile and DOM in permafrost thaw waters: ~50% biolabile; Bittar et al. 2015; Spencer et al. 2015). Qualls and Haines (1992) found tree-DOM (30–60% biolabile) to be more biolabile than DOM sampled from other points along the rainfall-to-runoff pathway (14–33% in litter leachates, soil solution, and stream water) but did not sample vegetation leachates. In studies where tree-DOM was not included, soil leachates have lower DOM biolability than tree-DOM (e.g., 7–15%; Wickland et al. 2007), whereas directly leaching vegetation can yield DOM that is similar to tree-DOM in that it is highly biolabile (11–93%; Wickland et al. 2007). DOM in blackwater rivers is generally of low biolability (e.g., 6 ± 4%) compared to plant leachates in the same study (38 ± 17%; Textor et al. 2018). These results indicate that tree-DOM is among the most biolabile forms of DOM in natural systems and that this high biolability is consistent with the sourcing of tree-DOM from vegetation.

The highly biolabile nature of tree-DOM suggests that it supplies a carbon and energy subsidy to ecosystems downstream of the forest canopy, including soils and streams. It is clear that tree-DOM reaches the forest floor and soils. However, the extent to which tree-DOM fuels total and spatial patterns in forest soil respiration is unclear. A rough comparison with soil respiration rates (Table 8.1) indicates that tree-DOM could support from around 1 to 9% of heterotrophic respiration in tropical, subtropical, and temperate soils and only 1 to 2% in boreal soils. While there remains a lot of uncertainty in these estimates, tree-DOM could be a significant source of biolabile carbon to soil microbes. The supply of tree-DOM is accompanied by a supply of water and other nutrients that wash from trees. Thus, the regions where the flow paths of stemflow and throughfall intersect with the forest floor may represent temporally dynamic biogeochemical hotspots that flare into action during storm events. It remains unclear how the spatially and temporally patchy delivery of water, carbon, and other nutrients to the forest floor in stemflow and throughfall during storms factors into net biogeochemical fluxes at the forest scale. Furthermore, the role of these patchy flow paths in shaping forest ecology, forest structure, and soil carbon stores is unknown.

Tree-DOM fluxes may also directly, from overhanging limbs and focused stemflow paths, or indirectly, via surface and soil water flow, enter freshwater systems. In tropical, subtropical, and temperate systems, tree-DOM yields exceed stream DOC yields by 3 to 20 times (Table 8.1). Thus, the potential for tree-DOM to contribute to stream DOM export is clear (Fig. 8.1). However, what is less clear is how much of the tree-DOM flux actual makes it to the stream. As discussed above, tree-DOM is highly biolabile and rapidly removed by microbes in incubation studies. Consequently, a fraction of tree-DOM can be expected to be consumed by microbes as it makes its way along flow paths to the stream. Where these flow paths intersect with litter and soil microbes, the loss of biolabile tree-DOM can be expected to be significant. The organic signatures of tree-DOM (Stubbins et al. 2017) also contain features that may sorb to soils. These and other biotic and abiotic processes along the flow path from tree to stream will likely remove a fraction of tree-DOM completely, plus alter the optical and chemical signature of the remaining tree-DOM obscuring its detection in streams. Despite the potential loss and obfuscation of tree-DOM chemical signals, there are a wealth of optical, molecular, and isotopic geochemical techniques that should help resolve the fate and role of tree-DOM as a carbon flux through and energy and carbon source within soil and freshwater ecosystems.



	Tillandsia usneoides			Oak (*Quercus virginiana*)				Cedar (*Juniperus virginiana*)		
Month	Flowering	Fruiting	Dormancy	Flowering	Fruiting	Leaf shed	Full leaf	Pollen	Seed	Full leaf
1			▨				▨		▨	▨
2		▨					▨	▨	▨	▨
3		▨		▨			▨	▨	▨	▨
4		▨		▨		▨		▨		▨
5	▨					▨				▨
6	▨						▨			▨
7	▨						▨			▨
8	▨						▨			▨
9	▨						▨			▨
10	▨				▨		▨			▨
11			▨		▨		▨			▨
12			▨		▨		▨			▨

Fig. 8.4 Example monthly phenology calendar of the dominant arboreal epiphyte, Spanish moss (*T. usneoides*), and each of the dominant tree species, oak and cedar, based on literature (Barve et al. 2015; Cavender-Bares and Pahlich 2009; Lawson 1985; Mack 1995; Mopper and Simberloff 1995) and field observations at Skidaway Island (GA, USA)

8.5 Temporal Drivers of Tree-DOM

Sources of DOM on canopy surfaces available to throughfall and stemflow may vary temporally in response to seasonal and human drivers. The most visible signs of seasonal change include the annual cycle (i.e., phenological) of the plants themselves. Events such as flowering, leaf shedding, fruiting, and pollen/seed production are unlikely to occur simultaneously for each plant within the vegetated ecosystem. For example, a "simple" phenological calendar for a forest canopy dominated by two tree species and a single epiphyte (based on Van Stan et al. 2017) shows that dynamics in potential DOM sources (leaves, pollen, etc.) likely follow different temporal patterns (Fig. 8.4). Shifting canopy source materials may alter the tree-DOM composition with the seasons and species-by-species. An example is the production of glucose-rich nectar from extrafloral nectaries (Campbell et al. 2013). Figure 8.4 is illustrative, not comprehensive, as plant phenological dynamics vary markedly across ecosystems and by species within ecosystems. Epiphytic vegetation is ubiquitous across ecosystems (Van Stan and Pypker 2015), and their abundance and seasonal dynamics may alter the amount and quality of DOM in throughfall and stemflow (Van Stan et al. 2017). Seasonal changes also occur that alter the source regions and provenances of air masses and, thus, the materials in dry and wet deposition (Greene et al. 1999). Both of these shifts can cause seasonal changes in the microorganisms deposited and living on plant surfaces (Copeland et al. 2015; Jumpponen and Jones 2010) and change epifaunal interactions with the plant by initiating insect infestation, bird roosting, or attracting insectivores—all of which may contribute materials to throughfall and stemflow (Beard et al. 2002; Bittar et al. 2018; Gilmore et al. 1984; Stadler and Michalzik 1998). Human interactions may influence the timing and intensity of these events, see discussions on climate change and infestation (Kurz et al. 2008) or fire frequency (Abatzoglou and Williams 2016), or the canopy organic matter pool directly through air pollution or land use change (Chantigny 2003; Fang et al. 2007).

8.6 Conclusions

Plants are the first interceptors of precipitation and the first potential source of DOM to vegetated ecosystems and the downstream aquatic carbon cycle. Stemflow and throughfall are highly enriched in DOM compared to precipitation above plant canopies and other waters. Little is known about DOM in throughfall and stemflow for any other type of plant beyond trees. Tree DOM chemistry varies between flow paths and species. Quantifying the proportion of tree-DOM that is autochthonous (i.e. of tree origin) versus that derived from deposition to the tree requires further research. The few studies to have quantified tree-DOM biolability to date place tree-DOM among the most biolabile forms of DOM encountered in natural systems. Tree-DOM flux is a significant term in forest ecosystem carbon budgets but constitutes a greater relative carbon flux in vegetation carbon-rich tropical and subtropical forests than in soil carbon-rich boreal systems. We recommend that the wealth of current optical, molecular, and isotopic geochemical techniques be applied to throughfall and stemflow waters to help resolve the source, fate, and role of tree-DOM in forest, soil, and freshwater ecosystems. We further recommend that studies of tree-DOM fluxes be expanded to other tree species and other forms of vegetation. Finally, additional studies are merited as tree-DOM is understudied with respect to its magnitude as carbon flux and its potential to shape terrestrial and aquatic ecosystems.

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Interactions of Epiphytes with Precipitation Partitioning

9

Glenda Mendieta-Leiva, Philipp Porada, and Maaike Y. Bader

Abstract

Epiphytes are structurally-dependent plants which grow on other plants without taking nourishment from them. Phylogenetic and ecophysiological differences divide them into non-vascular epiphytes (e.g. mosses and lichens), which are distributed worldwide, and vascular epiphytes (e.g. orchids and bromeliads), which are restricted to the tropics and subtropics. Within their distributional ranges, their abundance is strongly influenced by atmospheric water availability, since they have no access to soil water and are strongly coupled to the atmosphere. Epiphytes are most conspicuous in the tropics, in particular in cloud forests, but they can also be very abundant in cool-temperate wet forests. Their importance for precipitation partitioning rises from their widespread distribution, their location at the atmosphere-biosphere interface, and their adaptations specifically aimed at capturing and retaining atmospheric inputs. The interaction of epiphytes and precipitation partitioning is bidirectional: they deliberately contribute to partitioning and they depend on this partitioning (capture and retention of water and nutrients) for their survival. Additionally, they may be affected by partitioning by other canopy elements, taking advantage of throughfall and stemflow. Stemflow has been shown to be particularly important for non-vascular epiphytes on tree trunks, providing both water and nutrients. The presence of epiphytes increases the effect of forest canopy structure on the vertical and horizontal redistribution of precipitation by diversifying and changing nutrient pathways and by modifying water availability spatially and temporally. These functions are more pronounced in epiphytes than in the rest of the canopy, as epiphytes have developed a diverse array of strategies and mechanisms to cope with intermittent water supplies. Although quantitative information is scarce, it is clear that interception can be substantially increased by epiphytes, in particular by bryophytes and tank-forming bromeliads. In continuously wet environments, however, the potential water-uptake capacity of these groups may not be fully used because of low desiccation rates. Overall, much quantitative and process-oriented research into epiphyte interactions with precipitation interception is still needed to better understand the role of this functionally diverse group of plants in global climate and hydrological cycles. Mutual influence of epiphytes and precipitation redistribution will occur anywhere where epiphytes occur. However, the magnitude and exact mechanisms of the interactions will differ across climate zones and ecosystem types, based on epiphyte abundance, functional composition, and spatial distribution, as well as the frequency and intensity of precipitation as rain, fog and snow.

Keywords

Epiphytes • Canopy • Throughfall • Stemflow • Fog • Bryophytes • Lichens • Nutrient fluxes

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9.1 Precipitation and Epiphyte Ecology

Precipitation patterns are known to strongly affect the distribution and ecology of soil-rooted vegetation (Kreft and Jetz 2007). For plants with no direct access to soil water, such as epiphytes, the spatiotemporal patterns of precipitation are even more relevant. Epiphytes are plants that grow on other plants non-parasitically and are distributed throughout forest canopies globally, their abundance and taxonomic composition varying strongly among climate zones (Zotz and Hietz 2001; Vanderpoorten and Goffinet 2009). Having no direct contact with the soil, they capture most of their water and nutrients from the atmosphere in the form of dry deposition and precipitation (Feild and Dawson 1998). Additionally, they also recycle nutrients from the litter of their host tree and other epiphytes (Nadkarni and Sumera 2004). Thus, epiphytes depend strongly on patterns of direct vertical and horizontal precipitation as well as their subsequent partitioning into throughfall and stemflow, which determine the quantity and quality of water received in different parts of the canopy. This dependency highlights the critical importance of precipitation partitioning processes in forests where epiphytes occur. In this chapter we will present a general account of what is known about the ecology of epiphytes, including their role in forest water fluxes, which will help to understand how they depend on precipitation partitioning, supported by direct observations on this dependence where available.

Epiphytes can be divided into two main ecological groups: non-vascular (mosses, liverworts, lichens, algae and cyanobacteria, Fig. 9.1) and vascular epiphytes (e.g., orchids, bromeliads, aroids and ferns, Fig. 9.2). These groups differ in several respects but the most important, in the context of precipitation partitioning, is their physiology: non-vascular epiphytes are poikilohydric while nearly all vascular epiphytes are homoiohydric (Proctor 1990; Larcher 2003). Poikilohydric plants equilibrate their water content more or less freely with that of the atmosphere and most species are desiccation tolerant (Proctor 2009). As a result, their relationship with abiotic factors differs fundamentally from that of homoiohydric plants, which cope with fluctuations in water availability by controlling water loss. As a result, vascular and non-vascular epiphytes differ in their geographic distribution. Non-vascular epiphytes tolerate more extreme conditions (drought, cold) than vascular epiphytes while requiring high and constant humidity to attain high biomass (Gentry and Dodson 1987; Vanderpoorten and Goffinet 2009). For vascular epiphytes, minimum temperatures appear to be a serious constraint (Zotz and Hietz 2001), although at high elevations absence of substrate supersedes (Sylvester et al. 2014; Zotz et al. 2014).

While non-vascular epiphytes are distributed worldwide wherever hosts are available (on all continents except Antarctica, Vanderpoorten and Goffinet 2009), vascular epiphytes are constrained within the subtropics and tropics (Zotz 2016), with the exception of facultative epiphytes (terrestrial species found growing epiphytically under special circumstances) which can occasionally be found in temperate forests (Zotz 2005). Both groups show clear latitudinal and elevational distribution patterns, with biomass being the highest where moisture availability is highest and most constant, like in tropical montane and other cloud forests and coastal rainforests (e.g. Wolf 1993; Kessler 2000; Kessler et al. 2001; Kreft et al. 2004; Vanderpoorten and Goffinet 2009; Ah-Peng et al. 2012; da Costa et al. 2015; Sanger and Kirkpatrick 2015). Thereby, in tropical mountains, vascular epiphytes tend to have their abundance peak at lower elevations than non-vascular epiphytes, in particular, bryophytes (i.e. mosses and liverworts, Pócs 1982; Bruijnzeel et al. 2011). Both among vascular and non-vascular epiphytes, the functional composition of epiphyte communities are strongly climate dependent, with lichens preferring drier habitats than mosses, and, for example, tank bromeliads dominating in wet and atmospheric bromeliads in seasonally dry ecosystems (Fig. 9.2e).

Epiphytes are generally known to influence precipitation partitioning processes, including total interception, storage, and evapotranspiration, as well as spatial patterns in throughfall and stemflow (Zotz 2016). These effects have been rather widely studied (e.g. Van Stan II and Pypker 2015 and references therein, Porada et al. 2018; Gómez González et al. Accepted), although many questions remain unanswered. However, the reciprocal relationship, the importance of precipitation partitioning for the occurrence and performance of different types of epiphytes, has hardly been studied explicitly. Much can be learned, however, from the general ecology of epiphytes and how they manage their water and nutrient budgets. Thereby, the effect of epiphytes on partitioning can hardly be decoupled from the effect of this partitioning on the epiphytes, because much of the partitioning is deliberate. For example, fog and rain are captured and retained in epiphytes to safeguard their water supply, and canopy litter is retained between the leaves and roots of many epiphytes and help to increase the nutrient supply, also affecting the nutrient contents of throughfall and stemflow.

9.2 Effects of Epiphytes on Precipitation Partitioning

9.2.1 Effects on Interception

The most relevant feature of epiphytes determining their role in precipitation partitioning is their substantial interception and water storage capacity (Veneklaas and Van Ek 1990; Köhler et al. 2007). This capacity is particularly strong in the poikilohydric non-vascular epiphytes (Tobón et al. 2010), but some vascular groups, like tank-forming bromeliads, may also store significant amounts. Nonetheless, it is thought that the contribution to the overall forest water budget in the wettest and most epiphyte rich tropical forests may be limited because of very slow desiccation and therefore limited water uptake (Holscher et al. 2004; Tobón et al. 2010). In tropical cloud forests, non-vascular epiphytes may be constantly close to saturation since potential evaporation, which is controlled by radiation, is limited under constantly cloudy conditions (Proctor 1990; Miralles et al. 2011). It has been shown experimentally that variation in rainfall intensity did not affect interception efficiency of epiphyte-laden branches in a Pacific Northwest forest (Pypker et al. 2006a), which similarly to cloud forests are dominated by seasonal fog. On the other hand, variation in rainfall frequency, i.e. time for drying and level of saturation of the water storage capacity before rainfall events, should strongly affect interception. In line with global warming, the number of dry days in tropical montane cloud forests is increasing (Pounds et al. 1999, 2006). Although this may initially increase precipitation interception by the epiphytes, the increased drought stress may decrease epiphyte biomass (Zotz and Bader 2009) and hence, in the long run, will likely negatively affect interception volumes by epiphytes in these forests. In dry areas, where epiphytes are dry most of the time, they may considerably increase the proportional interception of water from light rains or fog. As a result, they may reduce throughfall and can negatively affect water input to the root systems of their hosts (Stanton et al. 2014) although on the other hand, they may increase air humidity around the plant shoots, decreasing water loss through transpiration (Stuntz et al. 2002).

Quantitative estimates of interception by epiphytes are very rare and variable. Generally, the estimated contribution of epiphytes is relatively large in relation to overall interception (interception of host branches and leaves). For example, Pocs (1980), in a submontane forest in Tanzania, estimated that the contribution by epiphytes to total interception capacity was of up to 51%, with bryophytes playing a dominant role (i.e. ca 48% of total interception capacity). This is in contrast to the estimate (based on an analytical model) by Holscher et al. (2004) who suggested that the contribution of non-vascular epiphytes was only 6% in a tropical montane rain forest in Costa Rica. Vascular epiphytes may also play an important role, depending on their growth form. For a subtropical forest in Georgia (USA), the total epiphyte contribution to interception (for a single *Tillandsia* species) was estimated to be 11% (Van Stan II et al. 2016). Very high interception in a cloud forest in Venezuela (Ataroff and Rada 2000) was attributed to the high abundance of “tank type” and “cushion type” epiphytes, although the contribution of epiphytes to total interception was not further quantified.

Divergence in estimates may be partially due to how potential and actual storage capacity of epiphytes are taken into account. In a detailed study, Gómez González et al. (Accepted) stripped epiphyte biomass from halves of trees in a lower montane cloud forest in western Panama. They estimated that epiphytes alone contributed to nearly half of canopy interception (20%, with total interception at 40%) when considering the potential storage capacity. However, it would be considerably less when taking into account that the capacity cannot be fully used under the permanently wet conditions in this forest (Gómez González et al. Accepted). In a global modeling study, Porada et al. (2018) found that non-vascular epiphytes substantially increase interception loss at the global scale. Compared to a simulation without epiphytes, the total value of interception in forest canopies as percentage of global evapotranspiration increased from 5 to 8%, which means that these epiphytes are responsible for almost half of the global interception loss from forest canopies.

9.2.2 Effects on Throughfall

Another important feature of epiphytes is their patchy distribution within canopies. Thereby, spatial patterns both in functional types and in biomass are important determinants of the effect on precipitation partitioning. For instance, in tropical montane forests, throughfall has reportedly a very high spatial variability (Zimmermann et al. 2007) which is not only due to the complex structure of these forests but also due to the incredibly high patchiness of epiphytic biomass (Werner et al. 2012). In turn, this spatial variability modifies the effect of precipitation on vegetation overall.

Throughfall is defined as the portion of incident gross precipitation, including fog, which drips through the canopy (Bosch and Hewlett 1982) or falls through gaps. It contributes the most to water input for terrestrial vegetation (Levia and


(a)
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◀ **Fig. 9.1** **a** Mosses (*Orthotrichum* sp.) growing on an aspen tree in a boreal forest in Turku, Finland (Photo: Tinja Pitkämäki). **b** Lichens (*Evernia prunastri*) and mosses on trees during winter in a temperate forest in Jena, Germany. **c**, **d** Mosses and lichens on stems in a boreal forest in central Norway (Hypnaceae, *Lobaria pulmonaria*, Parmeliaceae, e.g. *Parmelia sulcata* and *Hypogymnia physodes*). **e**, **f** Cactuses covered by lichens and lichen on a cactus spine in the loma-vegetation "las lomitas" in the National Park "Pan de Azúcar", Chile. **g** Lichen hanging from a southern beech tree in a temperate forest in the Southern Alps of New Zealand. **h** Bryophytes covering lianas and trees in a secondary tropical montane cloud forest of Wayquecha, Peru. **i** Liverwort (*Plagiochila* sp.) on an understory stem in a tropical lowland forest in Tiputini, Ecuador. **j** Epiphyll (liverwort growing on a leaf, Lejeuneaceae) in a tropical lowland forest in Paramaribo, Surinam. **k** Mosses (*Octoblepharum* sp.) growing on the lower trunk of a tree in "La Selva" tropical lowland forest, Costa Rica (Photo: Elodie Moreau). **l** Water droplets on a moss in a tropical montane cloud forest in Wayquecha, Peru. **m** Lichens on a fruit tree in agricultural land near Quito, Ecuador (*Ramalina* sp. and Parmeliaceae, e.g. *Usnea* sp.)

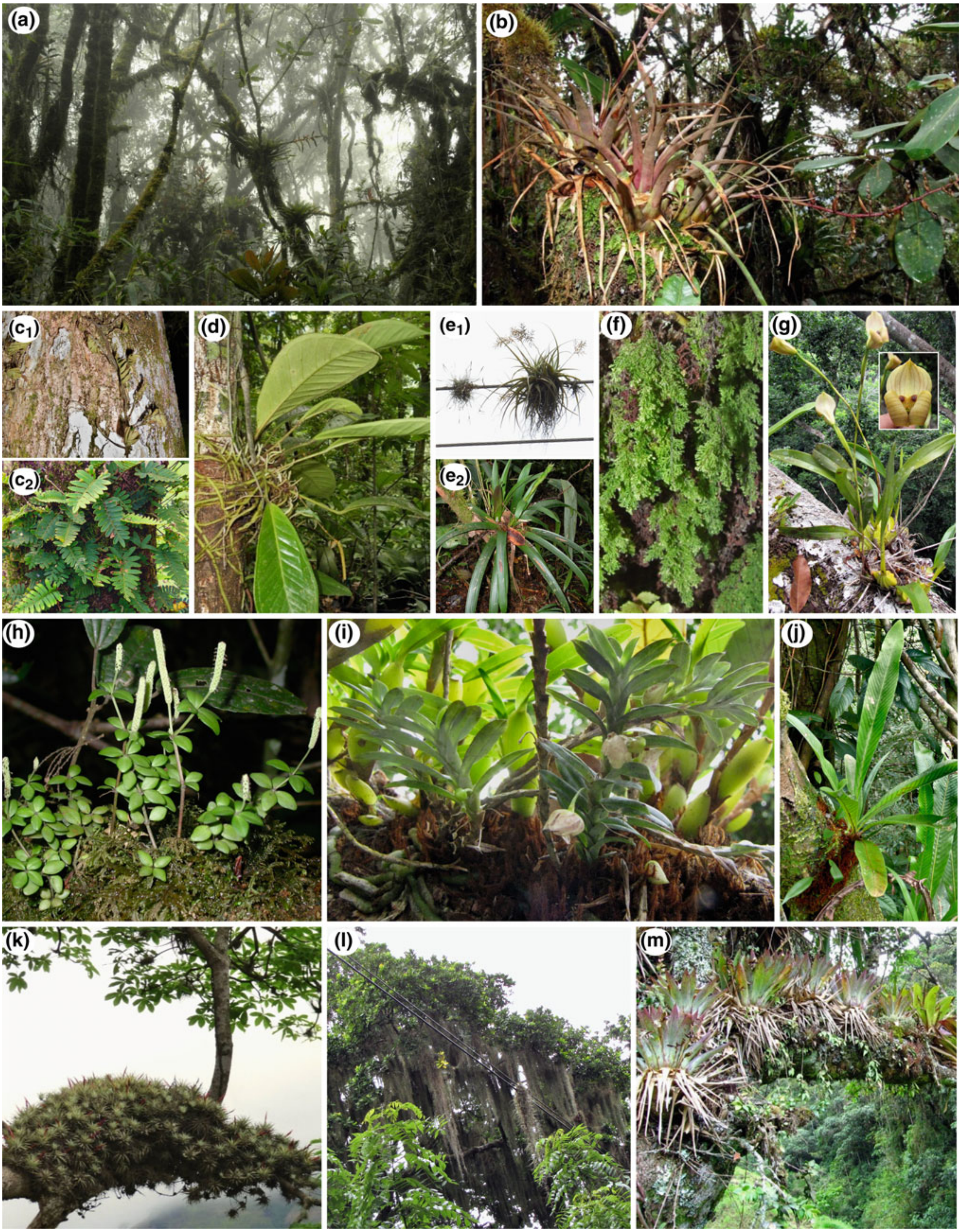
Frost 2006), between 47 and 73% of incident rainfall or up to 55–101% for lower montane forests and montane cloud forests of Ecuador and Honduras, respectively (Bruijnzeel and Proctor 1995; Fleischbein et al. 2005). This figure is generally reduced in epiphyte-laden canopies (Rosier et al. 2015), although with great spatial variation depending on forest structure, epiphyte biomass distribution, and the relative contribution of fog to precipitation (Veneklaas and Van Ek 1990). Throughfall also varies strongly with forest composition (Veneklaas and Van Ek 1990), since different host tree species have different leaf and crown shapes and harbor different functional groups of epiphytes (Wagner et al. 2015).

9.2.3 Effects on Stemflow

Stemflow is defined as the water draining over the exterior of a plant trunk or stem and it originates from rainfall and throughfall intercepted by branches. The latest global review of stemflow found that it can account for 0.01–33.9% of precipitation in forests (Van Stan and Gordon 2018). Tropical montane forests tend to show low estimates (<2.2%, e.g. Veneklaas and Van Ek 1990; Cavelier et al. 1997; Chuyong et al. 2004; Fleischbein et al. 2005). Outliers to these low stemflow percentages were documented at an upper montane cloud forest in Australia where estimated stemflow reach 11% of total precipitation, possibly due to high stem density and low LAI (McJannet et al. 2007). Stemflow exceeded 1/3 of precipitation for Hawaiian forests invaded by *Psidium cattleyanum*, where this extreme value was attributed to the smooth bark and steep branching of the species (Safeeq and Fares 2014), although the strong spatial variation in sampling could also be a cause. Additionally, in forests where fog deposition is prevalent, this can be a considerable source of stemflow (Levia and Germer 2015). Epiphytes affect stemflow by their role in interception, by changing the pathways of water along the stem, and by absorbing water as it flows down the stem. Non-vascular epiphytes, in particular, may be partially or completely dependent on stemflow. As they absorb water, they may decrease stemflow volumes (Köhler et al. 2007) as has been observed across several ecosystems (e.g. Fleischbein et al. 2005; Ponette-Gonzalez et al. 2010). On the other hand, epiphytes have also been shown to sometimes increase stemflow, with inconsistent effects across different trees in a tropical montane forest with high vascular and non-vascular epiphyte cover (Gómez González et al. Accepted). This inconsistency was probably due to the high variability in water capture and retention mechanisms found in different epiphyte groups and species. With the current information available, no overall estimation of the effect of epiphytes on stemflow can be presented.

9.2.4 Effects on Chemistry of Throughfall and Stemflow

Precipitation chemistry is certainly altered during the passage of precipitation through the canopy (Morris et al. 2003; Van Stan II and Pypker 2015). The degree to which throughfall and stemflow chemistry is modified is determined by forest canopy structure and the spatial distribution and the functional composition of canopy components. The mechanisms controlling the uptake, transformation and leaching of nutrients differ between epiphyte groups (Van Stan II and Pypker 2015). For instance, in forests where poikilohydric groups dominate, they can add cloud water into throughfall and stemflow (Reynolds and Hunter 2004). This can change their nutrient composition since fog water tends to have a higher ion concentration than rainwater (Schmid 2004). Also, epiphytes may harbor N-fixing bacteria and thereby contribute N to throughfall and stemflow. No legumes and very few other dedicated symbiotic plant groups are known as epiphytes (Zotz 2016), but the smaller cyanolichens, which contain N-fixing cyanobacteria, will certainly contribute N to the ecosystem (Pike 1978; Antoine 2004). Additionally, free-living N-fixers may play a role in epiphyte-derived canopy soil and in material trapped among epiphytes leaves, e.g. in basket ferns and tank-forming bromeliads.


(a)
(b)
(c1)
(c2)
(d)
(e1)
(e2)
(f)
(g)
(h)
(i)
(j)
(k)
(l)
(m)

◀ **Fig. 9.2** **a** Biomass and distribution of epiphytes in a tropical montane cloud forest during a foggy day at Wayquecha, Peru (Photo: Tinja Pitkämäki). **b** *Tillandsia* sp. on a liana with their base covered by *Hymenophyllum* sp. (filmy ferns) and *Peperomia* sp. (piperoids) in the understory of a tropical montane cloud forest at the "Estación Científica San Francisco", Ecuador (Photo: Florian A. Werner). **c** Resurrection-fern (*Polypodium polypodioides*) in the upper (1) and lower (2) parts of the same tree trunk near a lowland rainforest at the National Park Palenque, Mexico. **d** Variation in growth direction of velamentous roots in an aroid (*Anthurium acutangulum*, note roots growing upwards), this root type is more commonly known in orchids. **e** Bromeliad atmospheric form (1. *Tillandsia flexuosa* and *Tillandsia* sp.) growing on cables in a street of Vilcabamba, Ecuador and a bromeliad tank form (2. *Guzmania* sp.) growing on a treelet, with collected litter, in the understory of a tropical montane cloud forest, Ecuador (Photo: Florian A. Werner). **f** Filmy fern (*Hymenophyllum* sp.) growing on the base of a trunk in a tropical montane cloud forest at the "Estación Científica San Francisco", Ecuador (Photo: Florian A. Werner). **g** Orchid (*Trigonidium egertonianum*) growing on the bark of a *Brosimum utile* tree in open and exposed spots within the crown. **h** Piperoid (*Peperomia tetraphylla*) growing in the understory of a tropical montane cloud forest, Ecuador (Photo: Florian A. Werner). **i** Orchid (*Dichaea panamensis*) with green roots (which also carry out photosynthesis) growing on the roots of a fern (*Niphidium crassifolium*) in a Caribbean lowland forest in Panama. **j** Fern (*Niphidium crassifolium*) which forms a root basket to trap litter and dust with the fine rootlets covered in dark reddish-brown scales. **k** A stand of atmospheric bromeliads (*Vriesea espinosae*) growing on the bark of a ceibo tree in an equatorial dry forest in the Natural Reserve Laipuna, Ecuador. **l** Spanish moss (*Tillandsia usneoides*) growing on the crown of a tree and cables along the road to the cloud forest of Cerro Campana, Panama. **m** Bromeliad tank form (*Tillandsia complatana*) with their base covered by ericoids (*Sphyrospermun* sp.) growing on a remnant tree in a pasture near a tropical montane cloud forest, Ecuador (Photo: Florian A. Werner)

In temperate forests, non-vascular epiphytes dominate and are known to substantially contribute to nutrient fluxes (Coxson and Nadkarni 1995) by increasing the deposition of nutrients to the forest floor (Knops et al. 1996). In an experimental setup, it was observed that N concentrations in throughfall were strongly increased by the presence of lichens, although lichens did not affect P content (Knops et al. 1996).

9.3 Effects of Precipitation and Partitioning on Epiphytes

9.3.1 Effect of Humidity Gradients at Different Scales

Continuously moist conditions characterize the optimum habitat for both non-vascular and vascular epiphytes (Bates 2009; Werner et al. 2011). For non-vascular species, continuous humidity, due to prolonged or frequent precipitation (including fog) and slow evaporation, enables continuous photosynthetic activity and reduces the costs of desiccation (Wolf 1993). This is most probably why epiphytic moss cover reaches the greatest biomass in cool wet forests, in particular in high-elevation tropical cloud forests (e.g. Pócs 1982; Wolf 1993). In tropical lowland forests, however, the abundance of non-vascular epiphytes is relatively low, in spite of high humidity and moisture availability. This has been explained by high respiration losses relative to photosynthetic carbon gain for poikilohydric plants in these habitats, where fast drying in exposed positions in the canopy or very low light availability in the forest understory may frequently lead to negative carbon balances in these organisms (Richards 1984; Zotz et al. 2003; Wagner et al. 2014). Similarly, for vascular epiphytes, water availability is also a major factor determining species´ geographic and spatial distributions (Gotsch et al. 2017), with most species preferring continuously moist habitats (Gotsch et al. 2018), but some species able to grow in seasonally dry forests as well (Gentry and Dodson 1987; Kuper et al. 2004). Where vascular epiphytes need at least seasonal rainfall, some non-vascular epiphytes can make do with fog only, as exemplified in the coastal Atacama desert, where it will frequently not rain for years, but where fog oases with sparse vascular plant cover have a very high lichen cover on the resident cacti and desert shrubs (see Fig. 9.1e, f; Stanton et al. 2014).

Species-specific habitat preferences determine spatial distribution patterns among climate zones as well as within forests and canopies. These preferences are translated into partitioning along the vertical forest gradient, the best known spatial pattern of epiphytes. Thereby, sun-loving or desiccation-tolerant species are distributed in the upper tree crowns and shade-loving or desiccation-sensitive species are distributed in the understorey (e.g. Cornelissen and Steege 1989; ter Steege and Cornelissen 1989; Krömer et al. 2006; Pardow et al. 2012; Petter et al. 2016). Differences between non-vascular and vascular epiphytes lie in the amplitude of their distribution. In most cases, non-vascular epiphytes may have a narrower distribution than vascular epiphytes along the vertical gradient within a forest, although both groups contain both habitat generalists and specialists (e.g. Wagner et al. 2013; Oliveira and Oliveira 2016; Petter et al. 2016). Apart from showing strong vertical gradients, forests are also heterogeneous in terms of water availability, due to precipitation partitioning by the canopy and the epiphytes themselves. Water availability has been clearly shown to be a predominant control on the occurrence and growth rates of several epiphytic functional types (e.g. Schlesinger and Marks 1977; Zotz and Hietz 2001; Zotz et al. 2010; Wagner and Zotz 2018).

At the landscape scale, changes in humidity along topographic gradients are commonly associated with changes in epiphytes abundance and community composition. A noteworthy case is the tropical lowland cloud forest, which has been described in French Guyana but which may be much more widespread. This type of lowland forest is influenced by morning fog and shows epiphytic abundance and species richness comparable to that of montane forests and much higher than that found in lowland rain forests (Gradstein 2006, Pardow et al. 2012). Outside of the tropics, similar gradients can be found. For example, in *Nothofagus* forests of different ages in northern Patagonia, lichen biomass in low-precipitation sites was a mere 17% of that in high-precipitation sites, with differences in composition mainly driven by precipitation across forests of different age (Caldiz and Brunet 2006).

Nutrient availability, while not the most limiting factor for epiphyte distributions, does also limit the growth of epiphytes, which have no direct access to soil nutrients. Among ecological groups (e.g. mosses, ferns, and orchids) there is clear differentiation in strategies for nutrient acquisition (Clark et al. 2005; Cardelus and Mack 2010). Precipitation appears to be an important source of P and N to epiphytes (Asbury et al. 1994; Zotz 2016). A modeling study estimated that epiphytes, in particular non-vascular ones, capture a major part of N present in precipitation, while cations are leached from the canopy (Clark et al. 1998, 2005). This may indicate that precipitation is a source of N for epiphytes, while for the cations (P, Ca, Mg, K) terrestrial uptake by and subsequent leaching from the host is the more important source. Other sources of N include fixation by free-living bacteria in canopy soils and symbiotic cyanobacteria in epiphytic cyanolichens. This source may be particularly relevant in humid temperate forests of the Pacific Northwest of the USA, where epiphytic lichens have been shown to carry out considerable N fixation (Pike 1978; Antoine 2004).

So clearly, gross precipitation controls the distribution of epiphytes through determining the overall availability and input of water and nutrients. Once in the canopy, this precipitation is transformed, however, by the tree canopy as well as the epiphytes themselves, into throughfall, stemflow, water stores and water vapor. In the following sections, we will discuss how these different components may affect the distribution and performance of epiphytes within tree canopies.

9.3.2 Effects of Interception

Effects of epiphytes on interception are strongly controlled by the need of these plants to intercept water for their own use, i.e. by the central importance of interception for the epiphytes themselves. Epiphytes have found diverse ways to adapt to the lack of, or discontinuity in, their water supply, including changes in plant structure as well as physiology. Adaptations may be aimed at taking up water, storing it, avoiding its loss, or on tolerating desiccation. Uptake, storage and conservation together determine how much water is intercepted and how fast it is returned to the atmosphere.

Water and nutrient uptake by epiphytes from rain and fog is increased by e.g. foliar water uptake (via partially open stomata or through cracks in the cuticle, Darby et al. 2016; Berry et al. 2019), water-absorbing trichomes on bromeliad leaf surfaces, the absorptive tissue of the velamen radicum around the roots of orchids and some other epiphyte groups (Fig. 9.2d, g, i), and loose growth forms (e.g. pendants) in bryophytes and lichens (Fig. 9.1g). Water storage can be achieved through leaf, stem and root succulence in e.g. bromeliads, orchids and aroids, the formation of tanks by overlapping rosette leaves in many bromeliads, or specialized hyaline water-storing cells in some bryophytes (Figs. 9.2b, d, i, m and 9.1l). These adaptations are particularly important for interception and determine the water-holding capacity of the epiphyte vegetation. Avoiding water loss is aided in some species by e.g. leaf pubescence, reflective trichomes, impermeable cuticulas or by switching to crassulacean acid metabolism (CAM, Males 2016). Most non-vascular epiphytes, as well as filmy ferns (Hymenophyllaceae, Fig. 9.2f), are adapted to tolerate discontinuous water supplies through their ability to deactivate their metabolism upon desiccation and reactivate it when water becomes available again. Variation in this tolerance likely plays a significant role in determining differences in the distributions of species and functional groups, for example, the shift in dominance from bryophytes to lichens from the understory to the upper canopy and from wet to dry habitats, or the shift from dense moss cushions (a good shape for conserving water) to loose forms like pendant mosses (efficient for intercepting water, especially from fog) from dry habitats to cloud forests. Interception thus plays a crucial role in epiphyte distributions and growth. Yet, epiphytes are not passively affected by interception but are active engineers of the process.

9.3.3 Effects of Throughfall

In tropical montane forests in Puerto Rico, leaching of nutrients from host leaves and washing off of dry deposition can result in increased concentrations of nutrients in throughfall compared to gross rainfall (Asbury et al. 1994) suggesting that throughfall may be an important contributor of N and P for epiphytes (Clark et al. 1998). Variation in this contribution and the effect on epiphyte growth may even partly explain why some trees are better epiphyte hosts than others, as shown in experiments in a subtropical forest (Callaway et al. 2002). The importance of throughfall for epiphytes thus appears to be variable and is not quantitatively understood yet.

9.3.4 Effects of Stemflow

Although stemflow generally accounts for a very small proportion of rainfall partitioning, it can be an important source of water for epiphytic lichens and bryophytes, in particular. Up to a 40% of stemflow was estimated to be absorbed by bryophytes in a moist montane evergreen broad-leaved forest (Liu et al. 2002). This number may increase in forests where clouds are prevalent because of fog interception (Levia and Germer 2015). These percentages become significant considering that stemflow is known to be highly enriched in nutrients in comparison to gross precipitation or even throughfall (Carlisle et al. 1967; Parker 1983; Hölscher et al. 2003).

Therefore its contribution to epiphytes regarding nutrient input may be considerable, but it has not been studied explicitly in epiphyte-rich forests. In other forests, e.g. in a subtropical forest in the Himalayas, stemflow leachates have been identified to be the main source of N for five epiphytic orchids (Awasthi et al. 1995) and in oak woodlands in Britain, changes in stemflow chemistry due to air pollution had a very rapid effect on non-vascular epiphytes (Farmer et al. 1991). In evergreen forests it has been hypothesized that stemflow may determine species diversity, e.g. for lichens (Levia and Germer 2015), based on evidence indicating a strong effect of solute concentrations in stemflow on the presence and abundance of non-vascular epiphytes (Hauck et al. 2002; Hauck and Runge 2002; Schmull et al. 2002). Schlesinger and Marks (1977) suggested that mineral nutrients leached into stemflow may represent a transfer of nutrients from the host to the epiphyte, *Tillandsia usneoides* (‘Spanish moss’, which is not a moss but a bromeliad, Fig. 9.2l). A follow-up study indicated that as anthropogenic sources of mineral nutrient deposition to canopies increased (potentially associated with urbanization), the *T. usneoides* dependence on host-leached nutrients likely diminished (Husk et al. 2004). Stemflow, which can be spatially very variable along the trunk, also plays an important role in the small-scale distribution of epiphytes, with vertically extending patterns in epiphyte cover some tree along stems suggesting a relationship to stem flow patterns (Barkman 1958). Apart from providing water and nutrients, stemflow also plays a role in the dispersal of propagules, which may be part of the explanation why elongated patches of epiphytic mosses and lichens can often be found along stemflow paths on tree trunks. For vascular epiphytes the dependence on substrate water varies strongly. Some species forage for water with roots appressed to the branches or stems, while others use the substrate only for support and obtain their water from the atmosphere (i.e. fog, rain and throughfall). The latter group of species is likely only minimally affected by stemflow volume or chemistry.

9.3.5 Effects of Snow and Ice

Outside of the tropics and subtropics, epiphytes (non-vascular only here) may experience precipitation as snow, which is partitioned different from rain and fog and also has different effects on the organisms. Snow is hardly taken up into moss or lichen thalli, so that epiphytes should have a smaller effect on snow partitioning than they have on rain of fog partitioning. In temperate and boreal forests, the winter half-year may be the best growing season for non-vascular epiphytes on deciduous trees because of higher light levels combined with good moisture conditions. Some lichens may even be active below the snow. Significant net photosynthesis has been observed in a lichen down to −5 °C (Schroeter and Scheidegger 1995), and even at −24 °C, CO_2-uptake has been measured (Lange and Metzner 1965). Growth at these temperatures is unlikely, as no turgor can be built up, but at least carbon losses may be compensated, although activity at such extreme temperatures is not expected for most species. In addition to temperature, light becomes limiting at larger snow depths. Significant activity usually ceases if snow layer thickness exceeds 30 cm (Kappen et al. 1995). Such deep snow layers are unlikely to accumulate on tree branches, but at the stem base, epiphytes may be covered below thick layers of snow. Redistribution of snow and accelerated snow melting around the stem base then can become significant factors for the distribution of epiphyte species on the stem.

Sonesson et al. (2011) reported that snow cover affected the distribution of two epiphytic lichen species on birch trees positively and negatively, depending on their location on the tree. A species distributed at the base of the tree trunk survived burying under snow through large carbon storage and a low growth rate, which lead to low respiration under snow. The other species, distributed at higher positions on the trunk, had a higher growth rate and fewer reserves. It could, therefore, outcompete the first species but it could not survive under snow, leaving the trunk base to be dominated by the first species. Furthermore, lichen mortality has been often associated with heavy snow load, although quantitative estimates are not provided (Esseen 1985). Positive effects of snow and ice may be that they provide prolonged wetting when remaining on the side of stems and branches, allowing some low-level metabolic activity, and the protection of the epiphytes from extreme cold air temperatures due to insulation. On the other hand, most species can survive extreme temperatures when dry so that wetting during cold spells is not necessarily beneficial. Also, the snow layer may preserve cold conditions in spite of increasing air temperature and may thus delay activation in spring or during warm spells in winter (Pannewitz et al. 2003). While snow can obviously have various effects on non-vascular epiphytes, this aspect of epiphyte ecology has hardly been addressed in the literature so far and we are not able to conclude on any overall net effects.

9.3.6 Future Interactions between Epiphytes and Precipitation Partitioning

Understanding and quantifying the effect of epiphytes on precipitation partitioning, is particularly relevant under current threats of global change to epiphytes and hence to their ecosystem functions. Although in many ecosystems we expect the threat of climate change to be lower for epiphytes than for other forest elements due to the inherent drought and stress tolerance of epiphytes, epiphytes may be seriously threatened by drying trends in continuously wet habitats like tropical montane cloud forests (Zotz and Bader 2009). Other global or regional changes that may threaten epiphytes are air pollution, well-known to affect the quantity and composition of non-vascular epiphyte cover, and deforestation, leading to drier conditions and changes in species composition (Gradstein 2008; Werner and Gradstein 2009; Branquinho et al. 2015; Becker et al. 2017; Oishi and Hiura 2017).

A global modeling study suggests that non-vascular epiphytes contribute substantially to interception of rainfall at regional to continental scales. Since evaporation of intercepted rainfall has a cooling effect on the land surface, reductions in epiphyte biomass may lead to higher surface temperature, which would lead to even drier or less suitable conditions for the epiphytes and may result in a positive feedback with regard to global warming (Porada et al. 2018). Positive feedback (with negative results) can also be assumed at smaller scales, lower epiphyte cover leading to drier conditions in the canopy and on the branches themselves, with negative effects on the growth of remaining epiphytes. The loss of epiphyte biomass may have a negative cascading effect on the taxa depending on and interacting with epiphytes, the loss of epiphyte biomass constituting a habitat loss for many organisms (Thomsen et al. 2010).

9.4 Conclusions

Epiphytes are active and deliberate players in precipitation partitioning, as they depend heavily on being able to capture and retain atmospheric water. Stemflow and throughfall are important sources of water and solutes for many epiphytes (e.g., Veneklaas et al. 1990; Pypker et al. 2007; Holwerda et al. 2010; Oyarzún et al. 2010). Both processes are directly affected by forest structure (McJannet et al. 2007) in combination with the spatial distribution of epiphyte biomass and functional types (Hölscher et al. 2003; Zimmermann et al. 2007).

Although the mechanisms by which epiphytes can affect precipitation partitioning have been discussed extensively (e.g. Fleischbein et al. 2005; Pypker et al. 2006b; Zimmermann et al. 2009; Gay et al. 2015), quantifications of these effects or the reciprocal effect on the epiphytes are very rare, which may be partly due to methodological constraints. Differentiating and understanding the effects of each component of rainfall partitioning on epiphyte performance in different climate and forest types may be only possible through long-term experimental setups (Nadkarni and Sumera 2004; Van Stan II and Pypker 2015). Other open questions include the effect of epiphytes on fog capture, how they interact with snow, their effect on the chemistry and temporal dynamics of water fluxes through forest canopies, and the importance of epiphyte morphological and physiological traits for these functions. All these functions are far from being quantitatively understood, in spite of their importance for ecosystem functioning and local and global water and nutrient cycles.

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Relevance of Precipitation Partitioning to the Tree Water and Nutrient Balance

10

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Abstract

Canopy partitioning of precipitation into interception, throughfall, and stemflow can influence the dynamics of tree water and nutrient balances. Intercepted precipitation may evaporate back to the atmosphere or reach the forest soil via throughfall or stemflow; however, intercepted precipitation—and the minerals dissolved in the solution—may also enter the plant directly through foliar or bark uptake. Minerals deposited on canopy surfaces can be transferred along vegetation surfaces and to the soil via throughfall and stemflow. In addition to throughfall- and stemflow-mediated transport of nutrients originating from deposition, nutrients can also be leached from leaf surfaces via throughfall and stemflow. Nutrient concentrations in stemflow are typically higher than concentrations in throughfall, but throughfall volumes are much higher than stemflow volumes. Still, the majority of nutrient return to the soil occurs through leaf litter inputs and subsequent decomposition at the soil surface. Canopy partitioning of throughfall results in heterogeneous distribution of moisture which may directly or indirectly influence the heterogeneity of nutrient availability. Direct influence is based on dissolved minerals in throughfall or stemflow, whereas partitioning of throughfall may indirectly influence the heterogeneity of nutrient availability by influencing the microbial environment and community. The heterogeneity of belowground resource availability may impact fine-root density and spatial patterns of proliferation. Current knowledge is limited by a focus on how throughfall and stemflow water and nutrient pulses and patches influence individuals. We suggest that the path forward for improving our understanding of how precipitation partitioning influences tree water and nutrient balances should focus on a more holistic framework that investigates population or community level responses rather than just individual responses. Likewise, controlled manipulative experiments may prove more instructive in determining the mechanistic controls of canopy partitioning on tree water and nutrient balance than have observational studies.

Keywords
Precipitation • Throughfall • Stemflow • Roots • Nutrient cycling

10.1 Introduction: Water and Nutrients in Forested Systems

To understand how forest canopies partition precipitation into interception, throughfall, and stemflow influences tree water and nutrient balances, it is important to briefly discuss exactly why water and nutrients are important to trees. As with all life as we currently understand it, water is essential for fundamental physiological processes in trees. Indeed, individual plant cells are comprised of 80–90% water (Kramer 1955). Plant tissues are also comprised primarily of water. Although much variation exists among different species, ephemeral tissues responsible for resource acquisition above- and belowground (i.e., leaves and fine roots) generally exhibit water contents in the range of 70–90% (expressed as a percentage of fresh weight) (Kramer and Boyer 1995). Perennial woody tissues (i.e., stems and branches) are comprised mainly of dead cells

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that act as conduits for long-distance water transport (i.e., xylem) and generally exhibit water contents in the range of 40–60% (Kramer and Boyer 1995). Water content of seeds is quite variable among species, ranging from 5 to 80% (Kramer and Boyer 1995). Despite the high water content of plant cells and tissues, most water taken up by tree roots (~97–99%) is transient in nature—it simply passes through the vascular system as it cycles between its liquid state in the soil and its gaseous state in Earth's atmosphere through the process known as transpiration (Taiz and Zeiger 2010; Lambers et al. 1998). The process of transpiration is necessary for the uptake of CO_2 from the atmosphere. Approximately 400 H_20 molecules are transpired for every CO_2 molecule fixed in photosynthesis (Taiz and Zeiger 2010). Only a small fraction of absorbed water is incorporated into biomass, ~1% (Lambers et al. 1998), or to supply metabolic processes such as photosynthesis, another ~1% (Taiz and Zeiger 2010). This pathway of water transport is commonly referred to as the soil–plant–air continuum, which relies on the vapor pressure gradient between the atmosphere and inside the leaf mesophyll as the driving force to pull water from the soil into roots, through stems and branches, and out into the atmosphere through the stomatal pores of leaves (Huber 1924; Kramer and Boyer 1995). In addition to the direct impact of water on the physiology of plants, it is also critical for nutrient uptake and microbial processes that transform nutrients and thereby influence their availability for uptake by plants (Schlesinger and Bernhardt 2013; Kozlowski et al. 1991; Chapin 2011).

There are 16 mineral elements derived primarily from the soil (hereafter referred to as nutrients) that are classified as essential for plant growth, development, and reproduction (Epstein and Bloom 2005). Essential nutrients are often ranked relative to their concentrations in plant material. Despite them all being considered essential, there is a six order of magnitude difference between the nutrient of lowest (Mo) and highest concentration (N) in plant tissues (Epstein and Bloom 2005). Nutrients required in excess of 1,000 mg kg^{-1} dry mass are referred to as macronutrients (N, K, Ca, Mg, P, S, and Si) and those required in smaller quantities (i.e., <100 mg kg^{-1} dry mass) are referred to as micronutrients (Cl, Fe, B, Mn, Na, Zn, Cu, Ni, and Mo) (Epstein and Bloom 2005). Nutrients can also be placed into the following four groups based on their biochemical function: (1) those incorporated into carbon compounds (N and S); (2) those involved in energy storage or structural integrity (P, Si, and B); (3) those that remain in ionic form (K, Ca, Mg, Cl, Mn, and Na); and (4) those involved in redox reactions (Fe, Zn, Cu, Ni, and Mo) (Evans and Sorger 1966; Mengal et al. 2006). All of these nutrients are exposed to individual (i.e., geological, chemical, or biological) or combined (i.e., biochemical, geochemical, or biogeochemical) transformations and transport processes (i.e., nutrient or biogeochemical cycles) (Schlesinger and Bernhardt 2013; Marschner and Rengel 2007; Cronan 2018). For the purposes of this chapter, we will forgo detailed transformations and transport mechanisms of biogeochemical cycles that occur at landscape, regional, or global scales and instead focus on the inputs, outputs, and recycling of essential nutrients at the forest scale and the potential influence that precipitation partitioning may have on forest nutrient balances.

Following their importance to physiological function, tree growth and forest production are strongly controlled by water and nutrient availability. Forest productivity correlates most strongly with precipitation across global biomes (Foley et al. 1996; Kucharik et al. 2000). In other words, water availability is often the most limiting factor with respect to tree growth and forest productivity. Not surprisingly, dry forest sites tend to respond more strongly to increased precipitation or water amendments compared to wet sites (Huxman et al. 2004). However, too much precipitation can have a negative impact on tree growth and forest productivity (Schuur 2003). Even within the same site, species may respond to moisture additions to different degrees (Coyle et al. 2016). As a general rule, nutrient availability limits tree growth and productivity when soil moisture availability is adequate. Given the relatively large number of essential nutrients, there is potential for a number of different nutrients to limit or co-limit tree growth and productivity. However, the macronutrients, in particular N and P, are the nutrients that most frequently impose the greatest limitation on tree growth and forest productivity (Vitousek and Howarth 1991; Vitousek et al. 2010; Elser et al. 2007). Recent work has investigated the simultaneous limitation of multiple macronutrients (Alvarez-Clare et al. 2013; Wurzburger and Wright 2015; Kaspari et al. 2008) and have demonstrated a number of nuances with respect to soil parent material and forest history; however, it is reasonable to assert that N is the most limiting nutrient in most forests, but P can often be the most limiting nutrient in well-weathered soils due to differences in the cycling of these nutrients (Schlesinger and Bernhardt 2013). Indeed, numerous studies demonstrate increased tree growth and forest productivity in response to N availability as a function of N mineralization (Reich et al. 1997) and fertilization amendments (Albaugh et al. 2008; Coyle et al. 2016). However, nutrient availability becomes saturated at some point beyond an optimal and tree growth must then become limited by some other resource (e.g., light or CO_2) (Coyle et al. 2013). Although rarely reported to limit production directly (but see Kishchuk and Brockley 2002; Lehto et al. 2010), micronutrients may indirectly limit forest productivity through their influence on decomposition rates (Kaspari et al. 2008)—a process responsible for making macro- and micronutrients available for tree uptake. As we will discuss in slightly more detail later, decomposition is critical for making nutrients available to forest trees.

10.2 Plant Water Uptake and Loss

The water balance of a forest is the difference between inputs and outputs. Assuming no inputs from sources other than precipitation (i.e., no groundwater), then the inputs to the soil result from interactions between bulk precipitation and canopy interception. A portion of canopy interception may evaporate back to the atmosphere and another portion can drip through the canopy as throughfall or channel along branches and stems as stemflow. Water inputs to the soil are, therefore, the sum of throughfall and stemflow that penetrate through the leaf litter and enter the soil system. Evapotranspiration (ET), comprised of tree transpiration (following the soil–plant–air continuum as described previously) and evaporation from the soil, litter, and plant surfaces is the major output in forests. Transpiration is the dominant output component in forests, comprising 55–70% of ET (Schlesinger and Jasechko 2014). Indeed, transpiration is the single largest terrestrial water flux in the global water cycle (Jasechko et al. 2013). The primary mechanism of plant water uptake and transpiration is from the soil to the roots as described previously (i.e., the soil-plant-air continuum). Individual trees can transpire extremely large amounts of water. For example, a large overstory tree in the Amazon rainforest used 1,180 kg day^{-1} (Jordan and Kline 1977). However, most individual trees appear to use 10–200 kg day^{-1} (Wullschleger et al. 1998). Scaling individual tree measurements to forest stands indicate that forests may transpire 2.3–6.8 mm day^{-1} (Wullschleger et al. 1998). Transpiration measurements across annual periods indicate that some forests transpire an amount nearly equivalent to throughfall inputs (Caldwell et al. 2018). The water that reaches the soil and is not transferred to the atmosphere via ET leaches through the soil profile past the rooting zone to directly recharge the groundwater or travels as overland flow to recharge streamflow. Although transpiration water is largely sourced from the soil by tree roots, the pathway through the canopy provides additional water uptake opportunities.

Precipitation that is intercepted by tree canopies may evaporate back to the atmosphere or reach the forest soil via throughfall or stemflow; however, intercepted water may also enter the plant directly through foliar or bark uptake. Neither of these uptake processes is as well understood as root water uptake, but more is known about foliar water uptake compared to bark water uptake. A majority (85%) of plants that have been tested in the literature, comprising more than 70 species and 34 families, demonstrate the capacity for foliar water uptake (Goldsmith et al. 2013). Most of the previous research has focused on foliar water uptake as a subsidy in ecosystems where fog or dew commonly occur; however, it can also happen when leaves are wet by precipitation (Dawson and Goldsmith 2018). The actual mechanism of foliar water uptake is not well understood, but recent evidence suggests that stomatal pores may play a role (Burkhardt et al. 2012). Regardless of the mechanism, foliar water uptake rates are much lower than transpiration rates (Berry et al. 2019). Initial approximations of foliar water uptake indicate that the flux may be about 10% of leaf-level transpiration (Berry and Smith 2013). Perhaps not surprisingly, foliar water uptake may be more important for epiphytes, accounting for 30% (Darby et al. 2016) to 70% (Gotsch et al. 2015) of transpired water, than trees (Gotsch et al. 2014). In addition to its potential contribution to transpiration, foliar water uptake may also improve leaf water status (i.e., water potential) (Berry et al. 2019; Dawson and Goldsmith 2018). Bark water uptake has been documented in multiple coniferous tree species (Mason Earles et al. 2016; Katz et al. 1989; Mayr et al. 2014), but we lack an understanding of its importance relative to transpiration. However, there is emerging evidence that bark water uptake is a mechanism for repairing embolized xylem tracheids that would not maintain proper water transport function if left unrepaired (Mason Earles et al. 2016; Mayr et al. 2014). Although this potential repair mechanism has not been linked to leaves, it is possible that foliar water uptake may reverse embolisms in leaf veins. If leaves are capable of foliar water uptake, then it makes sense that they could also absorb some dissolved nutrients through the same mechanism, a topic which will be explored in the following section.

10.3 Plant Nutrient Uptake and Loss

Similar to the water balance, the nutrient balance of a forest is the difference between inputs and outputs. However, forest water and nutrient balances differ largely in their degree of openness, whereas water inputs and outputs are of large magnitude relative to their recycling within the forest (i.e., open system), nutrient cycling in forests is fairly tightly constrained (i.e., closed system). Specifically, the magnitude of nutrient inputs and outputs is much smaller than the magnitude of nutrient cycling between vegetation and soil pools. In other words, the annual recycling of nutrients represents the most significant source of nutrients available for tree uptake and use. At any given point, most nutrients are incorporated into plant tissue and these nutrients will not be available for plant uptake until after the tissue senesces and the organic material are mineralized through decomposition. Approximately 93% of N, 89% of P, 88% of K, and 65% of Ca that is available for uptake has been recycled (Chapin 1991). The highest concentrations of most nutrients are located in leaves, which are ephemeral organs. However, large quantities of nutrients are retranslocated from leaves prior to senescence and retained in perennial tissue, thus limiting the loss of nutrients from individual trees. The proportion of macronutrients resorbed prior to senescence represents 62%, 65%, and 70% of peak N, P, and K concentrations, respectively (Vergutz et al. 2012). Some micronutrients are not resorbed as readily as macronutrients with 11% and 29% of Ca and Mg, respectively (Vergutz et al. 2012). Similar retranslocation of nutrients may occur prior to senescence of ephemeral fine roots (Kunkle et al. 2009), but quantification of this mechanism of nutrient retention is much more challenging to establish belowground and, therefore, much less is understood about general patterns of belowground retranslocation relative to what is understood about leaves aboveground (Brant and Chen 2015).

Additional inputs of nutrients into forests can occur over longer time periods through chemical weathering of rocks, or in the case of N, at a faster rate through physical or biological fixation of atmospheric N. Nutrient inputs can also occur rapidly through dry and wet deposition. In the absence of major disturbance events, including forest harvesting, the loss of nutrients from forests is small. Estimated rates of mineral weathering for forest soils range widely across studies (Table 10.1; Andersson et al. 1997; Feller 1981; Cleaves et al. 1974; Marchand 1974; Mast 1991). Directly measured rates of mineral weathering for forest soils also exhibit wide variation among studies (Bergkvist and Folkeson 1995; Eriksson 1998). The biological fixation of N contributes the largest annual amount of N to terrestrial ecosystem soils from natural processes; however, an even larger quantity is added through industrial fixation to supply agricultural productivity (Schlesinger and Bernhardt 2013). For most forests, N inputs result from dry and wet deposition (Fig. 10.1a, b). The quantity of N inputs to forests can range from 5 to 30 kg N ha^{-1} y^{-1} for low and high elevation forests (Johnson and Lindberg 2013). Air quality near the forest, in addition to forest elevation, likely explains the majority of variation in N deposition rates on the forest canopy. After deposition on the forest canopy, N or other nutrients can be transferred along vegetation surfaces and to the soil via throughfall and stemflow. In fact, dry deposition rates are often indirectly estimated from variability in the concentration of solutes in throughfall and stemflow(Butler and Likens 1995; Kazda 1990; Lovett and Lindberg 1984; Draaijers and Erisman 1995; Staelens et al. 2008).

In addition to throughfall and stemflow-mediated transport of nutrients originating from deposition, nutrients can also be leached from, or taken up by, leaf surfaces (Lebedev et al. 1980; Tukey 1970) (Fig. 10.1c, d). The magnitude of K leaching is the largest of all nutrients (Parker 1983; Schaefer and Reiners 1990), whereas P leaching is higher than that of N leaching, which, in turn, is higher than Ca leaching (Schlesinger and Bernhardt 2013). Leaching rates may be the highest during leaf senescence (Schlesinger and Bernhardt 2013), so leaching of nutrients via throughfall and stemflow may exhibit seasonal patterns related to leaf longevity. Increased leaching contributions of Mg, Ca, and K to throughfall have been reported during leaf senescence (Van Stan et al. 2012). Although it has been argued that nutrient leaching differs among tree functional groups as pines appear to exhibit smaller nutrient leaching rates than deciduous hardwoods (Luxmoore et al. 1981), other data suggest that throughfall mediated nutrient return does not differ much between evergreen and deciduous species (Fig. 10.2; Chapin 1991). Although estimation of leaching rates began with direct observations of isotopically labeled nutrients (Long et al. 1956; Silberstein and Wittwer 1951), most modern estimates of leaching from forest canopies have been indirectly estimated from throughfall and stemflow chemistry, similarly to dry deposition rates on forest canopies (Butler and Likens 1995; Kazda 1990). Indirect estimates of nutrient leaching and dry deposition are, however, problematic as they may incorporate many other nutrient sources (like canopy detritus and epifauna waste—see Chap. 5). As a result, indirect leaching (and uptake) rates derived from throughfall and stemflow are typically called "canopy exchange" rates (Lovett and Lindberg 1984)—although this term still includes those canopy soil and epifaunal nutrient sources/sinks unrelated to exchange with leaf and stem surfaces.

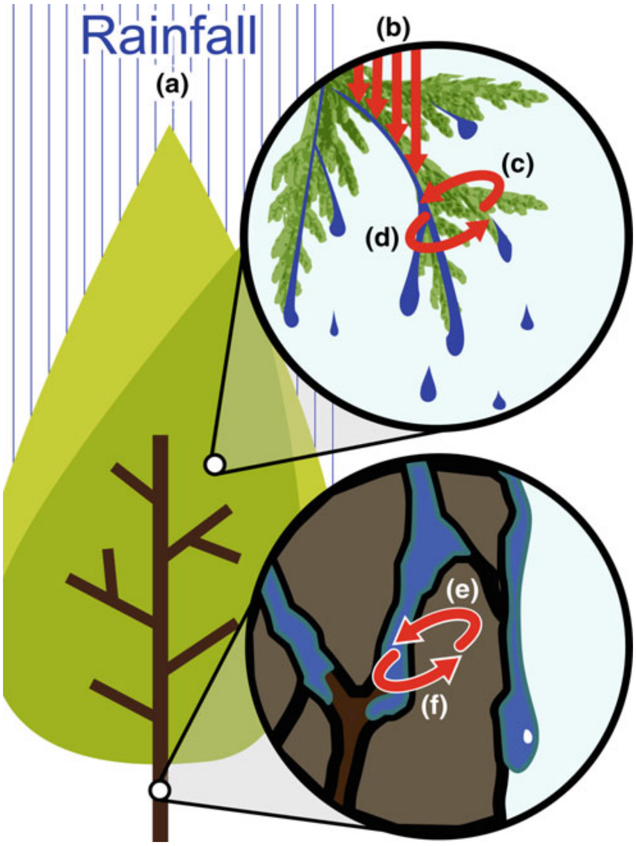
Nutrient concentrations in stemflow are typically higher than concentrations in throughfall, but throughfall volumes are much higher than stemflow volumes. Although it has been argued that stemflow returns a highly concentrated nutrient pulse to the base of trees (Gersper and Holowaychuk 1971), it is unlikely that the benefit is exclusive to the stemflow-generating

Table 10.1 Minimum and maximum mineral weathering rates of P, K, Ca, Mg, and Al expressed as kg ha^{-1} y^{-1}

	P	K	Ca	Mg	Al
Minimum	0.004[a]	<0.1[c]	<0.1[c]	0.7[e]	1.53[a]
Maximum	3.0[b]	28.4[a]	86[d]	52[d]	73.1[a]

Data from [a]Andersson (1991), [b]Feller (1981), [c]Cleaves et al. (1974), [d]Marchand (1974), and [e]Mast (1991)

Fig. 10.1 Principle mechanisms for atmospheric inputs and exchange of nutrients in forest canopies related to storms. **a** Wet deposition and **b** dry deposition provide nutrient inputs. Exchange with canopy surfaces as throughfall and stemflow drain to the surface can result in **c** leaf uptake or **d** leaching, depending on the specific solute. A portion of precipitation will also experience **e** bark uptake and **f** leaching. Rates of these inputs and exchanges for example forests and solutes are provided in the text



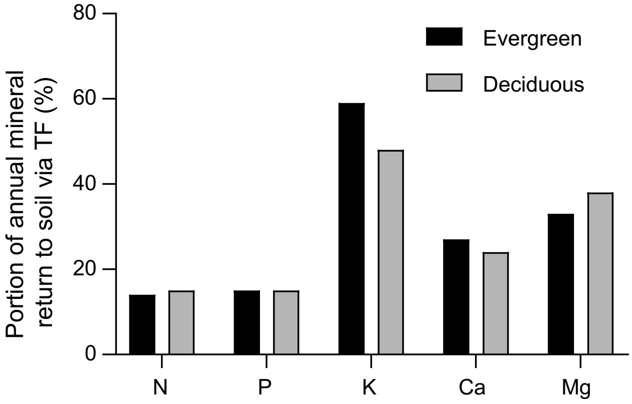


Fig. 10.2 The proportion of annual mineral return to the forest soil that occurs via throughfall for evergreen and deciduous forests (Chapin 1991)

tree since neighboring individuals are likely to be just as capable at acquiring those water and nutrient pulses. In a 22-year-old shrub chaparral ecosystem (Gray 1983; Schlesinger et al. 1982), throughfall comprised 2.6, 0.0, 23, 3.2, and 5.1% of total annual N, P, K, Ca, and, Mg returns to the forest soil, respectively (Fig. 10.3a). These returns accounted for 2.1, 0.0, 19.7, 2.8, and 4.7% of total annual N, P, K, Ca, and Mg uptake, respectively (Fig. 10.3b). Similarly, stemflow comprised 3.3, 0.0, 21.4, 8.2, and 14.1% of total annual N, P, K, Ca, and Mg returns to the forest soil, respectively

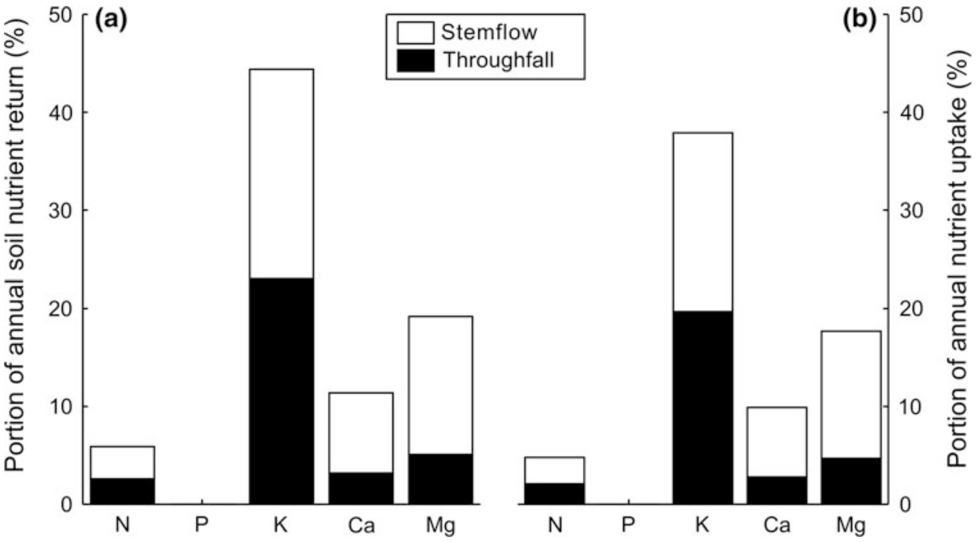


Fig. 10.3 Results from an example ecosystem, 22-year-old shrub chaparral (Gray 1983; Schlesinger et al. 1982), showing **a** the proportion of total annual canopy-to-soil nutrient returns represented by throughfall and stemflow. Depending on the nutrient studied, **b** throughfall and stemflow returns accounted large range of total annual nutrient uptake by the system

(Fig. 10.3a, b). These returns accounted for 2.7, 0.0, 18.2, 7.1, and 13.0% of total annual N, P, K, Ca, and Mg uptake, respectively. Together, the processes of throughfall and stemflow comprised 5.9, 0.0, 44.6, 11.4, and 19.2% of total annual N, P, K, Ca, and Mg returns to the forest soil, respectively, and 4.8, 0.0, 37.9, 9.9, and 17.7% of total annual N, P, K, Ca, and Mg uptake, respectively (Fig. 10.3). The majority of nutrient returns to the soil that becomes available for future uptake occurs through leaf litter inputs and subsequent decomposition (Tobon et al. 2004). This has held true across vegetated ecosystems, even drylands where stemflow was long-hypothesized to engender "islands" of nutrients around arid plant roots (Whitford et al. 1997). The only work to have thoroughly tested this stemflow-nutrient island hypothesis using long-term data (10 years) found that leaf litter inputs and subsequent decomposition appear to be the principal driver—stemflow, alone, was insufficient (Li et al. 2017).

Most nutrients necessary for tree physiological functions are acquired through the soil via root uptake. The bulk flow of water through soil toward roots that results from transpiration is one of the two major processes delivering nutrients to root surfaces (Nye 1977), and facilitates the other major process, diffusion (Oyewole et al. 2014). The passive uptake of nutrients dissolved in water entering plant roots via transpirational flow is suitable to meet tree requirements for many micronutrients and sometimes macronutrients (Turner 1982). Indeed, mounting evidence suggests bulk flow is the dominant process delivering nutrients to root surfaces and moving them inside (Cramer et al. 2009; Oyewole et al. 2014, 2017), so much so that reduced transpiration under elevated CO_2 has been implicated as a potential mechanism limiting nutrient availability to roots, and thus uptake and productivity (McDonald et al. 2002). However, the larger requirements of macronutrients and their relatively low availability in most soils necessitates other mechanisms of uptake. The absorption of nutrients directly into tree roots facilitated by enzyme transporters is also an important mechanism of nutrient uptake (Tischner 2000; Zhang and Forde 1998). The symbiotic relationship between mycorrhizal fungi and tree roots is yet another important mechanism of nutrient uptake (Chen et al. 2018; Dickie et al. 2015; Phillips et al. 2013; Smith and Smith 2011). While most nutrient uptake certainly occurs from soil through plant roots via the mechanisms described above, it is also possible for some uptake to occur directly in aboveground tree tissues.

Along with the direct uptake of intercepted water through tree leaves and bark, some dissolved nutrients can also enter the plant directly through foliar or bark uptake. As with foliar water uptake, the actual mechanisms of foliar nutrient uptake also remain poorly understood (Fernandez and Brown 2013; Eichert et al. 1998). Regardless, the foliar uptake of nutrients is a mechanism that was acknowledged as early as 1844 (Gris 1844) and has since been exploited in agriculture, horticulture, and forestry (Wittwer and Teubner 1959; Miller and Young 1976; Miller 1979). Since leaves impose the largest demand for nutrients, foliar nutrient uptake provides a relatively short and direct pathway for nutrient delivery to the ultimate endpoint (Fernandez and Brown 2013; Fernandez and Eichert 2009). While much more is known about foliar nutrient uptake in response to targeted nutrient applications, recent studies have demonstrated uptake in natural forest systems (Templer et al. 2015). Uptake (and leaching) of nutrients through bark (Fig. 10.1e, f) may be similar to the uptake of nutrients through suberized roots and may occur most rapidly in areas of active growth (Wittwer and Teubner 1959). Some indirect estimates of solute uptake (derived from throughfall and stemflow chemistry) from leafless canopies, and thus from the bark alone, indicate uptake rates from throughfall of ~4 μmol cm^{-2} mm^{-1} of rainfall for NH_4 and NO_3 (Potter et al. 1991), 9–16 μmol cm^{-2} mm^{-1} of rainfall for H^+ (Potter et al. 1991; Puckett 1990). Uptake rates of bark from passing stemflow have rarely been examined, but the few results are contradictory: one study found no solute uptake by bark for rough- and smooth-barked trees (Levia et al. 2011), but another found evidence of bark uptake for multiple solutes from similar tree species (Andre et al. 2008). Specifically, stemflow from the leafless canopies of smooth-barked *Fagus sylvatica* was depleted by 94, 79, 17, and 16 μeq m^{-2} mm^{-1} of rainfall for Ca, Na, Cl, and NO_3; while, rough-barked *Quercus petraea* stemflow was depleted by 53, 107, 41, 123, and 94 μeq m^{-2} mm^{-1} of rainfall for Na, K, NO_{3-}, SO_4 and H^+ (Andre et al. 2008). Again, as with water uptake, much more research effort has been placed in understanding foliar nutrient uptake compared to bark nutrient uptake.

10.4 Canopy Partitioning, Soil Resource Availability, and Roots

Canopy partitioning of throughfall results in heterogeneous distribution of moisture which may directly influence the heterogeneity of nutrient availability based on dissolved minerals in throughfall or stem flow, or indirectly influence the heterogeneity of nutrient availability by influencing the microbial environment and community. Areas that receive disproportionally high quantities of throughfall or nutrient inputs are referred to as hotspots and those that receive disproportionally low quantities of throughfall or nutrient inputs are referred to as cold spots. The same is true of stemflow, as some trees species may be efficient stemflow "funnelers" that provide greater water and nutrient supply than throughfall or rainfall alone (Herwitz 1986) and, thus, create isolated hot spots in soils near their stem base. However, a global review of stemflow production found that very few tree species supply a stemflow subsidy (in excess of what would be supplied by rainfall alone), with ~70% of all studied species yielding <2% of rain as stemflow, and many supply <1 g m^{-2} y^{-1} of nutrients (Van Stan and Gordon 2018). It is expected, then, that most near-stem soils will be cold spots of water and nutrient flux. A review and evaluation of throughfall and stemflow spatiotemporal patterns may be found in Chap. 6 of this volume. Two interrelated studies are oft-cited by throughfall and stemflow research as having correlated these patterns to fine-root patterns (Ford and Deans 1977, 1978); however, although these studies do contain detailed, thorough spatial analyses of fine-root patterns (Ford and Deans 1977) and throughfall patterns (Ford and Deans 1978), they do not contain any quantitative measure of correlation between these patterns. A more "direct" investigation suggests throughfall plays a role in fine-root proliferation (Kavanagh and Kellman 1992), but the authors caution readers against drawing generalizations from their findings as "the sites from which root growth were initiated were … not under close experimental control." This begs the question: what evidence does exist to evaluate the interaction between throughfall, stemflow, and fine-root distribution? In this section, I will introduce plant root forms and functions and our current understanding of controls over their patterns to place throughfall and stemflow into modern context.

Plant roots differ in their form and function. Accordingly, their chemical composition and physical structure reflect their function (McCormack et al. 2015). Typically, larger diameter roots function to transport soil resources, whereas smaller diameter roots function to acquire soil resources (McCormack et al. 2015). Of course, there are a number of other functions these roots provide, but we focus here on resource acquisition. A key physical difference between transport and absorptive roots is their chemical composition which influences their life span (McCormack et al. 2015). Transport roots, hereafter referred to as coarse roots (>2 mm diameter), are perennial structures—they are comprised of woody tissue that generally tends to increase in size (both diameter and length) throughout the life of the tree. The life span of coarse roots, therefore, may range from decades (e.g., eastern redbud), centuries (e.g., longleaf pine Chapman 1932; Wahlenberg 1946; Jose et al. 2006), to millennia (e.g., bristlecone pine Feng and Epstein 1994; Sonett and Suess 1984; Lanner and Connor 2001; Brunstein and Yamaguchi 1992). Coarse roots provide structural integrity and transport capacity, storage, and the overall spatial network necessary for distribution of absorptive roots (McCormack et al. 2015). Absorptive roots, hereafter referred to as fine roots (≤2 mm diameter), are ephemeral. Fine-root life span ranges from 0.5 to 2.0 y^{-1} (McCormack et al. 2015), with most ranging from 1.1 to 1.5 y^{-1} (McCormack et al. 2013),and can be influenced by a variety of factors, including diameter, depth, developmental state, and soil resource availability (Coleman and Aubrey 2018). Fine roots acquire soil resources, sense environmental cues (e.g., changes in water, temperature, or nutrient availability), form relationships with symbiotic mychorrhizal fungi and bacteria, and play an overwhelmingly important role in the forest carbon cycle (McCormack et al. 2015). Fine roots are, therefore, much more relevant to any discussion of precipitation partitioning impacts on tree water and nutrient balance, but coarse roots may also be influenced by the spatial partitioning of precipitation and nutrient pulses (Coleman 2007).

Water and nutrients are generally not distributed homogeneously in the soil through space and time (Fitter 1994). In fact, variation in nutrient availability within the rooting zone of a plant can be as large as variation at the plot-scale (Jackson and

Caldwell 1993a, b). To improve resource acquisition under the spatial and temporal heterogeneity in soil resource distribution, plant roots exhibit both physiological and morphological plasticity (Hodge 2004). Physiological plasticity is manifested through increased uptake capacity in areas (i.e., patches) or times (i.e., pulses) of high resource availability (Saker and Drew 1978; Robinson 1994), whereas morphological plasticity is manifested through increased root proliferation (Campbell et al. 1991; Wijesinghe et al. 2001), usually in response to extended periods of increased resource availability in a patch. Physiological responses to resource patches or pulses occur more rapidly than do morphological responses (Jackson et al. 1990; Jackson and Caldwell 1991), and may actually trigger morphological responses (Hodge 2004). While both physiological and morphological responses to resource patches and pulses are important, it remains uncertain which mechanism is more important than the other (Hodge 2006).

Much of what we know about root system responses to chronic or temporary shifts in resource availability has come from controlled manipulative studies. Irrigation via drip tubes is a common approach to manipulate soil water and nutrient availability and it results in a heterogeneous distribution of soil water and nutrient availability. Indeed, this heterogeneity can be viewed as analogous to the creation of hot spots and cold spots that result from canopy partitioning of precipitation. However, drip tubes result in chronic heterogeneity of resource distribution, unless the drip tube is repeatedly moved. It may seem reasonable to assume that chronic heterogeneity from drip tubes is of greater temporal stability than throughfall patterns; however, the temporal persistence of throughfall patterns are as persistent as canopy structure—being found to persist across variable storm conditions, seasons, and even years for nearly every forest type (Gerrits et al. 2010; Guswa and Spence 2012; Keim et al. 2005; Nadkarni and Sumera 2004; Raat et al. 2002; Zimmermann et al. 2007, 2009). Thus, the principal difference between drip tubes and throughfall–stemflow patterns may be the source of these patterns: one being derived from canopy structure, or the plant itself, the other being a manipulation. Studies investigating rooting dynamics in response to water and nutrient amendments supplied via drip tubes have observed consistent increases in fine-root biomass and density along the drip line in a variety of tree species (Coleman 2007; Fabiao et al. 1995; Pronk et al. 2002; Ruiz-Sanchez et al. 2005). Lab and greenhouse experiments with tree seedlings have observed similar root proliferation in response to high nutrient patches (Mou et al. 1995; Einsmann et al. 1999; Woolfolk and Friend 2003). However, the ability to proliferate roots in response to nutrient patches varies among species (Coleman 2007). Although fine roots are most likely to respond to hot spots over short periods, the entire root system (i.e., coarse roots as well) may respond when hot spots are maintained over longer periods.

10.5 Developing a Mechanistic Framework for Root–Interception Interactions

A review of the literature clearly indicates that precipitation partitioning processes have primarily and historically been examined from a pure hydrological or hydrometeorological perspective—and from a small community of scientists within these fields (see Chap. 1). A few decades after the advent of “ecohydrology” as an interdisciplinary subdiscipline (Hannah et al. 2004; Rodriguez-Iturbe 2000), the hydrological processes of interception, throughfall, and stemflow have been recognized as important drivers of ecological processes, particularly for intrasystem nutrient cycling (Chapin 1991). However, the difficulties inherent in rectifying the differences between hydrologic and ecological scientific perspectives involved in ecohydrological research—i.e., Newtonian versus Darwinian (Harte 2002; McClain et al. 2012; Rodriguez-Iturbe et al. 2005)—are apparent in publications from the precipitation partitioning community. That is to say, the Newtonian perspective is strong. Although this results in rigorous sampling campaigns, e.g., throughfall observations for each storm within a single plot can be as high as $n = 350$ (Zimmermann and Zimmermann 2014), it also results in little-to-no plot replication. In achieving a mechanistic framework of how the throughfall, stemflow, and interception hydrologic processes interact with plant roots, an integration of the Darwinian perspective will arguably be necessary. Thus, this section suggests two avenues for improved integration of ecological standards to promote the development of a mechanistic framework for future investigations of root interactions with precipitation partitioning.

10.5.1 Stemflow and Roots: Moving from Individualistic to Holistic Frameworks

Stemflow literature tends to focus at inappropriate scale or ecological level of organization when ascribing implications of partitioning. Specifically, the acute spatial partitioning resulting from stemflow is often and incorrectly linked to benefits of those particular individuals (Carlyle-Moses and Schooling 2015; Carlyle-Moses 2004; Carlyle-Moses and Price 2006; Levia and Germer 2015; Levia and Herwitz 2000; Siegert and Levia 2014). In fact, classic literature in the field even linked stemflow to evolutionary pressures, positing that adventitious roots may have resulted as an adaptation to acquire water moving along the stemflow pathway (Herwitz 1991). More broadly, the literature links fluxes of stemflow water and nutrient to benefits at the individual tree level. For example, in cases where stem size influences the quantity of stemflow delivered to the base of a tree, it has commonly been argued to represent a mechanism of providing more water and more dissolved nutrients to that individual tree. Unfortunately, this individualistic perspective ignores the extreme heterogeneity observed in the horizontal distribution of tree roots. In other words, the forest is not considered beyond the tree.

Analogous to leaf area dynamics aboveground that proceed through stand development to a maximum spatial occupation referred to as canopy closure, fine roots proceed through a similar developmental process of horizontal belowground area occupation referred to as root closure. During early stages of stand development, absorptive roots, and their mycorrhizal symbionts explore the soil as lateral roots extend further and further away from the tree stem. Indeed, tree roots can extend away from tree stems 1.5 to 2.5 times the tree height (Sudmeyer et al. 2004). Given that most closed canopy forests have stockings of hundreds to thousands of trees ha^{-1}, the intermingling of roots should be obvious. Although lateral roots continue to grow and extend, most of the area available for fine-root occupation is exploited within the first 4–10 years of stand development (Yanai et al. 2006), or even earlier under expedited growth conditions (Coleman 2007). Thus, most forest soils have a consistent stocking of fine roots. Moreover, the fine roots that are present at the base of a tree stem where stemflow is depositing moisture and nutrient pulses are likely roots belonging to a neighboring tree and not to the tree generating stemflow. Indeed, rooting density did not decline with distance from tree stems but rather appeared to increase, which is consistent with the concept of overlapping root systems of adjacent trees (Coleman 2007).

10.5.2 Throughfall and Roots: Moving to Controlled Frameworks

Interactions between roots and throughfall water/nutrient supply patterns have almost exclusively been examined in natural forest systems (Anderson et al. 1969; Bouten et al. 1992; Ford and Deans 1978; Reynolds 1970), with various uncontrolled elements (understory, storm and herbivory disturbances, heterogeneous epiphytic vegetation cover, etc.). The limited data supply from research conducted in forests with any silvicultural controls or manipulations is clear by the simplifications required of the few modeling efforts seeking to evaluate the role of "canopy versus roots" in the "production and destruction of variability" in soil properties and processes (Bouten et al. 1992; Guswa 2012). Studies employing manipulations of throughfall patterns to improve mechanistic understanding of fine-root properties and processes do exist, primarily via the large-scale reduction or removal of throughfall (Fisher et al. 2007; Hinko-Najera et al. 2015; Joslin et al. 2000; Moser et al. 2015). These artificial throughfall reduction/removal methods have yielded important advances, but they address only broadly sweeping mechanisms related to drought or disturbance where interception would be drastically and suddenly altered. However, to my knowledge, the relocation of throughfall (and stemflow), the co-monitoring of throughfall and stemflow as stand ages, or other such mechanistically oriented tasks have not yet been done.

10.6 Conclusions

Despite decades of research into canopy partitioning of precipitation and its implications on tree water and nutrient balance, many questions remain regarding fundamental principles and mechanistic controls. Indeed, compared to the broader literature base describing throughfall and stemflow dynamics, relatively few studies have placed those hydrologic and nutrient fluxes within the context of tree hydrologic and nutrient budgets. Mounting evidence suggests that foliar water and nutrient uptake may be important processes; however, further work is needed to contextualize bark water and nutrient uptake within broader plant hydrologic and nutrient balance. Drip tube studies indicate that persistent water and nutrient availability can simulate fine-root production and maintain higher densities of fine roots; however, the limited, un-replicated and loosely controlled data available on throughfall and fine-root patterns provide unclear results. Current work on stemflow–root interactions focuses on the potential of individual trees acquiring stemflow water and nutrient inputs; however, this focus requires more rigorous assessment of root closure and the intermingling of roots from a number of individuals. Future studies aimed at tracking the use of stemflow-mediated water fluxes may help reassess this currently untested assumption. An improved mechanistic understanding of the role throughfall and stemflow play in water and nutrient budgets and how they impact fine-root patterns and processes will require controlled experiments that deliver water and nutrient pulses and patches across a gradient of magnitude and time and observe short- and long-term physiological and morphological responses of roots.

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Throughfall
(Water+Solutes)
Litter
Decomposition

Role of Precipitation Partitioning in Litter Biogeochemistry

11

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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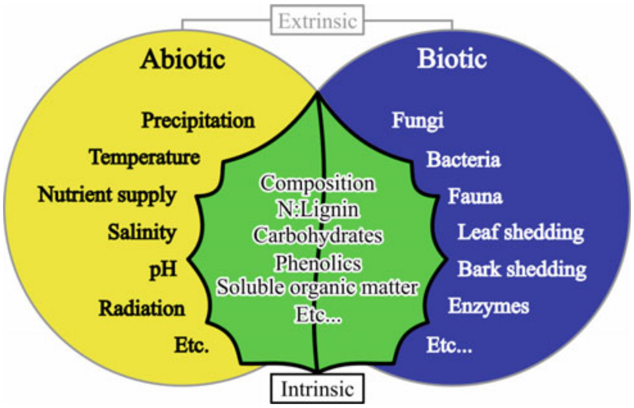


Fig. 11.1 Illustration showing common biotic and abiotic influences and their relationship with intrinsic and extrinsic factors affecting litter decomposition

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.

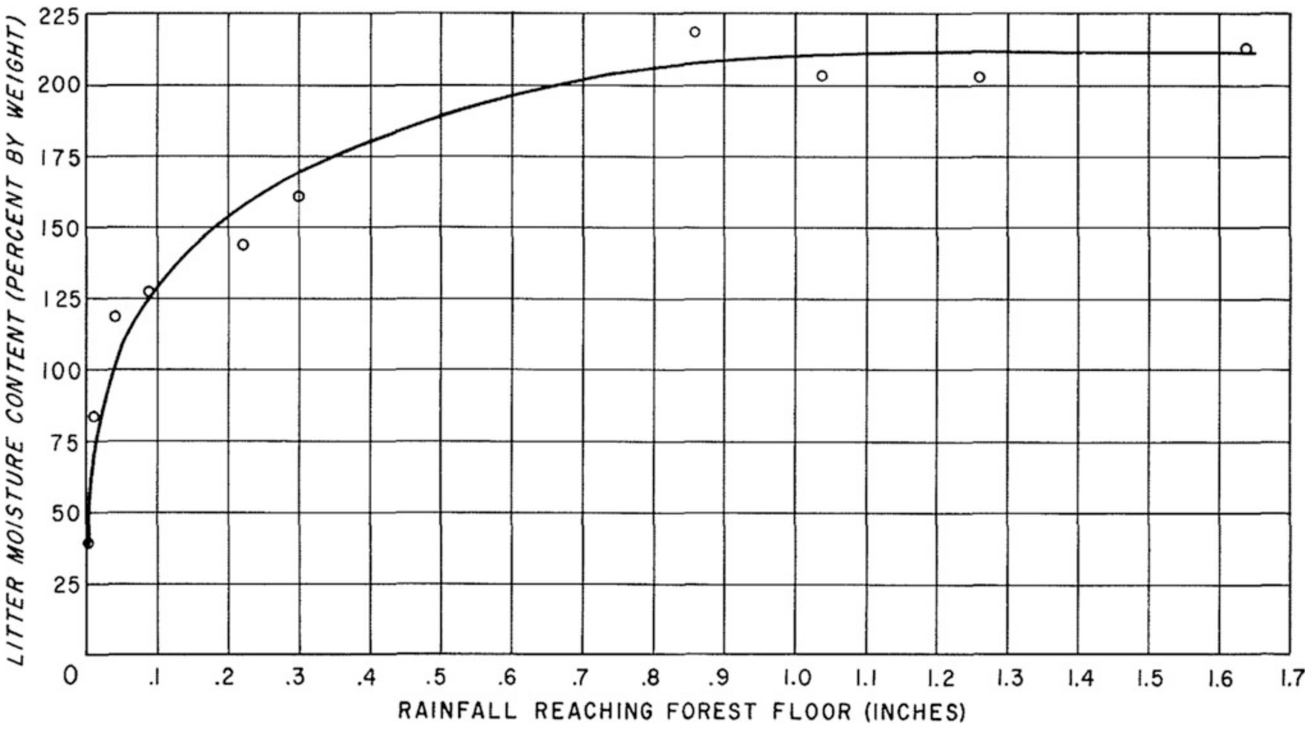


Fig. 11.2 The amount of throughfall necessary to wet the forest floor to its maximum water holding capacity after allowing it to drain for 24 h. While protected from evaporation (Reproduced from Helvey 1964, U.S. Forest Service). Measured in a mixed deciduous forest at the Coweeta Hydrologic Laboratory. 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:

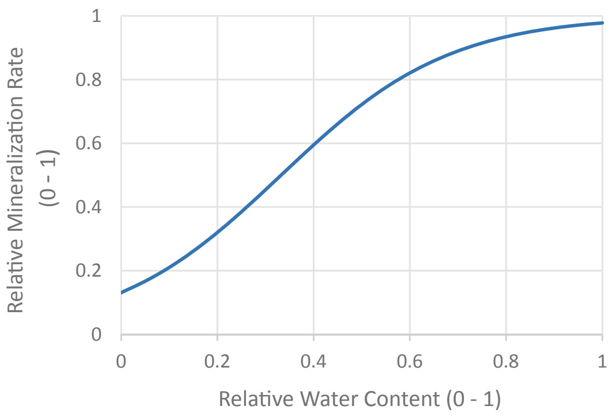
$$\text{N mineralization rate} = \exp\left[3.36\,(\text{T} - 40)/(\text{T} + 31.79)\right] \tag{11.1}$$

where T is temperature.

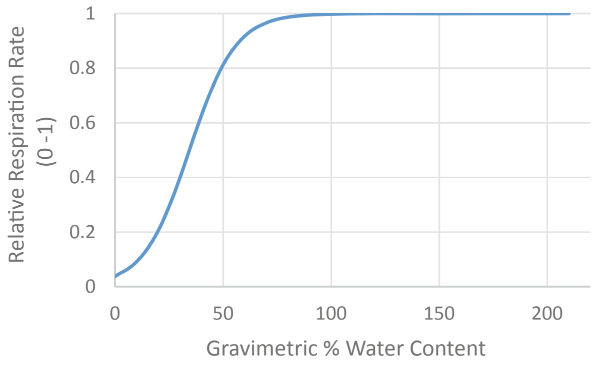
Curves of mineralization as a function of relative water content are generally hyperbolic or logistic, that is, they rise with water content with decreasing slope until a maximum is reached. The equation presented by Paul et al. (2003) relates the relative mineralization rate or respiration rate at a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



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

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:

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

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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12

A Review of the Effects of Throughfall and Stemflow on Soil Properties and Soil Erosion

David Dunkerley

Abstract

Over a large fraction of the global landsurface, precipitation interacts with standing vegetation or organic litter prior to reaching the mineral soil. This interaction has both benefits and costs for plants, and these arise over varying timescales from minutes or hours to years or decades. A two-way interaction emerges in which the precipitation-vegetation interactions can affect plant growth, which in turn may alter the nature of the physical processes responsible for the plant-precipitation interactions via changes in plant architecture. This chapter explores two important examples of these processes. These are canopy changes in the drop size characteristics of water reaching the mineral soil, and the occurrence of contact flow or 'stemflow'. Both may result in important hydrologic and erosional outcomes in forests, shrublands, and croplands, some of which are beneficial to plants, and some potentially detrimental. In particular, the effect of vegetation canopies in creating throughfall drops that are larger than those of open-field rainfall may result in higher sub-canopy erosivity. Likewise, the rainwater funnelling action of vegetation canopies and the resulting focussed delivery of stemflow may result in overland flow and scour of the soil surface around the base of some plants. Many of the interactions of precipitation and vegetation are conditioned by the characteristics of the open-field rainfall incident upon plant canopies; the chapter therefore also presents an overview of some of the key attributes of rainfall as they relate to processes acting on, within, and beneath vegetation. In many cases, the most important attributes of rainfall relate to the timescales characteristic of rainfall events, including event duration, depth, and intensity. These, and the nature of the vegetation and soils, exhibit wide geographical variability. This leaves many significant challenges facing the development of a full understanding of the interactions of rainfall, vegetation, and soils.

Keywords

Open-field rainfall • Throughfall • Impact droplets • Gravity droplets • Splash erosion • Stemflow erosion

12.1 Introduction

Over parts of the planetary landsurface, precipitation arrives directly at exposed rock, regolith, or mineral soils. This is the case over extensive portions of the global drylands where vegetation is largely lacking, as well as at high altitudes, on recent volcanic flows, on freshly deposited overbank sediments on floodplains, on exposed tors or granite domes, on recently deglaciated landscapes, coastal rock platforms, and elsewhere. However, where plant cover is more extensive, the first interactions of precipitation are frequently with plants in growth position, or with fallen plant parts (plant litter, including stems, leaves, branches, flower parts, bark, etc.) resting on the soil. Even in the case of dryland soils that lack a vascular plant cover, or on exposed bedrock, the first interactions with precipitation may be with microphytic plants such as lichens and mosses (Porada et al. 2018), which are capable of holding water equivalent to 6–10 times their dry weight (Link et al. 2004). Many areas of the landsurface are now cultivated, and in these areas, the first interactions of precipitation may be with

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managed canopies such as those of cereal crops, or tea and coffee plantations, softwood or hardwood plantations, vegetable gardens, or urban forests. In such cases, there may be particularly strong seasonal changes in the nature of the interactions with precipitation, as a function of stage of growth, harvest cycles, or deliberate vegetation thinning and other management interventions such as branch removal or understory litter and weed control (Dietz et al. 2006; Ganatsios et al. 2010; Molina and del Campo 2012; Hakimi et al. 2018). Interactions with precipitation may be functionally important for many plant taxa, perhaps improving plant water relations and facilitating increased photosynthesis (Dawson and Goldsmith 2018; Gerlein-Safdi et al. 2018).

There are many forms of precipitation, including rain, hail, dew, mist and fog, snow, and rime ice. All interact with vegetation, though through different mechanisms. This chapter willl consider only precipitation consisting of liquid water, since the behaviour of snow and ice on vegetation involves different mechanisms that would require a separate treatment. The principal kinds of interactions between liquid water precipitation and plants or plant litter (see other chapters in the present volume) include the progressive wetting-up of standing vegetation, including foliage, branches, and stems (bearing in mind that rain frequently arrives obliquely, driven by wind; Hörmann et al. 1996). There may be a maximum depth of water that can be retained, the 'canopy storage capacity', before additional water overflows and is released by dripping or trickle flow along the plant parts. Splash on wet plant or litter surfaces is another important interaction. Splash primarily occurs on surfaces that are already wet, and does not occur at all on dry, smooth surfaces (Mutchler and Larson 1971). Splash may release small water droplets in huge numbers, and these may undergo rapid evaporation, such that many may be lost or swept away by wind. Plants may release gravity-driven drip from wet foliage or branches, or from ground litter. These 'gravity drops' may cascade through the vegetation canopy, having multiple interactions with plant surfaces during passage toward the ground. Frequently accompanying splash or drip is trickle flow, generally referred to as 'stemflow', even though this may occur on petioles, twigs, leaves, and branches, as well as on stems. In this case, water flows in contact with the plant surface, often to reach the ground after many meters of travel along the trunk of a tree, for instance (Fig. 12.1). Because of the diverse forms of trickle flow, the essence of which is that water moves over the surface of some plant part, Moss and Green (1987) proposed that this form of water movement be termed 'contact flow', and this is probably a preferable term, despite not having been widely adopted, since this form of flow is certainly not limited to the stems of plants. However, in the remainder of this chapter, reference will generally be made to 'stemflow', following common usage. All of the above processes may also occur on fallen litter, which can be wetted-up, may generate splash if already wet, or drip if lying above the soil surface. Contact flow may also occur on fallen plant parts, which can be abundant in many forests.

In all of the above processes, both solutes and particulates may be carried with the dripping, splashing, or flowing water. Spores may also be dispersed by splash on plant canopies (Paul et al. 2004). Materials carried in splash, drip or stemflow can result from dry or wet deposition on the aerial parts of the vegetation, or may be sourced by flushing and leaching from the vegetation itself. As a result of this family of mechanisms, water delivered by precipitation may finally reach the mineral soil in vegetated areas via a range of pathways, each with their own potential to scavenge and deliver solutes and particulates. As a result, the water is commonly enriched in terms of its dissolved load, in comparison with the incident rain.

There are potential erosional and other consequences of the interactions of precipitation with plant parts, as a result of the change in the ways (rates, pathways, locations) in which water arrives at the soil surface. These form the principal subject of this chapter. We can classify the changes into several categories:

- delivery of throughfall drops in the absence of rainfall (fog drip)
- A change in the drop size (diameter) and fall speed of drops within the canopy, compared with open-field rainfall;
- a change in the flux of drops and in the timing of their arrival at the soil surface, in comparison with the intensity fluctuations of the open-field rainfall;
- altered locations struck by incident drops at the soil surface, including some areas that may receive fewer drops than would be expected if the ground was exposed to open-field rainfall (e.g. if sheltered by an overlying branch), and some that may receive more (e.g. locations beneath drip points);
- focussed delivery of stemflow to the soil around the base of a plant (corn plant, desert shrub, rainforest tree, etc.), possibly gathered from a large canopy above the stem.

It is also necessary to remember that weathering and other geochemical processes beneath a plant canopy or a litter layer may be different from those in the open, in ways that may be related to the physical, chemical or microbiological effects of roots, fungi, earthworms, termites, ants, and other organisms, as well as to the characteristics of throughfall and stemflow. Microclimatic conditions including solar radiation, wind, and humidity are also altered by the presence of a vegetation cover.

Fig. 12.1 Flow paths of stemflow (contact flow) are visible owing to wet and dry areas on the branches and trunks of smooth-barked Eucalyptus trees, Melbourne, Australia. Complex wetting patterns are evident, including wet upper surfaces of branches, and trickle flow wrapping around the branches to gather in integrated, pendant flow paths down the undersides of branches (Photos: author)

These influences may affect soil properties, including texture, infiltrability and nutrients. Via a feedback loop, these soil changes may affect plant growth, and hence may result in modifications to the plant canopy and hence its interaction with precipitation. The interactions of precipitation with vegetation are therefore bi-directional in nature, although the interactions occur via different pathways and probably at very different rates. For example, at an unusual Italian field site where some soils were acidic and some alkaline (Corti et al. 2019), throughfall and stemflow generated by Turkey oaks (*Quercus cerris* L.) only 50 m apart had distinctively different chemical composition despite being the same age and growing on the same rock type and in the same climatic conditions. Where tree roots extend into the regolith, there are various processes that affect weathering, including the mechanical effects of the roots in cracking and prising. However, the mycorrhiza are potentially more significant, as they greatly extend the area of the root system across which chemical reactions may deliver nutrients to the plant (Pawlik and Kasprzak 2018). In this chapter, we will primarily focus on processes acting over timescales from minutes to years; those occurring over the millennial timescales of weathering and soil development are not considered further.

This chapter then is concerned primarily with the ways in which soil properties and soil erosion are affected by the influence of vegetation on the manner in which precipitation finally reaches the soil surface. Soil erosion can result from diverse processes, including the action of wind, tree throw, soil creep, solifluction, ice heave, the scour caused by flowing water, and the movement of particles caused by the physical impact of water drops in rainfall or throughfall. In what follows, we are only concerned with the processes that are influenced by throughfall and stemflow. Even this is a large subject, given the global range of soil types, climatic conditions, and forms of vegetation that could be considered. It will become clear that even though there is a very large literature on this subject, much remains to be learned about the nature of the interactions between precipitation and vegetation across the global landsurface, and their consequences for soil properties and erosion.

We begin by considering rainfall and its properties prior to interactions with plant materials: ‘open-field’ rainfall. We then consider the large water drops that can fall from above-ground plant parts, and which can be very erosive (Sect. 12.3). The much smaller impact (or splash) droplets, which are hydrologically important (see Chap. 3 on evaporation) play a minimal role in soil properties and erosion. Stemflow and its effects are considered in Sect. 12.4. Section 12.5 considers the challenges of quantifying the erosivity of rain and throughfall, and the erodibility of soil materials, as the two key aspects of understanding (and perhaps predicting) soil detachment and transport. Finally, some conclusions and a view to the future of research in the areas covered by this chapter are considered in Sect. 12.6.

12.2 Open-Field Rainfall: A Brief Overview of Key Characteristics

The nature of the rain arriving at the top of a plant community greatly affects the subsequent interactions on and within the vegetation. The fate of water delivered to vegetation communities depends on many aspects of the local rainfall climatology, including the timing of rainfall (diurnal/nocturnal, seasonal, time between showers), rainfall depth and intensity, and drop sizes and their fall speeds, which are linked to rainfall intensity. Many of these important aspects of precipitation exhibit large variations in time and space, and differ among regions and environments (arid, temperate, wet tropical, and so on). In this section, we examine briefly some of these important rainfall characteristics, since they are major determinants of subsequent splash, drip, and stemflow processes.

12.2.1 The Nature of Water Drops in Open-Field Rainfall

Open-field rainfall over the continents is the product of the cloud microphysical processes of nucleation, condensation, and droplet growth. Cloud droplets are too small to precipitate, and only when droplets have grown to ~ 0.1 mm diameter do they begin to fall as precipitation. Sustained rainfall is supported by moisture convergence and uplift, so that drops falling from the cloud base must have sufficient mass that they are not swept up in the rising column of air. In more intense rainfall, there is a tendency for larger drops to form an increasing proportion of the drop population (Kelkar 1945, 1961); in drizzle, small drop sizes dominate (Westbrook et al. 2010). For Malaysia, for instance, Yakubu et al. (2016) defined an exponential relationship between the median volume raindrop diameter (d_{50}, mm) and the intensity (I, mm/h):

$$d_{50} = 3.27 - 1.63\,\exp(-0.04\,I)$$

This relationship was based on intensity data extending to >100 mm/h.

The surface tension force becomes insufficient to hold drops in a spherical shape as their diameter and mass increase, so that large drops exhibit unstable shapes, and tend to become oblate as they fall through the atmosphere (McDonald 1954). Pressure forces on large falling drops may cause them to break apart into smaller, more stable drops, and this instability determines the maximum possible raindrop diameter. The precise nature of droplet breakup is still debated, but it has been hypothesised that the exponential distribution of drop numbers by diameter reflects this process (Kostinski 2009; Barros et al. 2010). It is likewise not completely certain what the maximum size of raindrops is. Gatlin et al. (2015) confirmed that maximum drop diameter increases with rainfall rate (intensity), but found that only 0.4% of drop spectra contained drops >5 mm diameter. They noted that ‘giant’ raindrops >8 mm diameter do occur, and found that the largest recorded in their data had a diameter of 9.7 mm. This drop was associated with a thunderstorm in Oklahoma. Hobbs and Rangno (2004) also reported ‘super-large’ raindrops of >8.8 mm diameter, and possibly 1 cm diameter, in the Marshall Islands, and

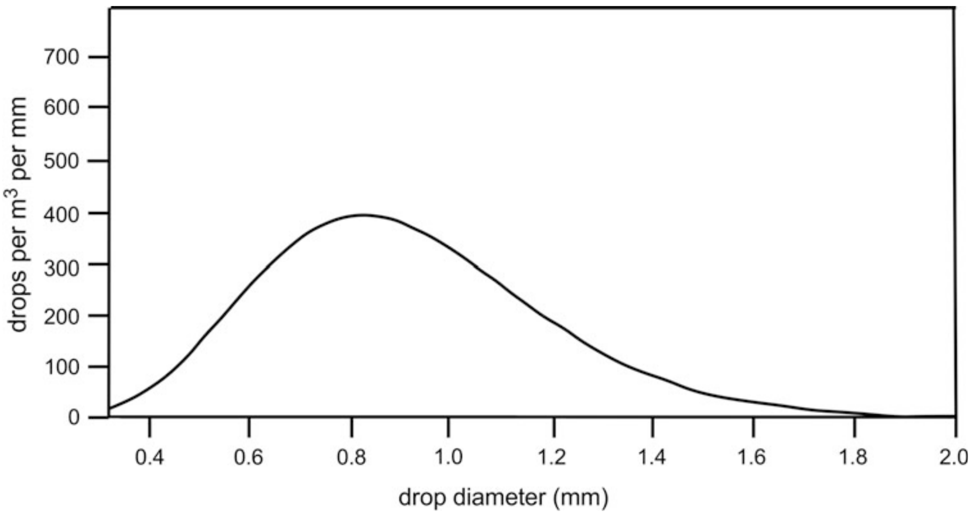


Fig. 12.2 A gamma distribution of drop diameters, as is commonly seen in rainfall. Other distributions, including log-normal, are frequently also used to describe drop size distributions. The raw disdrometer data to which the gamma distribution was fitted were collected at Chilbolton, England, during rain at 2.1 mm/h (Adapted from Ekerete et al. (2015), Radio Science 50, 876–885)

following a bushfire in Brazil. However, the majority of raindrops are <5 mm in diameter, and smaller drops are far more abundant than larger drops. For at least the larger raindrop diameters, the relation follows the exponential number distribution introduced by Marshall and Palmer (1948). This relation is

$$\mathrm{N_d} = \mathrm{N_0 e^{-\lambda d}}$$

where N_d is the number of drops of diameter d per m^3 of air, N_0 is a constant that represents the number of drops for d = 0, and λ is a fitting constant that varies with rainfall rate. N_0 is large for drizzle and declines for more intense rainfall (Joss and Waldvogel 1969). The interaction of drops falling at different speeds, as a function of their diameter, may result in collisions, whose outcome may be droplet bouncing, breakup or coalescence; these interactions may modify the distribution of drop sizes (Low and List 1982; Villermaux and Eloi 2011). For small drop diameters there is a decline in abundance, so that for the entire drop size population, a log-normal or gamma distribution, with a mode in the range 1–2 mm, is often exhibited (Konwar et al. 2006; Mazon and Viñas 2013; Ekerete et al. 2015) (Fig. 12.2). Whether an exponential or a gamma distribution provides the best fit to observed distributions of drop size depends partly on the intensity, and may differ between stratiform and convective rainfall (Caracciolo et al. 2008). For additional information on precipitation and associated microphysical processes, reference may be made to texts such as Pruppacher and Klett (1997).

An important characteristic of rain drops is their terminal velocity in air. Upon commencing to fall from an updraft, drops are reasoned to accelerate from rest. Wang and Pruppacher (1977) investigated the fall distance required for terminal velocity to be reached, a condition where gravitational pull and frictional drag are in balance. For virtually all raindrop diameters, they showed that ~12 m is sufficient fall distance for terminal velocity to be reached; small drops require shorter fall distances to reach their terminal velocity than large drops (Fig. 12.3). There are many studies of terminal velocities (Gunn and Kinzer 1949; Best 1950; Berry and Pranger 1974; Yu et al. 2016). Terminal velocity increases with drop diameter, but at a diminishing rate for larger drops; the relation is generally described by a polynomial equation. Larger drops take on a flattened (oblate) shape as they fall, and this affects the airflow around the drop, and the frictional drag that it experiences. Approximate, indicative speeds are 4 m/s for a 1 mm drop, 6.5 m/s for a 2 mm drop, 8 m/s for a 3 mm drop, and 9 m/s (~32 km/h) for a 4 mm drop. Drops smaller than about 1 mm diameter have been recorded as falling faster than their expected terminal velocity (Larsen et al. 2014). The phenomenon of such 'superterminal' raindrops is not fully understood, but has potential relevance to erosion by open-field rainfall.

Estimates of terminal velocity V_t (cm/s) for drops of diameter d (mm) can be found from the empirical formula presented by Reynolds et al. (1987)

$$\mathrm{V_t} = 880.0\left[1-\exp\left(-\left((\mathrm{d}+0.115)/1.718\right)^{1.336}\right)\right]$$

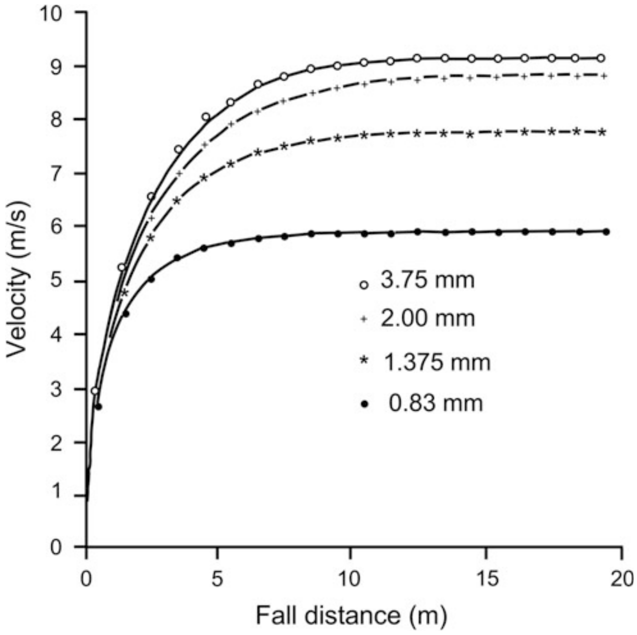


Fig. 12.3 The relationship between fall velocity of water drops with distance from a release-point. The experimental data show that larger drops achieve higher terminal velocities, but require a larger fall distance to reach this than do smaller drops. A fall of 10–12 m is sufficient for all drop diameters shown to reach terminal velocity, but much of the acceleration occurs in the first metre of fall. Adapted from Wang and Pruppacher (1977), Journal of Applied Meteorology 16, 275–280, by kind permission of the American Meteorological Society

These speeds are affected by height above sea level, which affects the density of the atmosphere and hence the drag felt by a falling drop, as well as by wind and atmospheric turbulence. Strong winds can deflect drops from the vertical fall expected in still air, and in a size-selective manner, such that small drops are most easily deflected. Oblique rain is thus common, and raises questions about the most appropriate orientation of rain gauges where topography may cause location-related deflection of wind (Blocken et al. 2006). Oblique, wind-driven rain is known to be able to drive the splash-saltation of grains across the ground (Vieira et al. 2004).

Among the properties of raindrops that have been explored in terms of their connection to soil erosion by splash are terminal velocity, kinetic energy (Rosewell 1986), impact force, and momentum (Goebes et al. 2014). The kinetic energy is given by

$$\mathrm{KE} = 0.5\mathrm{mV}^2$$

where KE is the kinetic energy in joule, m is drop mass in kg and V is fall velocity in m/s. Given that rain is composed of a distribution of drop sizes, the energy per mm of rain may be estimated by summing the KE across all droplets. A raindrop of 3 mm diameter has a kinetic energy of $\sim$ 0.4 mJ (millijoule) at a terminal velocity of 8 m/s, and this energy can be partially transferred to splashed soil particles upon impact. Summed across all drop sizes, the total amount of kinetic energy delivered to the ground by rainfall can be expressed as J/m^2/mm or as J/m^2/h; the total kinetic energy delivered of course increases with rainfall intensity, and often reaches several kJ/m^2/h, or 20–30 J/m^2/mm (Shin et al. 2016).

12.2.2 The Nature and Occurrence of Rainfall Events

Open-field rainfall arrives in episodic falls separated by rainless periods. During the separate falls (which can be identified by a defined MIT, or minimum inter-event time, often taken to be 6 h with no rain), termed ‘rainfall events’, the intensity fluctuates with time, the temporal sequence of intensities being termed the ‘event profile’ or ‘intensity profile’. Each rainfall event can also be characterised by a definable duration (h) and a depth (mm), as well as an average intensity and various measures of peak intensity in periods of a few minutes or tens of minutes (e.g. I_5, I_{30}, I_{60}). Events can also be characterised by the duration of the rainless periods that precede (the ‘waiting time’) and follow them. Rainfall most commonly falls at an intensity of a few mm/h, and exceptionally intense rainfall may occur at 50–100 mm/h or more. Convective rainfall frequently exhibits highest intensities early in the course of an event, and then a waning intensity, whilst stratiform or frontal rainfall may show less time variation. During rainfall, vegetation canopies become progressively wetter (uppermost foliage first, and foliage deep within the canopy later) and they progressively dry out between showers. Most studies estimate the time for full drying to be ~ 6 h (Dunkerley 2008). A plant canopy can notionally hold, under static and windless conditions, a depth of rainfall that is typically up to ~ 100 g/m^2, or the equivalent of a few mm of rainfall. Beyond this, if rain continues to fall, the canopy sheds water as drip or stemflow at increasing rates. Shaking as a result of wind empties the canopy faster, and splash (once the canopy is wet) produces impact droplets which may number in the thousands per drop impact, and which may evaporate rapidly owing to their large surface area-to-volume ratio. The release of drips may be encouraged by leaves that droop under the weight of accumulated water, and the intensity of the rainfall increases the apparent storage capacity, since foliage is wetted faster than it can empty by drip or trickle flow.

Having described something of their sizes and fall speeds, we can now proceed to consider some of the effects of water drops (rain drops or drops released by wet vegetation during and after rain) on erosional processes.

12.3 Background: The Impact of Water Drops on Soil Erosion

In many situations at hillslope or field scales, or locally beneath some plants, the physical impact of water droplets is the dominant agency dislodging soil particles. Water drops are held under positive pressure by the surface tension forces linking molecules near the drop surface. The pressure difference between that inside a water droplet and the surrounding air is called the Laplace Pressure, and can reach 1 kPa or more for small drizzle droplets. Even for a 1 mm raindrop, the pressure is about 140 Pa. The internal pressure becomes higher for smaller drops. The relevant relationship is

$$\Delta P = 2\gamma / R$$

where ΔP is the Laplace pressure (Pa), γ is the surface tension of water (72 mN/m at 25 °C) and R is the drop radius (mm).

As a result of the confining surface tension forces, small water drops do not readily break apart when they strike a water surface, wet soil, or a wet leaf or branch; splashing is primarily the ejection of water lying on the wet surface that is struck by an incident drop. Owing to the confining effect of surface tension, an incident water drop is thus able to displace some of the pooled or 'target' water from the point of impact and its close surroundings. Some of the movement is lateral, away from the point of impact, and thus generates shearing forces across the soil surface that would not be present in the case of a drop striking dry soil.

The mechanics of splash impacts on erodible soil (and on rigid surfaces) have been extensively investigated, both by empirical observation and through modelling efforts (Harlow and Shannon 1967; Al-Durrah and Bradford 1982; Sharma et al. 1991). Splash on smooth surfaces covered by films of water of various depths was explored by Mutchler (1971). He showed that the number of impact droplets ejected by the impact of a large water drop comparable in size to a gravity drop increased as the water film became thinner. Numbers of impact droplets from a single impact reached >4500 for a 5.6 mm drop striking a water layer 0.1 mm thick. The production of impact droplets by splashing on wood has also shown that large numbers of droplets are ejected at high speed from drop impact points (Chiang et al. 2017). When the water film is moving, as would often be the case with contact flow on plants, splash crowns become asymmetrical, and splash crown height and diameter are altered in comparison with stationary water films. Large numbers of splash droplets are nevertheless ejected, as clearly visible in the high-speed photographs presented by Cossali et al. (1997) and by Burzynski and Bansmer (2018). Other factors, such as the impact speed of the incident drop, and the roughness of the surface, also influence splash droplet production (Roisman et al. 2015; Koch and Grichnik 2016). Early studies established the speed with which the vertical velocity of an incident drop is converted into flow radially outward from the point of impact (Engel 1955). At the soil surface, an impact pressure is exerted, and this may be conveyed into the soil through saturated pores; there is also a surface shearing force related to the radial flow and lateral jetting (Bako et al. 2016). As noted earlier, the presence of a water layer overlying the soil, perhaps during ephemeral ponding caused by bursts of intense rain, or by shallow overland flow, modifies the impact forces generated by an arriving drop. If the ponding or overland flow is sufficiently deep, the soil surface experiences lower shear forces from drop impact, and scour by overland flow may become the dominant erosive force (Vaezi et al. 2017). Soil properties, including texture, shear strength and hydrophobicity, affect the damage to the soil surface resulting from drop impacts (Nearing and Bradford 1985; Sharma and Gupta 1989; Mouzai and Bouhadef 2011; Ahn et al. 2013). Small craters in the soil surface often result from drop impact and splash. These craters have been measured using

X-ray computed tomography, in a study that showed that soils with higher matric potentials restrict crater development (Beczek et al. 2018). Soil particles can be splashed tens of cm (Leguédois et al. 2005), but the amount transported declines exponentially with distance from the impact point (Legout et al. 1995). The chemistry of the soil solution is also influential in the outcome of splash, including osmotic disruption effects that arise when dilute rainwater encounters soil pores containing a higher salt concentration (Hu et al. 2018). Soil texture and particle aggregation are important too, and in drylands, soil binding by fungal hyphae in the uppermost few mm of the soil can confer stability against erosion by splash as well as by overland flow (Dunkerley 2011).

Data on the proportion of the mass of the incident drop that forms splash or impact droplets have been collected by colouring the incident drops with fluorescein (Timmons et al. 1971). Water resting on a soil surface is thrown outward from the location struck by an incident drop, in the form of fast-moving lateral jets. These jets, whose velocity may reach twice that of the incident drop (Huang et al. 1982) are responsible for breaking apart soil aggregates, and for displacing the breakdown products laterally. Soil particles may be thrown into the air by drop impacts, for instance during intense rainfall, and as a result may move both upslope and downslope following a curving path through the air (the process is called ‘airsplash’). Having been loosened or completely separated from the surrounding soil, they may also be carried downslope in flowing water, and in this case their transport may be assisted by the impact of drops on the water surface (rain-assisted flow transportation), or, having been dislodged by drop impact, by flowing water alone. The speed of overland flow is much lower than the speed of the lateral jets thrown out by a raindrop impact, and this accounts for the reduced capacity of overland flow to disrupt and carry away soil particles in the absence of raindrop impacts. Detailed study of the effects of water drop impacts were pioneered by Mihara (1952), who, beginning in the 1940s, measured drop impact and splash processes. Mutchler and Hansen (1970) explored the influence of the depth of a water film present on the surface, and showed that the maximum influence on splash occurred when the film had a depth equivalent to about 0.3 incident drop diameters, deeper films cushioning the drop impacts. Hartley and Alonso (1991) used computational fluid dynamics methods to show that the intensity of shear at the soil surface depended on the water film cushioning depth. The shear force became negligible for water depths $> \sim 3$ incident drop diameters. Hobbs and Osheroff (1967) had previously established that various splash characteristics reached a maximum for surface water that was about 3 incident-drop diameters deep. For those requiring a fuller treatment of soil erosion processes than can be provided here, there are a number of comprehensive texts (e.g. Carson and Kirkby 1972). Weggel and Rustom (1992) presented a brief overview, which touches also on options for erosion control, and Fernández-Raga et al. (2017) reviewed the literature on splash erosion, highlighting a number of knowledge gaps.

Equipped with this understanding of drop impact processes, we turn next to the ways in which vegetation may influence the size and other properties of water drops, such that drops arriving at the ground beneath vegetation are distinctively different from those arriving under open-field rainfall conditions. We will see that in some cases, the presence of vegetation is protective against soil erosion, whilst in others it exacerbates soil erosion, sometimes markedly. Subsequently, we shall see that under some circumstances, stemflow can also be more erosive than open-field rainfall.

12.3.1 Effects of Vegetation on the Sizes of Water Drops Arriving at the Ground

12.3.1.1 Conversion of Fog and Mist Droplets to Gravity Drops

Under suitable climatic conditions, vegetation may have seasonal interactions with fog, cloud, and other atmospheric water droplets. Mist and fog consist of water droplets that are sufficiently small and light that they are kept aloft by even slight wind and air turbulence. When they drift against standing vegetation, the small water droplets can adhere, sometimes causing foliage to sag owing to the increasing weight of water. During foggy hours, the plant surfaces become increasingly wet, and the water can gather (coalesce) into droplets large enough to drain across the leaf surfaces and drip from the plant toward the ground (Fig. 12.4). The attached droplets are referred to as sessile droplets; the processes involved in their coalescence remain incompletely understood (Andrieu et al. 2002). Fog droplets are generally <100 µm in diameter (Pérez-Díaz et al. 2017), whilst the resulting fog drips may be 4–5 mm in diameter. Thus, the wetted foliage increases the drop diameter by perhaps 50 times, and the mass (proportional to the cube of the drop radius) by 125,000 times. The enlarged drops can strike plant parts and trigger splash as described earlier, or reach the soil, where the drop impact may be erosive.

The process by which trees collect water from low cloud or fog has been termed ‘cloud combing’ (Rigg et al. 2002) or ‘cloud stripping’ (McJannet et al. 2007), and if there is the release of collected water toward the ground, this is called ‘fog drip’ (del Moral and Muller 1969). In some wet tropical locations, such as Mt Bellenden Ker (summit elevation 1593 m) in the wet tropics of northern Queensland, Australia, fog drip delivers more than 2 m (29%) to the total precipitation recorded at the ground, and averages 5.9 mm/day (McJannet et al. 2007). Even at a subtropical location in south east Queensland,

Fig. 12.4 Upper: Fog droplets adhering to a Eucalyptus leaf following a foggy night, Melbourne, Australia. Some droplets have coalesced to form larger sessile drops. Lower: localised pooling of water delivered by fog drip to the sealed surface of a car park. Significant amounts of water are evident. Photo taken on the same morning as the upper photograph, Melbourne, Australia (Photos: author)

Hutley et al. (1997) found that fog drip provided the equivalent of an additional 40% of the rainfall. High values of fog drip (7–28%) were also reported by Cárdenas et al. (2017) from the Colombian Andes, and by Domínguez et al. (2016) from San Cristobal Island in the Galapagos. Precipitation of fog water can result in negative estimates of canopy interception (Gomez-Peralta et al. 2008). Global estimates of fog input were reported by Bruijnzeel et al. (2011). By collecting fog droplets, a vegetation canopy can cause water to reach the soil surface when no rainfall has occurred, and in much larger drops, formed on the leaves, than were present in the fog itself; this is referred to as occult precipitation. The process can be especially important in winter, or where warm oceans adjoin uplands where air may be forced to rise and cool. Fog drip is evidently of considerable hydrologic importance in areas such as the California Coast Range (Sawaske and Freyberg 2015), and warrants additional field-based study. The delivery of fog drip to the ground can be reduced or lost altogether after logging of forests (Harr 1982), since there are fewer surfaces upon which fog droplets can accumulate, or following wildfire, for the same reason (Fig. 12.5). The loss of fog drip may reduce soil moisture and streamflows. Fog drip can also deliver materials to the soil, including toxins washed from foliage that may have the effect of inhibiting the growth of sub-canopy plants (del Moral and Muller 1969). Small droplets arriving as drizzle or light rain can be converted to larger drops by the same mechanism. However, in this case the incident drops are much larger than fog and mist droplets, having diameters of up to several hundred µm in drizzle (Westbrook et al. 2010). Finally, it is worth noting that dew deposition, another form of occult precipitation, can also contribute a significant source of water to plants. Shure and Lewis (1973) showed that dew can be delivered as stemflow; for common ragweed (*Ambrosia artemisiifolia*) growing in New Jersey, USA, stemflow supplied by dew amounted to 2.85 mL/plant/night during their study.

12.3.1.2 Gravity Drops: Their Production and Erosivity

By accumulating droplets from mist, fog, or drizzle, which then coalesce, foliage may release enlarged drops. A pioneering study of these large drops, termed ‘gravity drops’, was presented by Moss and Green (1987). They sprayed leaf specimens

Fig. 12.5 Hillslope following wildfire, Colorado, USA. The absence of foliage in such conditions, or following timber harvesting, may reduce fog interception and fog drip (Photo: author)

from 28 different plant taxa with a fine water mist, and also exposed them to simulated rainfall, and recorded the large water drops that were released from the leaves at regular intervals. Spray irrigation of crops can result in the same mechanism, in which the crop plants modify the size, energy, and fall location of water drops reaching the soil surface. Moss and Green showed that the gravity drops had a mean diameter of 5.3 mm, and that among the individual taxa, the range of mean gravity drop diameters was 3.7–6.7 mm. Most drops in ordinary rainfall are considerably smaller, drops larger than 3–4 mm being uncommon; the number mean drop diameter is often in the range 1–3 mm, but drop size distributions can fluctuate markedly during rainfall (Friedrich et al. 2016). The volume (or mass) of a spherical drop is proportional to the cube of the diameter; therefore, though a 6 mm gravity drop has twice the diameter of a 3 mm raindrop, it has a volume and mass 8× larger. In comparison with a more typical 2 mm raindrop, the volume or mass of a 6 mm gravity drop is 27 times larger.

The gravity drops produced by the interaction of fog or rain with vegetation are thus quite large (larger and heavier than almost all raindrops) and may fall from heights of many metres, depending on the structure of the vegetation. The erosive effects of gravity drops are a function of their size, fall height, and the texture and condition of the soil surface. A thick cover of leaf litter may protect the soil from splash dislodgment of soil particles. However, in cropping fields, on the bare soils left after management fire or wildfire, or on bare soils exposed by tree-fall in tropical rainforest, unprotected soil may be exposed to the direct impact of gravity drops. Ruxton (1967) described the effects of splash erosion by gravity drops in creating what he termed ‘earth pillars’ in rainforests of tropical Papua New Guinea (Fig. 12.6). In forest gaps, these were seen to be partly the result of raindrop impacts, but beneath the forest canopy, were primarily attributed to gravity drops. One major difference between raindrops and gravity drops is the location where they strike the soil surface. Raindrop impact locations change from moment to moment. In contrast, gravity drops, especially if they are being generated from dripping branches or stems, may repeatedly fall to almost the same location on the soil surface. In this way, the erosional effects can be magnified. Signs of splash by rain or by gravity drops can be seen where stones, plant parts, roots, etc. protect the soil surface from the drop impacts, resulting in the formation of protected pedestals. Figure 12.7 shows such pedestals capped by fragments of charred wood that were the product of recent wildfires; the inference can be made that the splash erosion was facilitated both by the bare post-fire soil surface and by the unobstructed path of gravity drops falling from the extensive branches of the defoliated trees. Annual burning of savannah woodlands during the late dry season in northern Australia leaves the soil exposed to drop splash from trees and from heavy monsoonal rain in the subsequent monsoon rain season, and striking erosion results (Fig. 12.8). Artificial capping materials made from plastic strips attached to the soil surface have been used as a means of recording surface lowering via the production of soil pedestals under the plastic strips (Okoba and Sterk 2006).

Fig. 12.6 Soil pedestals beneath tropical rainforest on the Atherton Tableland, in the wet tropics of north Queensland, Australia. **a** and **c**: fragments of rock form the protective cap on these splash pedestals. **b**: a single fallen leaf has resulted in a steep-sided splash pedestal. **d**: small fallen branches have resulted in linear, wall-like splash pedestals (Photos: author)

The production of gravity drops from plants is strongly influenced by the characteristics of the vegetation, including plant architecture and leaf and branch properties (Nanko et al. 2013; Goebes et al. 2015); differences in production also occur for leafed and leafless stages in deciduous plants (Nanko et al. 2016). The erosivity of gravity drops depends on their size and fall height, which again are related to vegetation characteristics. Hall and Calder (1993) used a disdrometer to establish that throughfall had a median drop diameter of 2.3 mm (*Pinus caribaea*), 2.8 mm (*Eucalyptus camaldulensis*) and 4.2 mm (*Tectona grandis*) in southern India. Nanko et al. (2004) recorded throughfall and rainfall drops in a Japanese cypress (*Chamaecyparis obtusa*) plantation, and found a maximum throughfall drop diameter of 6.35 mm, compared with the largest drop in open-field rainfall, which was 3.31 mm. However, in this study, only two rainfall events were recorded, and sample areas for throughfall drop collection were very small (10 × 40 mm). Nanko et al. (2006) showed that throughfall had both more large and more small droplets than open-field rainfall, and hypothesised that these differences were linked to the production of impact and gravity drops; they also showed that under the same rainfall, throughfall d_{50} (the median value of drop diameter) differed among three species of plant.

An important but often neglected aspect of rainfall (and throughfall) is the areal drop arrival rate. This is the rate at which drops strike the ground, expressed in terms of impacts/m^2/s. If for sake of illustration we consider rain consisting of 2 mm drops falling at 5 mm/h (a moderate intensity), then 1 h of rain involves 5×10^6 impacts/m^2. The arrival rate is then almost 1400 impacts/m^2/s. If the incident rain was all converted to gravity drops of 6 mm diameter, then there would be only $\sim 44 \times 10^3$ impacts/m^2, and the arrival rate would fall to ~ 12 impacts/m^2/s. These numbers would not correspond to any actual field conditions but serve to show that conversion of rain to gravity drops can greatly reduce the drop arrival rate.

Fig. 12.7 Soil splash pedestals developed after wildfire in the upland forests of eastern Victoria, Australia. **a** and **b**: charred fragments of wood and bark form the caps of many small splash pedestals. **c** and **d**: area of abundant splash pedestals around the base of trees whose foliage was consumed in the fire, and likely to be the result of persistent drip from the bare branches. The coin in **d** (at lower centre) provides a scale, and is ~24 mm in diameter (Photos: author)

The importance of this is that drop impact points can lose soil by splash at a greater rate than it is returned by splash from surrounding locations, if those splash points are more widely-spaced. Further information on drop arrival rate can be found in Dunkerley (2008). A fuller evaluation of drop impacts and splash erosion, allowing for the full distributions of drop size in rain, can be found in Ma et al. (2008).

What happens when a large gravity drop strikes an erodible soil surface? Moss and Green (1987) used fixed 5.1 mm drops and a standard sand to quantify this. The fall height of the gravity drops was varied to explore the effects that vegetation structure and height might have. For drops falling from 11.2 m, drops reached a terminal velocity of 8.8 m/s. Upon impact, these ejected (‘airsplashed’) sand grains laterally, most splash distances being <0.3 m but in some cases >1 m. For two drop diameters, Fu et al. (2016) showed that the mass of material splash declines rapidly with distance from the impact point, becoming very small at a distance of 50 cm (Fig. 12.9). Splash droplets rose to ~0.6 m above the surface. As fall height was reduced, there was a decline in airsplash distances, and grain displacement became negligible at 0.2 m fall height (fall velocity 1.9 m/s) and ceased altogether for fall heights of 0.1 m (fall velocity 1.4 m/s). This suggests that even the gravity drops released from understory plants such as shrubs may reach sufficient fall speed to be erosive.

On sloping ground, splash dislodgment of soil particles can result in net transport of particles downslope, since airsplash trajectories in that direction are longer than those directed upslope. In terms of the flux of material in splash transport (expressed in g/m/s), drop size is a major influencing factor. Laboratory experiments have shown that 5.1 mm diameter

Fig. 12.8 Soil splash pedestals resulting from monsoon wet season rainfall on recently burnt savannah woodland, eastern Arnhemland, Northern Territory, Australia. Upper: view of intense splash erosion of soil, with many small pedestals capped by stones. Lower: a single large splash pedestal capped by a large stone. The camera lens cap is 45 mm in diameter. Pedestals sheltered by tree roots can be seen in the background (Photos: author)

drops splash medium sand downslope twice as rapidly as 2.7 mm drops, 225 times faster than 1.27 mm drops, and 15,000 times faster than 0.81 mm drops (Moss and Green 1987).

A frequent but perhaps unsurprising finding, in light of the foregoing, is that erosion beneath a vegetation canopy, driven primarily by the impact of gravity drops (intermixed with other throughfall drops), can be more erosive than open-field rainfall (Shinohara et al. 2018). This can readily be accounted for by the population of larger drops in the throughfall than in the open-field rainfall. Gravity drops can be more erosive than raindrops at terminal velocity if their fall height from the standing vegetation is sufficient. Whether erosion is actually greater beneath a vegetation canopy also depends on whether the soil surface is protected by leaf litter (Miura et al. 2002, 2003), or, in agroforestry, by understory plants such as coffee (Nanko et al. 2008). Brandt (1998) showed that in Brazilian rainforest, throughfall energy was increased by the vegetation, from 18.2 J/mm/m^2 in rainfall to 31.8 J/mm/m^2 in forest where the understory had been removed, and to 22.1 J/mm/m^2 in intact rainforest. Correspondingly, splash was 6.65 × greater without understory, but only 0.4× under intact forest. Under agroforestry, conditions may be akin to the understory removal treatment of Brandt (1998). Liu et al. (2016) studied splash

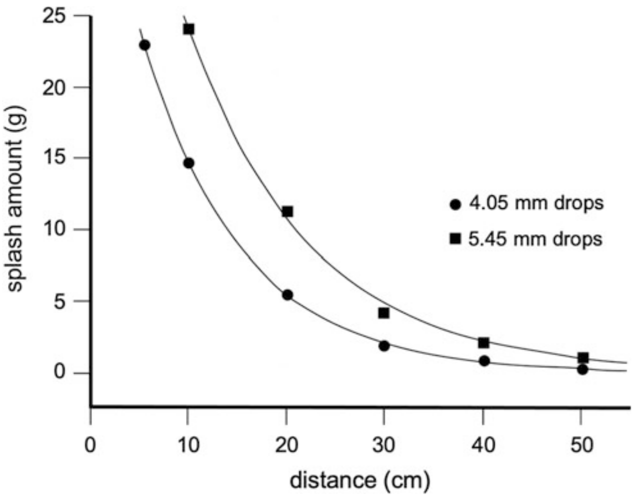


Fig. 12.9 The relationship between the mass of sand splashed by incident drops of two diameters and the distance from the impact point. Note the exponential decline of the splash mass, reaching very low values at a distance of 50 cm. Adapted from Fu et al. (2016), Soil Science Society of America Journal 80, 1071–1077

erosion under rainforest and under monoculture rubber plantation (with tree height >17 m) in SW China, and also under various agroforestry systems that had understory plants including tea, coffee, and cacao. They used conventional sand-filled splash cups (Geissler et al. 2010, 2012) to quantify splash erosion. Their results showed that mean sand splash was 3.12× greater under a rubber monoculture than in the open; importantly, in small storms the difference was larger (up to 9.3× more splash under rubber monoculture). The effects of splash under rubber plantation are clearly evident in the photograph in Fig. 1 of Li et al. (2012). Evidently, in small storms where intensity and dropsize are modest, the gravity drops are proportionally more erosive than in larger, more intense storms when open-field raindrop diameters are themselves larger. Among rainfall characteristics accounting for splash loss statistically, maximum open-field rainfall intensity (mm/10 min) was more important that total rainfall amount (Liu et al. 2016).

It is important to remember that greater splash erosion or throughfall kinetic energy under forest does not mean that overall erosion rates at hillslope or catchment scale are also larger. The connectivity of splash erosion sites with streams able to remove splashed material needs to be considered; forested land very often exhibits lower overall erosion rates than areas cleared of forest (e.g. Zhou et al. 2002), despite splash erosion being locally active.

Soil dislodgment by throughfall drops and gravity drops, and indeed by open-field rainfall, is a complex process (Yariv 1976; Kinnell 1983, 2005, 2012). Knowledge of the mechanics of splash, as outlined earlier, does not provide a complete understanding, because soil solution chemistry affects cohesion in the soil, and soil moisture content affects the detachability of soil particles. This can be illustrated by a study of erosion under Brussels sprout plants (Noble and Morgan 1983), which showed that soil splash erosion was not reduced by the presence of the plants, which ranged in height from 0.98 to 8.75 m. The reason for this was not clear, as only small amounts of the rainfall were converted to gravity drops. Noble and Morgan speculated that the gravity drops might cause local soil saturation beneath drip points such that even the smaller free throughfall drops were able to drive enhanced erosion. The activity of soil organisms can also influence splash processes, as was the case with earthworm (*Lumbricus terrestris* L.) activity in a forest in Luxembourg (Van Hooff 1983). There, large areas of the forest floor are normally protected against splash erosion by leaf litter (Fig. 12.10). However, these areas are seasonally bare owing to earthworm breakdown of the fallen litter, facilitating splash erosion and scour by overland flow. It is also important to remember that not all tree species are associated with increased size or kinetic energy of throughfall drops. For instance, Song et al. (2018) used standard sand-filled splash cups to explore the spatial variability of erosion beneath subtropical forests in China. They found that among three broadleaved taxa, *Sapindus saponaria* increased throughfall kinetic energy, whilst *Lithocarpus glaber* and *Schima superba* reduced it.

12.3.1.3 Splash and Desert Shrub Mounds

One of the locations where the interaction of rain with plant canopies affecting splash transport appears to be important is in the formation of shrub mounds that are often associated with dryland plants (Fig. 12.11). Shrub mounds may have diverse origins: deposition of dusts from wind transport contributes to some (Quets et al. 2016), whilst others may simply be residual

Fig. 12.10 Ground cover of fallen leaves and bark can protect the soil beneath plants from splash erosion. **a**: broad sheet-like fragments of fallen Eucalyptus bark, Melbourne, Australia. **b**: mixed ground litter of Eucalyptus bark, twigs, and leaves, Canberra, Australia. **c**: thick ground cover of leaves under deciduous trees, Rotterdam, Netherlands. **d**: narrow strips of Eucalyptus bark, Melbourne, Australia (Photos: author)

features left by erosion of the more exposed soils between shrubs (Lee 1986; Rostagno and del Valle 1988). In many situations, the presence of the shrub canopy means that splash dislodgment of sub-canopy soil is less active than in surrounding open spaces. This can result in more soil particles being splashed inward, and coming to rest beneath the shrub canopy, than are splashed outward in the reverse direction. As a result, the relatively protected sub-canopy of the shrub becomes a location of net accumulation, and a shrub mound grows (Furbish et al. 2009; Hoffman et al. 2013). Small particles are most readily splashed, and particles of ~0.1 mm diameter (fine sand) are especially mobile. This is ecologically important because the shrub mound has enhanced infiltrability owing to its texture (enriched in inwardly-splashed fine sand) and structure, and is more readily able to absorb throughfall and stemflow. These properties further benefit the shrub in the moisture-scarce dryland environment. This ‘fertile island’ effect is a clear example of the feedback loop mentioned earlier, in which vegetation may influence erosion processes, and these in turn affect the growth and development of the plants. Many dryland shrubs can live for decades. The mechanisms resulting in mound formation benefit the shrubs through this substantial period, integrating the particle splash occurring through perhaps hundreds of storm events.

12.3.1.4 Drip Tips and Gravity Drops: Possible Effects on Splash Erosion

Leaf size, shape, and surface texture may all affect the size and hence erosivity of gravity drops. Leaves may possess a form that includes an extended tip, or ‘drip tip’ (Fig. 12.12). The possible evolutionary development of drip tips because of some advantage conferred on the plant is debated (Lightbody 1985; Goldsmith et al. 2017). Hypotheses include the idea that drip tips allow water to escape more readily from the leaf, so permitting faster leaf drying after rain (confirmed experimentally by

Fig. 12.11 Shrub mounds beneath dryland plants, western New South Wales, Australia. Upper: mounds beneath Maireana spp. (bluebush) shrubs, produced primarily by the net inward splash of soil particles from the shrub interspaces. Lower: mounds associated with small Atriplex spp. Shrubs on a rocky slope. In this case, deposition of the mound materials from wind-transported particles is likely (Photos: author)

Dean and Smith 1978). This has been reasoned to reduce the time available for disease such as fungal infection to develop on the leaves, but there are other hypotheses, including reduced leaching of nutrients from the leaves or reduced reflectance of sunlight (Ivey and DeSilva 2001; Malhado et al. 2012). In the Amazon and elsewhere, plants with drip tips are associated with wetter areas (Malhado et al. 2012). Williamson (1981) speculated that since leaves with drip tips drain more readily, and consequently release smaller gravity drops, they might function to reduce splash erosion beneath the canopy. He showed that drop size indeed declined linearly as drip tip width declined (Fig. 12.13). Williamson et al. (1983) collected leaf shape data from the La Selva research station in Costa Rica, and showed that for understory plants in the height range 10 cm–1.6 m, leaf tips became more acuminate (having the form of a long narrowing point) for taller plants. Their interpretation of this finding was that given the low fall height of gravity drops from short understory plants, there would be little effect of drip tips on splash erosion, and hence little evolutionary benefit to be had from their development. This idea was further explored by examining the frequency with which drip tips are present on soils of presumed different erodibility (Rebelo and

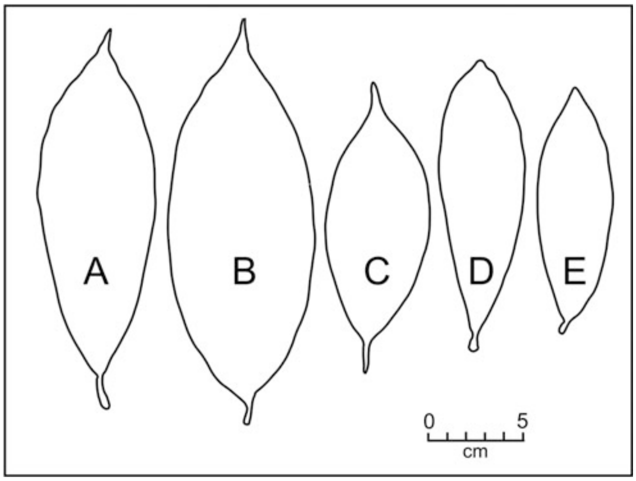
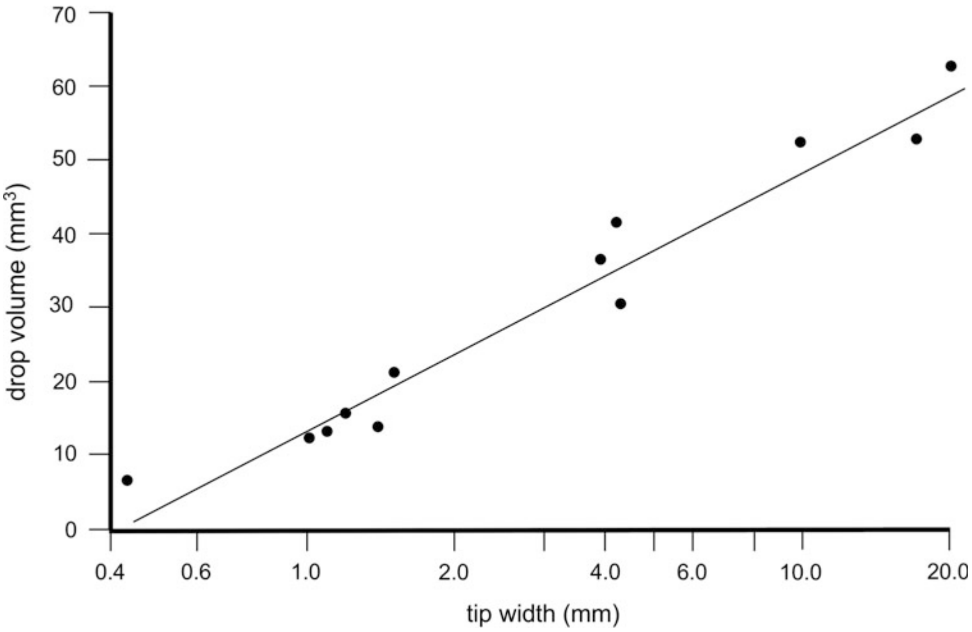


Fig. 12.12 Leaf shapes from tropical rainforest plants growing on the Atherton Tablelands, north Queensland, Australia. **a**, **b**, **c**: leaves equipped with drip-tips. **d**, **e**: leaves with acute tip shapes, lacking drip-tips. Scale of cm is shown for reference (*Source* author)

Fig. 12.13 The relationship of drop size (drop volume) released from experimentally-wetted leaf specimens to the width of leaf tips measured at 3 mm from the tip. Note log scale on X-axis. Adapted from Williamson (1981), Biotropica 13, 228–231



Williamson 1996). These authors examined plants on sandy soils and on clay soils in the same general climatic zone of the central Amazon. Drip tips, expressed by the leaf width at 3 mm from the tip, were more abundant on the clay soils. Leaf litter that might otherwise protect the soil was reasoned to decay relatively rapidly, and to leave the mineral soil at least partially exposed to the impact of gravity drops. These ideas are certainly interesting, but more data, for instance confirming that the clay soils were indeed more vulnerable to splash, and quantifying the erodibility of the soils, are needed.

12.3.1.5 Overall Transformation of Drop Sizes: Summary

We have seen that raindrops may be converted to impact droplets or drips with different diameters and velocities of movement, as well as into trickle flow composed of a stream of flowing water (considered next). Not only may drop size and velocity be altered; so too may be the location where the water ultimately arrives at the soil surface, as occurs where the architecture of a plant results in persistent drip points that are active in successive storms. Thus, the timing, intensity, location, and energetics of the original precipitation (as it might be measured by instruments mounted on a tower or mast above the vegetation, or in a clearing) are no longer directly relevant to processes at the soil surface beneath vegetation.

For instance, leaf drip may continue to arrive at the soil surface long after rain has ceased, as the wet vegetation slowly drains. In this way, occurring through a longer period of time than the rainfall event (storm) that delivered the water, the mean intensity or flux of water arriving at the soil may be lower than that of the open-field rainfall. However, as we have seen, the erosivity of the water arriving at the soil can, if conditions are right, be larger than that of the open-field rainfall. In this case, erosion beneath a vegetation canopy can be more active than in the open, where the ground is exposed only to the smaller drops comprising the open-field rainfall. The enhanced erosion potential is a hazard that may require management action in order to maintain agricultural or silvicultural productivity. Many of the processes that we have considered are affected by properties of the open-field rainfall (depth, duration, intensity), and by the properties of the vegetation, litter, and underlying soil. Considered within the wide range of global environments and climates, our understanding of these processes must be regarded as well-developed in only a small number of locations.

Unsurprisingly, therefore, much remains to be discovered about drop size distributions in throughfall under different kinds of vegetation; a review highlighting key knowledge gaps was presented by Levia et al. (2017). In some plants, leaves change their characteristics as the plant develops from juvenile to mature; this heteroblasty may be reflected in different leaf sizes and shapes (Gras et al. 2005), though little is known about how this affects splash or drip.

12.4 Stemflow and Soil Physicochemistry

Stemflow (including contact flow on branches and other plant parts) occurs where water remains in contact with the plant, rather than dripping or splashing. It can deliver very large volumes of water to the base of a plant that has a large collecting area of foliage and/or branches, perhaps facilitated further by inward-sloping branches down which water can trickle, and smooth, non-absorbent bark. Slatyer (1959) reported that mulga trees (*Acacia aneura*) in central Australia shed stemflow after as little as 2–3 mm of rain, and in many storms delivered about 40% of the rainfall over the projected canopy area (Fig. 12.14). He stressed that the 100 L or so of stemflow delivered to the base of a tree in a rainfall of 15–20 mm amounted to an important water source for the plant in the dryland conditions of inland Australia. Working in south–west Queensland, Pressland (1973, 1976) drew additional attention to the fate of the stemflow, noting that it had been observed to infiltrate within 50 cm of large trees, and 30 cm of small trees. In this way, he showed that the increase in effective depth of

Fig. 12.14 Mulga (Acacia aneura) growing on the dryland Burt Plain, Northern Territory. Note the multiple, steeply-inclined stems. Water is intercepted on upwardly-inclined phyllodes, which readily carry flow to the stems and hence to the soil (Photo: author)

precipitation over the area around the base of the plants, and within which the stemflow was absorbed, reached almost 200% of the open-field rainfall for a 10 mm rainfall over a small tree. Water repellency (hydrophobicity) of soils around the base of a plant may however serve to reduce soil infiltrability there. In the absence of such hydrophobicity, Prebble (1987) estimated that all stemflow could be absorbed within 3 cm of the trunks of *Eucalyptus pilularis* and *E. intermedia* growing in dune sand in eastern Australia, where infiltrability (K_{sat}) was 600 mm/h, such that ponding and overland flow would not normally be expected to occur. Evidence of overland flow resulting from stemflow was reported by Iida et al. (2005). They recorded zones where litter had been carried radially outward from tree stems near Tsukuba, Japan. Signs of rill erosion and surface flow were also reported by Chinen (2007) around the base of *Acacia albida*, *Balanites aegyptiaca* and *Hyphaene thebaica* near Niamey in Niger. Traces of rilling and overland flow extended for 4–7 m downslope of these plants, but there was no scour upslope, confirming that widespread overland flow had not occurred (see Fig. 4 in Chinen 2007). These were observations made after one or two rain days when the intensity of rain was thought to have been ~60 mm/h, and additional systematic investigation would be needed to explore relationships of the erosion to storm depth, intensity, soil, and plant characteristics. Similar signs of scour related to stemflow were detected around oil palm trees (*Elaeis Guineensis*) in Malaysia (Rashid and Askari 2014), and though all of these observations are qualitative, they suggest the stemflow may often lead to localised overland flow and the scour of organic litter and soil around the base of affected plants. In this way, of course, the occurrence of stemflow may leave the soil increasingly bare and vulnerable to the impact of gravity drops falling from the foliage and branches above.

Pressland's (1976) work was pioneering in its focus on the area over which the stemflow was absorbed to become soil moisture. Since his work, various means have been used to characterise stemflow; it has commonly been considered in the context of a 'funnelling ratio', F (Herwitz 1986; Tanaka et al. 2017). Other descriptors of stemflow are in use, including stemflow volume per unit of rainfall (Zhang et al. 2017). Funnelling ratio (F) is defined as the ratio of the stemflow amount (or depth) to the amount that could be expected over the basal area of the trunk in the absence of the canopy. Thus,

$$F = V/BR$$

Where V is the volume of stemflow (mL), B is the basal area of the trunk or stem (cm^2), and R is the depth of incident rainfall above the canopy (cm). The effective collecting area from which water is funnelled to the base of the stem is then given by

$$C = V/R$$

Herwitz (1986) reported F values >150, especially from rainforest canopy emergent trees, whose spreading branches extended above the bulk of the forest canopy below. These funnelling ratios are akin to the multiplying factors presented by Pressland (1976) but pay no attention to the fate of the stemflow once it arrives at the soil surface. Though they are widely employed, funnelling ratios are not directly relevant to understanding erosion arising from stemflow, which depends more on the volume and flux of stemflow at the base of a plant at any moment, rather than on a time-integrated funnelling ratio. Likewise, stemflow may drain down one side of a stem more than the other, or be channelled by soil microtopography around the base of a plant, and these influences cannot be accounted for by the value of F. Funnelling ratios tend to be largest for small plants with some canopy but a small stem diameter, and stemflow in this situation can be erosive (Fig. 12.15).

12.4.1 Stemflow and Geomorphic Processes

In terms of soil erosion, it is necessary to consider what occurs in large or intense rainfalls, that might saturate the soil around the base of a tree. The infiltrability of soils declines with time as rain continues, and the wetting front reaches deeper within the soil. Thus, in prolonged rain, the ability of the soil to take in stemflow may decline. In the very wet Mt Bellenden-Ker area of northern Queensland, Australia (where daily rainfalls of ~300 mm can occur), Herwitz (1986) observed that infiltration excess (Hortonian) overland flow could be generated near trees exhibiting very high funnelling ratios. This was possible despite soil infiltrability in the top 5 cm being 372 mm/h, which exceeds any recorded hourly rainfall. Infiltrability declined with depth, to about 70 mm/h at 50 cm depth. A set of trees equipped with stemflow collars recorded 13.6% of rainfall delivered as stemflow, and funnelling ratios of >100 were recorded. The extremes of rainfall were observed by Herwitz (1986) to be important to the conversion of stemflow to overland flow at the tree base. Extreme rainfall rates included 51.6 mm in 42 min (73.7 mm/h), and within this event, a short burst of 11.8 mm in 6 min (118 mm/h). By assuming that any excess stemflow would drain downslope, Herwitz (1986) calculated that the length of possible flow paths

Fig. 12.15 Erosion resulting from concentrated, downslope-directed stemflow. The most prominent stemflow scour, which resulted in the incision of a rill channel, was the result of stemflow from a small Eucalyptus sapling visible at the top of each photograph. Scour downslope of several other plants can also be seen. Both photos show the fan of sediment deposited on a cement path at the base of the steep garden bed. Monash University campus, Melbourne, Australia (Photos: author)

was >11 m, sufficient for the water to reach adjacent stream channels. In this way, stemflow may be capable of contributing directly to streamflow, at least in rainfall events of sufficient intensity and duration, and from trees with efficient stemflow delivery.

Herwitz (1986) recorded soil scour downslope of trees with high funnelling efficiencies, notably emergent trees with small trunk diameters. He speculated that large throughfall droplets (perhaps including gravity drops) might be responsible for soil dislodgment, the particles then being carried away by the runoff arriving at the tree base as stemflow. These processes have been examined in few other studies. The erosive role of tree stemflow was investigated by Prebble (1987), working on steep vegetated sand dunes at Cooloola, Queensland, Australia. There, signs of scour downslope of tree trunks suggested at least periodic erosion of the dune sands related to stemflow (see Fig. 2 in Prebble 1987). Experimental manipulations were set up to divert stemflow or overland flow away from some trees, while others were kept as controls. Mean stemflow fraction was found to be 2–4%, but up to 5.3%. For individual events when bark was already wet, stemflow fractions of up to 16% were noted. Stemflow volumes were significant, including 4775 L for one tree over 12 months, and 402 L in 14.5 h. Nevertheless, the field data on downslope sand transport arising from the exclusion experiments suggested that the dominant agency removing sand was not overland flow generated by stemflow, but rather was airsplash resulting from drop impacts.

Crop plants may also generate problematic volumes and fluxes of stemflow, an instance being the Australian Macadamia nut plantations studied by Keen et al. (2010). These authors estimated stemflow to average 7% of rainfall, but concentrated at the base of the trees, it caused soil loss (surface lowering) averaging 6.5 mm/a, based on gridded soil surface elevation data. Some cereal crops, notably corn and maize, convert very large fractions of incident rainfall (or spray irrigation) into stemflow. Martello et al. (2015) for instance recorded 78% stemflow and only 22% throughfall in a study of a Maize crop under natural rainfall in Legarno, Italy. Using intense rainfall simulation, Bui and Box (1992) studied stemflow in corn and sorghum. In the case of corn their data suggested that a proportion (perhaps a third) of the stemflow had become overland flow. Nevertheless, they concluded that erosion related to the stemflow was negligible in comparison with the erosion resulting from throughfall drop impacts at the soil surface.

Stemflow may also affect the mechanical properties of soil, including the extent of local saturation around the point-source represented by the stem. Numerical models of the factor of safety against hillslope mass movement have suggested that by generating local zones of soil saturation, stemflow may increase the risk of failure, and that the risk may develop sooner in wet weather than would be the case in the absence of stemflow (Liang et al. 2010, 2011).

The few studies cited above represent much of what is known about soil erosion driven by stemflow. Such erosion appears to be localised. This must be seen as an interim conclusion, however, because our knowledge of these processes as they occur in other forms of vegetation is incomplete, and currently we know too little to be able to evaluate in a systematic way the influence of plant characteristics, climate, soil type, or rainfall characteristics, on erosion driven by stemflow.

12.4.2 Stemflow and Soil Moisture Levels

Apart from erosion, stemflow exerts a number of other influences on soils. In plants where stemflow is a recurring phenomenon, soil moisture may be delivered to the base of the stem in larger amounts than would otherwise reach the soil there. As described above, except where the stemflow is funnelled in very large fluxes, it is generally able to infiltrate within quite a small annulus surrounding the stem. This annulus may be from a few cm to a few tens of cm in width. Gomez et al. (2002) reported that stemflow in a Spanish olive grove was able to infiltrate within 50 cm of the tree trunks. As a result, stemflow may amount to a localised ‘point-source’ of soil water recharge that may benefit the plant. This is presumably the evolutionary advantage that would drive dryland plant architecture toward a form that is very efficient at generating stemflow and at the same time not losing too large a proportion of rain to canopy interception, as in Australian mulga (Slatyer 1959, Pressland 1976) or heath vegetation (Specht 1957). Taniguchi et al. (1996) studied stemflow recharge in an area of pine forest at Tsukuba, Japan. Stemflow was mostly <10% of net precipitation (throughfall plus stemflow), amounting to 5–20 mm, equivalent to just a few percent of the rainfall. Taniguchi et al. also estimated groundwater recharge using the chloride balance method. This showed that stemflow contributed 10.9–19.1% of the annual recharge. This large contribution reflects the focussed stemflow recharge points located at trees that deliver large stemflow volumes. Thus, although stemflow volume might be small in absolute terms, it is of greater importance to recharge than the small amounts, or proportions of incident rainfall, might at first suggest. Tanaka et al. (1996) introduced a cylindrical infiltration model to account for the stemflow contribution to recharge, and to relate this to the trunk diameter trees contributing the stemflow (Fig. 12.16). This is an example of mechanisms through which vegetation affects groundwater recharge (Le Maitre et al. 1999).

The generality of these findings across different plant taxa in different environments (trees, shrubs, grasses, crops, wet tropical, temperate, dryland, etc.) is far from securely established, owing to the limited number of careful field studies. Forests are relatively well-studied; for example, Bialkowski and Buttle (2015) found that the water delivered by throughfall and stemflow close to the stems of sugar maple in southern Ontario were 3–4× the gross rainfall, and resulted in higher soil moisture contents close to the tree bole than in soils further away. Similar findings were reported for red pine (*Pinus resinosa* Ait.) in Ontario (Buttle et al. 2014). Increased soil moisture resulting from stemflow was also reported from remnant forest in Brazil, where the stemflow only represented 0.17% of the rainfall above the forest canopy (Terra et al. 2018). However, the

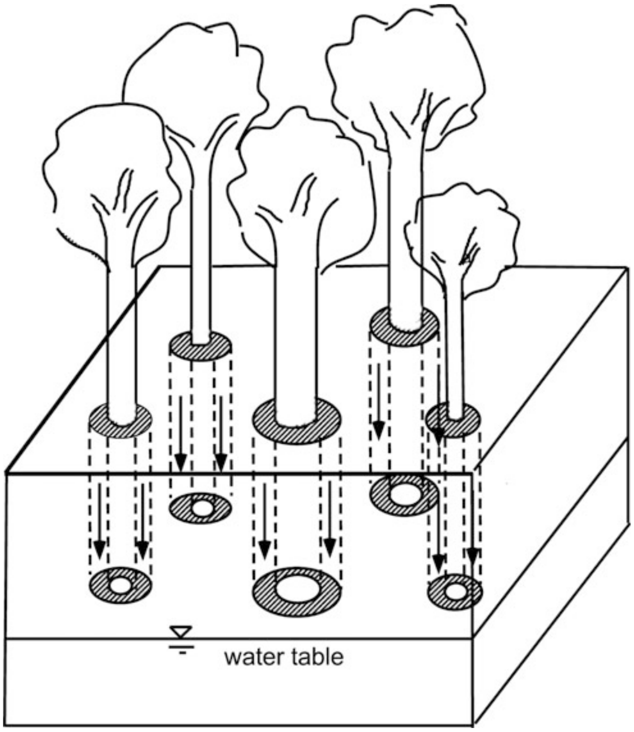


Fig. 12.16 Schematic of the role of concentrated stemflow in establishing annular sources of groundwater recharge surrounding the stems of trees. In nature, patterns of movement of water into and through the soil and regolith would be much less regular than shown in this diagram. Adapted from Tanaka et al. (1996), Hydrological Processes 10, 81–88

enhanced soil moisture was only recorded for depths to about 0.2 m. For dryland shrubs, efficient harvesting of stemflow to enhance available soil moisture stores is perhaps more critical than in humid forest environments. As a result, stemflow in drylands has been investigated further since the pioneering work of Slatyer (1959) and Pressland (1976) referred to earlier. High funnelling ratios have been reported from a number of dryland plants, which suggests that stemflow is ecohydrologically important. For drylands on the Eyre Peninsula in South Australia, Swaffer et al. (2014) found funnelling ratios of 74 for *Eucalyptus diversifolia* and 147 for *Allocasuarina verticillata*. These are comparable to the values seen in the forest trees of wetter environments.

Li et al. (2008) measured stemflow and soil moisture for three shrubs, *Tamarix ramosissima*, *Caragana korshinskii* and *Reaumuria soongorica* in the dryland loess area of China. They found that around the stems, the wetting front had progressed up to 4.5× deeper than in the shrub interspace; root zone soil moisture was also higher around the stems. Li et al. (2008) stressed that the deeper soil moisture recharge resulting from stemflow probably facilitated conservation of the moisture, benefiting the plant in subsequent rainless periods. These results were later echoed by Wang et al. (2011) for *C. korshinskii*. Likewise, for the two dryland shrubs *C. korshinskii* and *Hippophae rhamnoides*, Jian et al. (2014) reported that wetting depths beneath the shrubs were twice the depth seen in the interspaces, and that soil water content was likewise higher beneath the shrubs. This was attributed to stemflow arising from efficient funnelling of water, the rainfall event funnelling ratio averaging 156.6 for *C. korshinskii* and 49.5 for *H. rhamnoides*. For the same two dryland shrubs, Jian et al. (2018) recorded stemflow using collars, and soil moisture was logged at 20 depths extending to 2 m below the soil surface. They found that stemflow was carried deeper into the subsoil around the stem than outside the shrub canopy; wetting front depths after natural rainfall events were up to 6.7× and 2.9× deeper beneath the canopy than outside. Even at 2 m depth, soil moisture was about 25% higher in the area around the stem than away from the shrubs.

The kinds of findings referred to above, suggesting that stemflow yields additional plant-available soil moisture, were contradicted by Metzger et al. (2017). Their study was made in a temperate beech forest in Germany, where they recorded throughfall, stemflow, and soil moisture. Metzger et al. (2017) found that in their environment, the effects of soil wetting by stemflow and throughfall during rainfall events were short-lived, and that a more temporally-stable soil moisture pattern, related to soil structure and hydraulic properties (such as field capacity) was soon re-established. Surprisingly, they also found that at all times soil moisture was lower close to tree stems than further away. However, this was hypothesised to reflect the channelling of stemflow deeper beneath the soil surface, below the rooting depth of the trees. How these results might apply to other climates and vegetation types is not known.

The available evidence therefore leaves as an open question the extent to which stemflow benefits plants across the bioclimatic zones, from wet tropics to drylands. Evidently, what occurs during and immediately after rainfall is part of a more complex water availability dynamic, that involves also the time between storm events, and the nature (size, duration, depth, intensity) of the rainfall events themselves. These characteristics are not constant between climate zones, nor between wet and dry years (Dunkerley 2013; D'Odorico et al. 2001), and they are likely to change the warmer climate of coming decades (Ye et al. 2016; Schroeer and Kirchengast 2017). There is certainly scope for ongoing work on the connection between stemflow and soil moisture, which is probably most needed in dry environments where soil moisture is more frequently limiting to plant growth, and where many climate change scenarios suggest further climatic drying in the future (Trenberth 2014).

Rainfall event characteristics and plant architectural attributes such as branch angle, bark texture and bark water holding capacity affect the delivery of stemflow water to the base of a plant (Herwitz 1987; Levia and Herwitz 2005). Its fate there, and the dimensions of the zone into which it infiltrates (or over which it runs off as overland flow), are, however, also influenced by the local soil properties, such as density, porosity and macroporosity, and infiltrability. There exists a two-way interaction here, since the growth of roots and the delivery of nutrients and other materials (including possibly agro-chemicals, isotopes, and pollutants washed from foliage) are affected by the stemflow, and in turn, are affected by it. These interactions are once again incompletely explored, especially across the global bioclimatic zones. Let us consider a few instances of these interactions.

12.4.3 Stemflow Effects on Soil Properties and Chemistry

Stemflow affects properties of the receiving soils beyond the increased wetting depth and soil moisture levels just discussed. Though the effects of stemflow on soil chemistry and nutrient effects are beyond the scope of this chapter, some brief observations are included here as a guide to the kinds of findings that have been made. The chemistry of stemflow is known to differ from that of open-field rainfall (Koichiro et al. 2001). Stemflow is enriched in a number of elements including N (Langkamp et al. 1982), but the cycling of nutrients to the soil and their return to the plant are complex. Other effects, such as the delivery of allelopathic chemicals in stemflow, may inhibit the growth of understory or other plants nearby (May and Ash 1990). There are also physical effects within the receiving soil. For instance, Li et al. (2009) showed that for the dryland shrubs *Salix psammophila* and *Hedysarum scoparium* growing in north China, root macropores comprised a set of preferential flow paths along which stemflow was dispersed unevenly into the subsoil, so increasing the spatial heterogeneity of soil moisture.

Bollen et al. (1968) estimated that nutrient delivery in stemflow was small in proportion to the aggregate inputs from rain and throughfall, but did enrich a narrow zone around the stem of a single red alder *(Alnus rubra)* tree in Oregon, USA. These findings were confirmed by Crozier and Boerner (1986) in a mixed-species forest in Ohio, and by Chang and Matzner (2000) for beech (*Fagus sylvatica* L.) in Germany. Gersper and Holowaychuk (1970) studied soil morphology in a beech-maple woodland in Ohio, USA. They found a less dense A1 horizon and a thicker A2 horizon close to the stems. Silt content was reduced in the A horizon, and increased in the B horizon, compared to locations removed from trees. Gersper and Holowaychuk (1971) reported that elements including C, K, Ca, Na, Mg and P were delivered to the soil beneath three taxa (American beech (*Fagus grandifolia*), red oak (*Quercus rubra*), and sugar maple (*Acer saccharu*) in Ohio, USA. Some plants exhibited radially-symmetrical patterns of soil chemical properties that changed with the distance from the stem. These included a pH increase with stem distance, and a decline in organic C and exchangeable K. Stemflow may commonly contribute only small fluxes of solutes (Van Stan and Gordon 2018) but the cumulative influence on soil nutrient properties may not be negligible. Studies of the influence of stemflow on the soils beneath individual plants, or of leaching from specimens removed from growing plants (Levia and Herwitz 2002), though informative, do not fully account for the landscape-scale effects of stemflow on soil composition and chemistry. Extensive forests or other plant communities, including crops, may exhibit marked spatial variability in rainfall and soil properties, and summing stemflow effects at the scale of an entire forest or ecosystem, possibly with diverse taxa and varying stages of growth, is not straightforward. In the modern landscape, forest patches are common, and in this situation, edge effects on the rainfall catch and on stemflow deposition result in stemflow being different in magnitude at edges than at sites well within the forest (Soulsby and Reynolds 1994), establishing a challenge for field measurement. The chemical enrichment of stemflow and throughfall are also known to exhibit considerable variability related to tree species (Schroth et al. 2001; Legout et al. 2016), which further complicates a full analysis of the effects of stemflow in a diversity plant community.

Levia and Frost (2003) and Levia et al. (2011) provide reviews of the inter-connections of ecohydrology and biogeochemistry for various biomes and agricultural ecosystems. Increasingly, attention is also being paid to stemflow composition and its effects in urban trees and forests, where additional contaminants may be delivered (Takagi et al. 1997; Schooling et al. 2017). Ecosystems are also exhibiting recovery from influences such as acid rain linked to industrial pollution, with consequences for element cycling in throughfall and stemflow (Vanguelova et al. 2010). General reviews of forest biogeochemistry provide additional overviews of the relevant literature for these important ecosystems (Koslowski and Pallardy 1997; Waring and Running 2007; Likens 2013; Cronan 2018).

12.5 Quantifying Erosivity and Erodibility: Complex Issues

Finding suitable measurement methods represents a major challenge facing the collection of field evidence to advance the kinds of studies referred to in this chapter. How can we quantify the propensity of rainfall or throughfall to cause soil erosion upon striking the soil surface? This is termed the ‘erosivity’ of rainfall. Likewise, how can we quantify the vulnerability of soils to dislodgment and erosion under the widely-varying conditions encountered in the field, and under throughfall or rainfall of varying dropsize, kinetic energy, etc.?

Rainfall erosivity can be measured through empirical observations of soil loss from plots, fields, or hillslopes, correlated with the KE, momentum, or peak intensity of rainfall during a rainfall event. However, in this context, even seemingly simple parameters such as rainfall intensity become challenging to explore. The measure of intensity used might be the mean for a rainfall event, or the mean of all rainfall events in the wet season; alternatively, it might be a measure of short-term peak intensity, such as I_5 or I_{30}. Multiple studies have pointed to the importance of short bursts of intense rain, perhaps set within longer events of lower intensity. For instance, Mizugaki et al. (2010) showed that splash dislodgment of soil on Japanese forested hillslopes was strongly related to maximum rainfall intensity assessed at 10–30 min periods (I_{10}–I_{30}). Likewise, Wagenbrenner and Robichaud (2014) highlighted the importance of I_{10} in post-fire sediment movement in the western USA.

An alternative approach to the assessment of erosivity is to expose a standard erodible material, such as a well-sorted sand, to the impact of throughfall drops, and record the mass of sand dislodged per event or per mm of rainfall or throughfall, or per mm of rainfall or throughfall at more than some nominated threshold intensity. This is the approach used in standard splash cups, mentioned earlier. Given the complex form and structure of plant canopies, and the consequent varying heights from which released throughfall may fall and accelerate, the erosivity of throughfall cannot be regarded as constant, but as spatio-temporally variable across a forest floor, and perhaps less variable beneath a crop of uniform age, such as a citrus or olive grove. It would also vary during a storm event, as the canopy progressively wets and up later drains of excess intercepted water. As a result, field sampling needs to be carried out at sufficient locations, and with sufficient temporal resolution, for the results to be representative and informative.

The nature and erodibility of the soil of course also affects particle dislodgment by rain, throughfall, or concentrated stemflow. The concept of erodibility of soil is also a complex one, and ‘erodibility’ is not a straightforward parameter to quantify. Indeed, it can be regarded as a ‘latent’ measure, akin perhaps to human intelligence, that is not easily defined or measured, except under limited, specific conditions (e.g. in the case of intelligence, by assessing discrete attributes such as language or numeracy as surrogates for the underlying ‘intelligence’). Erodibility is certainly not a ‘manifest’ parameter, such as soil bulk density or porosity, that can be measured with reasonable confidence using an established method. Certain properties tend to make a soil more readily erodible by splash or flowing water: absence of cementing agents such as clays; friability related perhaps to organic matter content; particle sizes of around 0.1 mm diameter (smaller particles become more cohesive, and larger ones heavier, since volume of mass rise with d^3 whereas fluid drag only rises with d^2). A widely-used approach to quantifying soil erodibility is the use of the K factor in the Universal Soil Loss Equation (USLE). The K factor is derived using data on the soil texture, organic matter content, structure, and infiltrability. Details lie beyond the scope of this chapter, but can readily be found in the literature (Yang et al. 2018 provide a recent example using Australian data).

12.6 Conclusions and a View Forward

This chapter has presented a necessarily selective review of some of the ways in which soils and soil erosion are affected by the diverse interactions between precipitation and vegetation. There are both short-term effects, exemplified by soil splash caused by the large dropsize of throughfall in a single rainfall, to long-term effects relating to the effects of stemflow and throughfall chemistry on nutrient cycling and soil properties. On both timescales, growth conditions for the plants can be influenced by the interactions with rainfall, in a bi-directional interaction.

The literature presented above makes it clear that whilst much is known about the interactions for a few well-studied taxa growing in a limited number of climatic regions, the diversity of vegetation communities and climatic conditions ensures that there remains much that has not been explored. Throughfall, stemflow, and associated effects on the soil have been recorded in some crop plants, but many have not been investigated. Crops whose cultivation is expanding rapidly, such as oil palm or soybean, certainly warrant closer examination.

A major challenge that remains in most studies is to upscale our understanding from individual test plants to whole forests, shrublands, or crops. To fully understand the controls on erosion driven by throughfall and stemflow in a species-diverse forest with a complex understory, plants of different growth stages, variable soil conditions, and annually varying climate, is no small task. When human management actions such as tree thinning or the use of management fire for hazard management are added to this mix, the task becomes more challenging still.

A major additional challenge is now emerging: the effects of ongoing global and regional climatic and environmental change. Rising levels of atmospheric CO_2 bring with them the prospect of shifts in plant characteristics such as leaf form and plant LAI (leaf area index). The water balance of plant communities may change owing to stomatal changes. Simultaneously, the floristic composition of plant communities may well respond to changes in ambient temperature, humidity, rainfall amount and seasonality, and other parameters, linked to climate change. Not least among the important changes may be those relating to rainfall intensity and the size of rainfall events, which may increase owing to invigoration of the hydrological cycle in a future warmer world. Even in the absence of changes in plant form or in the floristic composition of vegetation communities in a warmer world, changes in rainfall characteristics such as those discussed earlier in this chapter will result in altered splash, drip, and stemflow. These change in turn may pose future risks for sustainable agroforestry and cropping. Certainly, for those seeking to understand the ongoing interactions of rainfall and plant communities, ample challenges remain.

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Flow Pathways of Throughfall and Stemflow Through the Subsurface

13

Jan Friesen

Abstract

Net precipitation recharges soil- and groundwater beneath vegetation canopies and litter layers. Interactions between subsurface water and net precipitation fluxes differ, however, as there are multiple types of net precipitation: free throughfall (rain that passes through canopy gaps), throughfall, and stemflow (rain that drains down plant stems). Rates and infiltration areas for these different hydrologic fluxes interact with soil properties to result in complex wetting fronts, preferential flow paths along roots and through macropores, and localized soil water recharge. How far net precipitation travels through the subsurface and whether it contributes to streamflow or groundwater recharge is reviewed in this chapter. Past and current methods for monitoring throughfall and stemflow infiltration patterns are reviewed, and a critical synthesis is provided for our understanding of subsurface–precipitation interactions to date.

Keywords

Stemflow • Throughfall • Groundwater • Ecohydrology • Forests • Infiltration

13.1 Introduction

Under plant canopies, precipitation is redistributed to the soil at the base of their stems (via stemflow) and as a spatially variable drip flux (called throughfall). For stemflow this redistribution can result in substantially higher, localized water fluxes to soils as rainfall, snow, or ice captured by the large canopy surface area is channeled down branches toward the comparatively smaller basal area of the stem (Miller 1966; Herwitz 1986). Although throughfall is redistributed beneath the entire projected canopy area and typically must pass through litter, it can also be concentrated by canopy drainage pathways as "drip points" to localized soil areas (Lloyd et al. 1988; Zimmermann et al. 2009). Throughfall and stemflow patterns are often hypothesized to drive spatiotemporal variability in soil water content (see references listed by Metzger et al. (2017); however, observational data from concomitant monitoring of net precipitation and soil moisture patterns is limited to few studies (Raat et al. 2010; Metzger et al. 2017). Arguably, the most intensive of these studies (Metzger et al. 2017) found soil moisture patterns rapidly responded to throughfall and stemflow patterns but were weakly correlated and dissipated rapidly after rainfall (see Chap. 6 for further details).

These rapid soil moisture responses, alongside other studies to be discussed in this chapter, raise several questions: How do throughfall and stemflow patterns propagate through the subsurface? Do these net precipitation patterns attenuate or result in preferential flows within soils? Of course, precipitation is responsible for recharging groundwater, generating interflow, filling variable source areas, etc., yet the aboveground mechanisms (throughfall and stemflow) that introduce spatially heterogeneous precipitation inputs to the surface are rarely evaluated. In fact, large uncertainties exist as to whether throughfall and stemflow interactions in the subsurface differ temporally or spatially enough to merit separate consideration in hydrologic models at all. To inspire discussion and future research into these uncertainties, this chapter describes the

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current understanding of throughfall and stemflow interactions with subsurface water, common methods used to trace these hydrologic fluxes' subsurface movements, and estimate their contributions to soil-, ground-, and streamwater.

13.2 Aboveground Motivations for Belowground Throughfall and Stemflow Research

From the first known studies that report quantitative measurements of throughfall and stemflow (Krutzsch 1855; Riegler 1881; Ney 1894), it was obvious that these net precipitation fluxes follow inherently different spatiotemporal patterns. Spatially, throughfall is a drip input through gaps and from branches, leaves, and epiphytes, distributed heterogeneously below the entire canopy, while stemflow is a "contact flow" directly input at the base of the trunk. Temporally, throughfall (from gaps) begins immediately with the commencement of a precipitation event, then increases when branches and leaves become saturated by rain (Leyton et al. 1967) or when snow melts or falls from branches (Lundberg and Halldin 2001). In this way, aboveground observations of the timing of throughfall indicate that throughfall should begin wetting the surface and infiltrating earlier in a storm than stemflow. Stemflow experiences a longer delay because, conceptually, it begins after (i) throughfall-generating areas of the canopy are saturated and (ii) enough water has drained to the stem to saturate its storage and evaporative demands during rainfall. The stemflow delay may be substantially longer for intercepted snow and ice requiring (i) air temperatures to rise above freezing, (ii) the tree's internal heat, and/or (iii) absorption of radiation by exposed bark surfaces to cause melt. Thus, aboveground observations of the timing and spatial patterns of net precipitation fluxes indicated that belowground throughfall and stemflow pathways initiate at different times during storms and enter the subsurface from different areas of the forest floor.

Aboveground observations have also found that the surface characteristics of areas receiving throughfall and stemflow differ. Stemflow may bypass litter layers or push litter away from the stem base, as indicated physically by litter "infiltration rings," for which photographic evidence has been provided for a few sites (Tanaka et al. 1991; Iida et al. 2005; Rashid and Askari 2014). The author notes, however, that direct aboveground observations of how much stemflow bypasses the litter layer have not yet been reported. Throughfall, on the other hand, must percolate through any litter layer between it and the mineral soil layer—which can substantially reduce and chemically alter throughfall (Michalzik et al. 2001; Van Stan et al. 2017). The litter cover and composition of the surface that receives throughfall is also spatiotemporally variable, depending on season (Coenders-Gerrits et al. 2013) and an area's effectiveness at accumulating litter (Kappes et al. 2009). Aboveground observations of surface exposure to atmospheric conditions (i.e., evaporative drivers) also indicate differences between areas receiving throughfall versus stemflow.

With these aboveground observations in mind, researchers generally hypothesized that throughfall and stemflow inputs result in differential subsurface hydrological processes (e.g., Specht 1958; Eschner 1967) and studies began searching for infiltration patterns unique to each flux. Given that throughfall drip points and stemflow are of substantial amount and persistence, there are different hypotheses as to where and how far net precipitation travels belowground (Fig. 13.1).

13.2.1 The Many Possible Pathways for Precipitation Water in the Subsurface

Precipitation that reaches the mineral soil surface of a vegetated ecosystem may follow several possible pathways—not all of them being infiltration into the subsurface. When soils are saturated, which occurs during wet seasons or during the latter part of a storm, or when water input rates are higher than soils can accept, overland runoff may occur (Herwitz 1986; Bui and Box 1992; Cattan et al. 2007; Banabas et al. 2008); however, little work has assessed the occurrence or spatial extent of overland runoff from throughfall and stemflow (see Chap. 12). Within the upper portion of mineral soils, net precipitation is again partitioned into evaporation, transpiration, and deeper subsurface flows. This partitioning of net precipitation in mineral soils naturally depends on the local conditions such as tree species, understory, stand characteristics, soil type and depth. (Brantley et al. 2017). For example, in a scots pine stand on sandy soil in North East Germany, Müller and Bolte (2009) estimated 88% for total evaporation (including evaporation from interception, soil evaporation, and transpiration) and 12% seepage (bottom outflow from lysimeter units). Net precipitation that has infiltrated deeper into mineral soils can end in different sinks (Fig. 13.1).

Deep sandy soils, of course, provide a high potential for deep soil infiltration and even groundwater recharge (Müller and Bolte 2009). Structured soils with shallow impermeable or low conductive soil layers can result in perched water tables (Germer 2013). Hillslope settings with shallow soils and bedrock interfaces can result in interflow and subsequent streamwater generation (Spencer and van Meerveld 2016). In addition, event-specific characteristics such as the saturation

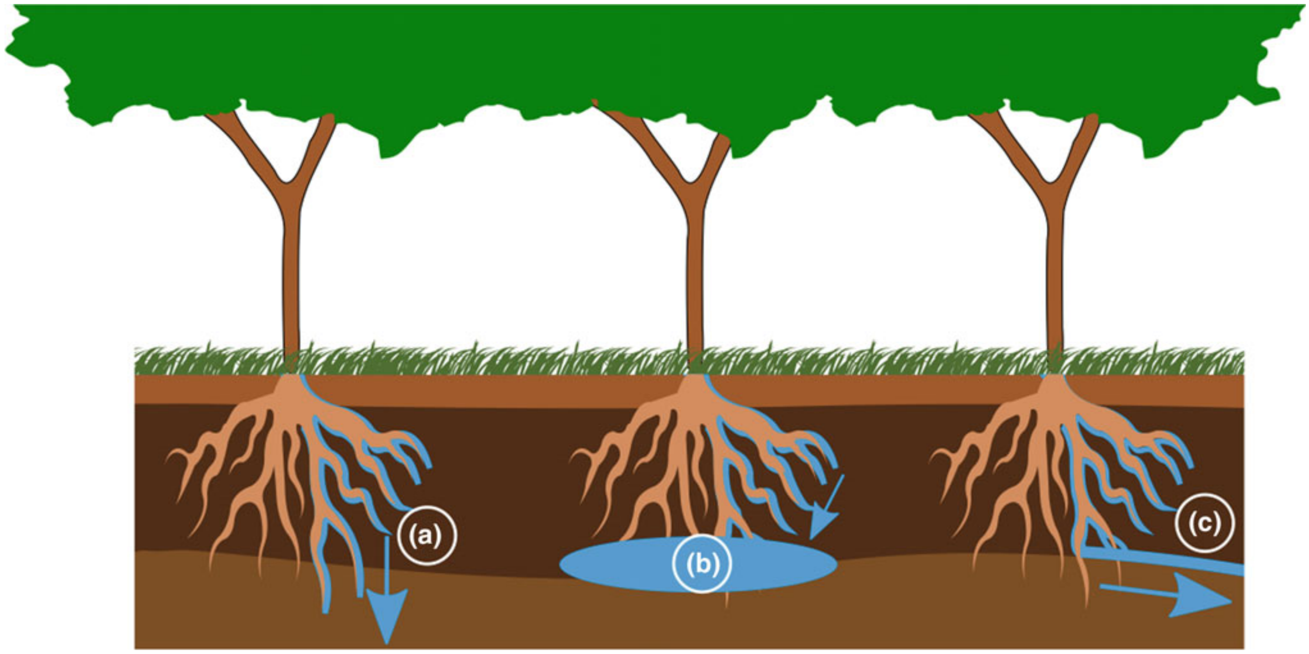


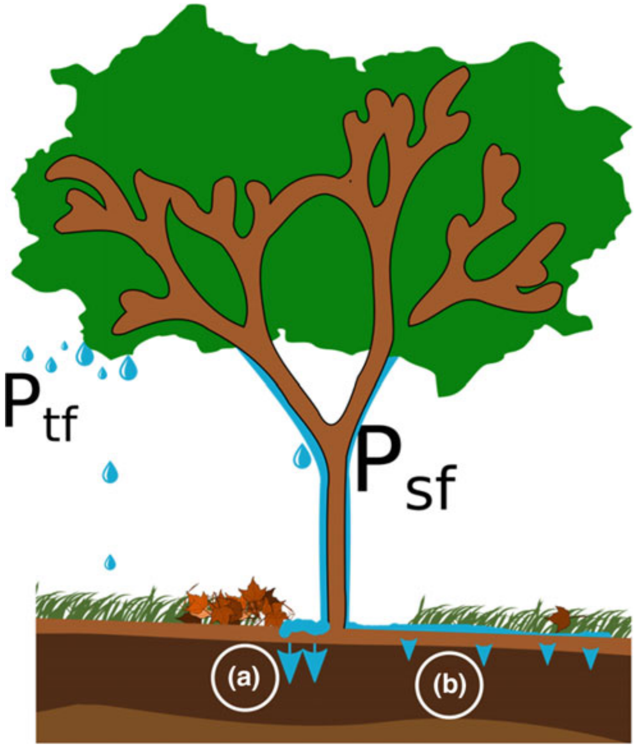
Fig. 13.1 Hypothesized recharge from net precipitation. **a** Preferential flow along roots to deep infiltration, **b** perched water tables soil layers with low conductivity or bedrock (**b**), and subsurface transport as interflow to wetlands/streams

degree of the soil, the event duration, as well as the intensity play a role of whether excess net precipitation for deep infiltration and recharge is available. In most soils, to reach deeper subsurface regions require net precipitation fluxes to access preferential pathways that bypass the unsaturated soil matrix. This has been conceptualized as "double funneling" for stemflow (Johnson and Lehmann 2006; Schwärzel et al. 2012; Spencer and van Meerveld 2016) which describes fast flow through macropores (e.g., earthworms, soil cracks) as well as flow along root systems. Macropore flow through the subsurface is also considered possible for concentrated throughfall drip points (Guswa and Spence 2012; Klos et al. 2014).

13.2.2 The Importance of Infiltration Area

The area over which any net precipitation flux infiltrates is an important factor determining how it will enter and move through the subsurface. As the bulk of net precipitation is used for evapotranspiration, an important issue, especially for stemflow, is the infiltration area applied for the flux estimate and the subsequent potential recharge. Historically, the area of the stem base was assumed to be the infiltration area for stemflow (Eaton et al. 1972; Mahendrappa 1974; Herwitz 1986); however, stemflow clearly cannot infiltrate where the stem itself is positioned. So, this may be an incorrect estimate conceptually, but, in reality, stemflow may spread out around the base to an area approximately equal to basal area (Fig. 13.2; Table 13.1). The amount and extent of overland flow generated by stemflow is both under-researched (Herwitz 1986) and debated (Carlyle-Moses et al. 2018; Van Stan and Gordon 2018). It has been suggested that stemflow will preferentially infiltrate in a narrow band at the base of individual flow paths down the stem (Fig. 13.2) so long as the stemflow rate is lower than soil saturated conductivity (Carlyle-Moses et al. 2018). Infiltration areas of individual stemflow pathways (<0.01–0.03 m^2 $tree^{-1}$) have only been once reported by dye tests on small pine trees (Carlyle-Moses et al. 2018). However, an area of soil may not always be conducting water at the theoretical or field/lab estimated rate. Patterns in soil hydrophobicity are highly variable in space and time (Doerr and Ritsema 2005) and water repellency appears to be present in surface soils of all major soil textural types at vegetated sites (Doerr et al. 2006; de Jonge et al. 2009; Goebel et al. 2011). Even an assumption of infiltration supported by visual confirmation of "normal wetting" behavior could be in error—by an order of magnitude compared to estimates based on nearby soils (Wallis and Horne 1992). In fact, patterns of surface hydrophobicity develop often during inter-storm dry periods for natural forests and have been found to influence infiltration patterns (Ferreira et al. 2016; Gimbel et al. 2016). For the soils of urban forests, they are well-known to become water

Fig. 13.2 Infiltration areas for stemflow. **a** Proximal to the stem (<1–2 m^2) or **b** as overland flow on the downward slope



repellant (Craul 1985) or have significantly reduced infiltration through compaction (Jim 1993; Mullaney et al. 2015). As a result, all other observed stemflow infiltration areas have been orders of magnitude larger than observed by Carlyle-Moses et al. (2018) and more dynamic (Table 13.1).

Stemflow infiltration areas are dynamic, indeed, depending on storm characteristics, soil type, soil saturation, and land use (Pressland 1976; Gomez et al. 2002). Whether the generally high stemflow flux rates generate Hortonian or saturation excess overland flow or infiltrate through the soil matrix or along preferential pathways highly depends on this infiltration area. However, there are a few studies discussing the infiltration area of stemflow for trees: ranging from an infiltration area nearly 12 m^2 to <0.01 m^2 tree^{-1} (Table 13.1). It has been said that stemflow infiltration areas “in the range of 1–2 m^2 [tree^{-1}] are almost always associated with extreme precipitation conditions,” (Carlyle-Moses et al. 2018), but several past studies have found large stemflow infiltration areas in this range (and larger) without extreme conditions (Table 13.1). Iida et al. (2005)

Table 13.1 Stemflow infiltration areas reported from previous work alongside storm conditions during which these areas were observed

Study	Infiltration area		Storm conditions			Tree size
	Min	Max	Amount	Intensity	*n*	Range
	(m^2 tree^{-1})	(m^2 tree^{-1})	(mm)	(mm h^{-1})	(storms)	(cm DBH)
Pressland (1973, 1976)	0.34	1.37	0.3–120.0	–	46	6–38
Tanaka et al. (1991)	0.19	1.34	2.0	–	1	9–44
Chinen (2007)	1.12	4.75	20.7	~60.0	1	17–40
Gomez et al. (2002)	0.04	1.12	0.6–77.1	–	12	26
Herwitz (1986)	0.13	3.09	11.8–51.6	73.7–118.0	2	30–48
Iida et al. (2005)	0.40	1.28	18.0–88.5	1.1–2.3	2	31–63
Rashid and Askari (2014)	6.80	11.83	–	–	–	58–97
Carlyle-Moses et al. (2018)	<0.01	0.03	5.9–16.0	–	3	2–5

found stemflow infiltration areas >1 m^2 $tree^{-1}$ under low rainfall intensities, 1–2 mm h^{-1}, and provided photographic support. Tanaka et al. (1991) found similar stemflow infiltration areas for a small storm, ~2.0 mm. One study was not included in Table 13.1 because it was a simulation; Schwärzel et al. (2012) applied stemflow volumes generated by a moderate 18 mm rainstorm, yet the smallest stemflow infiltration area achievable under the following circumstances was 0.245 m^2: (a) "forest litter around the sample tree was removed" (as this could have redistributed stemflow) and (b) "the soil surface was wetted with a spray of water [prior to the application of simulated stemflow]" explicitly to "enable a better observation of the water entry into the soil, and if necessary (when water spread over the soil surface), to reduce the irrigation rate [or, simulated stemflow rate]." Van Stan (2012), under a range of modest storm conditions on a hillslope, found stemflow dominated the shallow (>20 cm) soil water chemistry ~1 m from the stem of both a voluminous stemflow-generating and a low stemflow-generating tree species.

For smaller vegetation, where stemflow may play a major role (e.g., grasses) no infiltration areas are known, yet. As a result, stemflow's infiltration area remains broadly unobserved and, therefore, unknown. Resolving this unknown is easily accomplished by collecting direct observations of stemflow infiltration areas across storm and site conditions—which could be done using in situ video monitoring of near stem soils, or simulation of stemflow at various known rates.

13.3 Methods to Monitor Throughfall and Stemflow Infiltration

Measurement, and more often modeling, of subsurface hydrological processes has not only been a challenge for scientists interested in following the infiltration of throughfall and stemflow (Johnson and Lehmann 2006; Tanaka 2011), but it has also been a long-standing challenge for the broader field hydrology (Dane and Molz 1991). Monitoring and modeling methods used to determine water infiltration depths and pathways by throughfall and stemflow have been diverse (Fig. 13.3). Some of the most recent methods have included a combination of precipitation budgeting and soil water monitoring (Fig. 13.3a). For greater experimental control and measurement precision, the infiltration of throughfall and stemflow beneath plants have been monitored within weighing lysimeters (Fig. 13.3b). The budgeting and weighing lysimeter approaches give insights into infiltration depth and timing; however, these methods do not typically provide information on the shape of throughfall and stemflow infiltration pathways, or information about the conduits (e.g., roots versus water repellent soils) carrying throughfall and stemflow. Studies seeking to investigate the shape and drivers of infiltration pathways beneath plant canopies can apply dye or chemical tracers (Fig. 13.3c). Researchers have also used naturally present, assumed conservative, solutes in throughfall, and stemflow as "geochemical tracers" (Fig. 13.3d) which have been

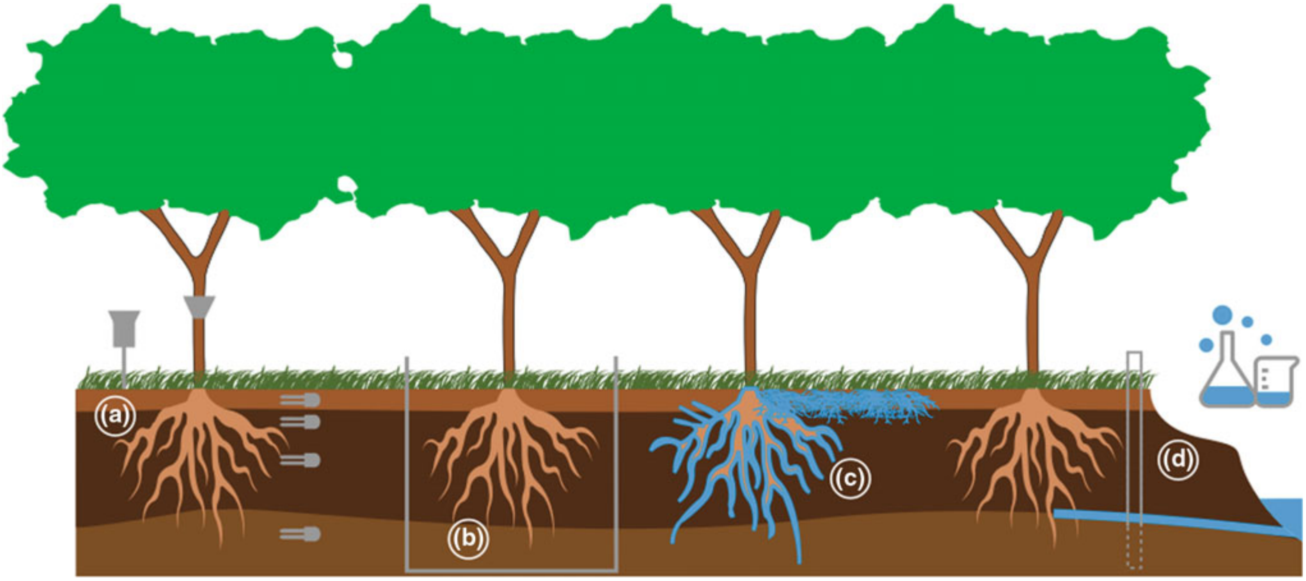


Fig. 13.3 Different monitoring methods to identify subsurface infiltration of stemflow and throughfall from **a** precipitation budgeting and soil water measurements, **b** forest lysimeter studies, **c** color or chemical tracer studies, and **d** chemical budgeting studies such as the chloride mass balance

very useful at study sites where dyes or chemical tracers cannot be applied. The different methods presented are often not used singly but in combination (e.g., lysimeters are often equipped with soil water sensors).

13.4 Mass Balances and Mixing Models

The chloride mass balance (CMB) has been widely applied to estimate groundwater recharge (Allison et al. 1985; Wood and Sanford 1995; Scanlon et al. 2002). By balancing the mass flux of chloride at the surface to the mass flux of chloride at depth, i.e., in groundwater, the recharge rate can be estimated. Taniguchi et al. (1996) applied the CMB to chloride concentrations of stemflow, soil water, and groundwater using Eq. 1.

$$R_{sf} = R\left(C_i - C_g\right)/\left(C_i - C_{sf}\right), \tag{1}$$

where R_{sf} is the recharge rate by stemflow, R the total annual groundwater recharge rate, C_i the chloride concentration of soil water at i cm depth, C_g the chloride concentration of soil water at the groundwater level depth, and C_{sf} the chloride concentration of stemflow. Using the mass balance of chloride in this way assumes that chloride behaves conservatively as it flows through the soil column (only removed by evapotranspiration).

Studies have also used other anions and major ion fluxes and budgets in combination with water budgets to monitor throughfall and stemflow infiltration (Gersper and Holowaychuk 1971; Koch and Matzner 1993; Chang and Matzner 2000). In fact, "mixing" models to partition streamflow and runoff into possible sources and examine their possible hydrologic flowpath through catchments have been used extensively over the past several decades (Inamdar 2011 and other studies cited therein). Mixing models simply solve the mass balance equations for water and any geochemical tracers selected to represent each flux of interest (in this case, throughfall and stemflow):

$$S_t = \sum_{i=1}^{n} S_i,$$

$$S_t C_t^j = \sum_{i=1}^{n} S_i C_i^j \text{ where } j = 1\ldots(n-1)$$

where S_t and $C_t{}^j$ are the subsurface flow of interest (soil solution, groundwater, etc.) and its concentration of tracer j; respectively, and S_i and $C_i{}^j$ are the contribution from an "end member," or net precipitation flux component, in this case, i and its concentration of tracer j. Solving this equation requires a minimum of $n - 1$ tracers chemicals given the following key assumptions:

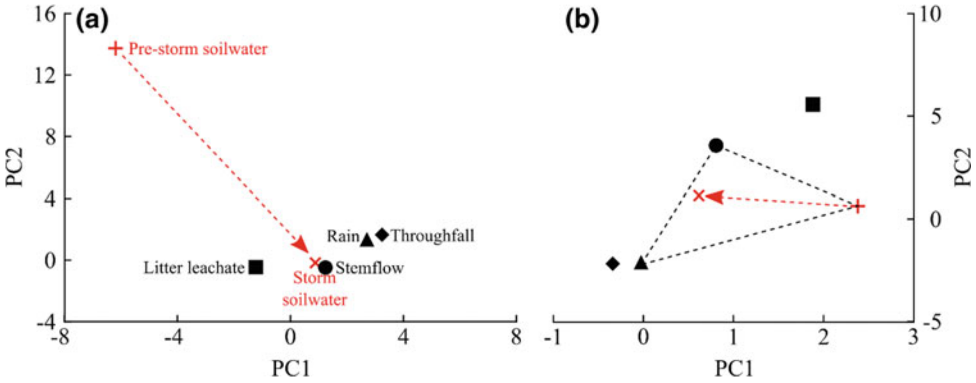


Fig. 13.4 An example mixing diagram derived from a principal components analysis illustrating the evolution of soil solution from before-to-after a storm event near a **a** voluminous stemflow-generating *Fagus grandifolia* tree and **b** a low stemflow-generating *Liriodendron tulipifera* tree—modified from Van Stan (2012). Visualization shows that soil solution during storms near *F. grandifolia* was nearly identical to stemflow; yet, for *L. tulipifera*, storm soil solutions may be a mixture of stemflow, throughfall (including gap rainfall) and pre-event soil solution. Tracers used to develop these EMMA mixing diagrams were: Na, Ca, Mg, Si, and dissolved organic carbon (Van Stan 2012)

1. Selected tracers behave conservatively (i.e., do not vary within the model time scale);
2. Mixing of tracers is linear; and
3. Net precipitation flux (end member) tracer composition is invariant across space and the time scale of the model.

More tracers than required can be used with principal component analysis to reduce the data dimensionality to, typically, two principal components (in a three end member model) that are used to solve the mass balance equations—in a process typically called "end member mixing analysis" or EMMA (Hooper et al. 1990). A benefit of EMMA is that the principal component analysis produces a mixing diagram (by plotting end members into the principal component space) that enable visualization of both S_t and its potential end members (Fig. 13.4). A complete description and theory are provided by Hooper (2003).

13.5 Lysimeters

Lysimeters are tanks that are filled with disturbed or undisturbed soil columns and are usually planted. By measuring the input in terms of precipitations, soil moisture as well as the outflow (seepage), soil water budgets can be calculated. Lysimeters are usually weighed which allows for evapotranspiration estimates as well as dynamic monitoring of the water storage. Only few lysimeter experiments are known for tree-scale applications (Fritschen et al. 1973; Edwards 1986; Müller and Bolte 2009), as lysimeters are usually used for crops or grassland. Long-term forest lysimeter experiments even have planted trees in lysimeters (Knight and Will 1977; Müller and Bolte 2009). Such tree-scale lysimeters experiments yield groundwater recharge (seepage) values, however, lack the monitoring of lateral flows.

13.6 Dye Tracer Experiments

Dye tracer experiments use dyes such as "brilliant blue" to visualize stemflow and throughfall infiltration pathways by dying soils that encounter infiltrating water carrying the dye. Dyes are usually applied using sprayers to simulate stemflow or throughfall (Spencer and van Meerveld 2016) or using sprinkler hoses clamped to the stem to simulate stemflow (Schwärzel et al. 2012), using amounts that represent observed stemflow and throughfall events. Dyes applied during "dry" periods provide limited insights due to the absence of all other subsurface hydrologic processes that would normally interact with infiltrating stemflow and throughfall water. To dye soils during rain events, some studies have applied dye in powder form (Li et al. 2009) so that the dye is infiltrated through rainfall. After excavating soil trenches the colored soil patterns then indicate flow pathways as well as infiltration depth (see Fig. 13.5). Flury and Wai (2003) provide an extensive review on

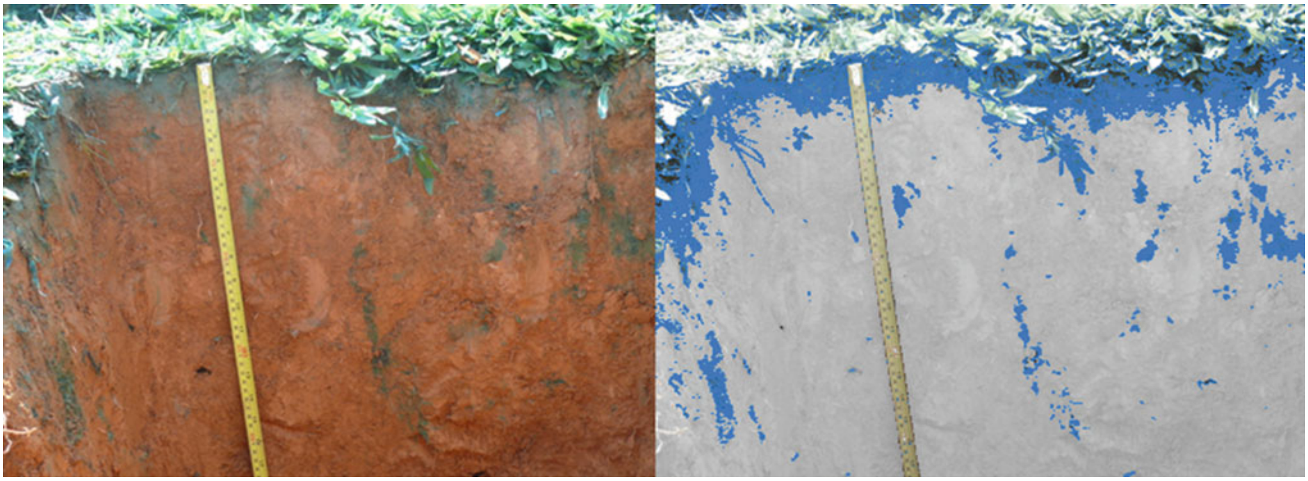


Fig. 13.5 Photo of dyed soil under grassland from Brilliant Blue sprinkler experiment (left) and filtered image highlighting the infiltration areas and pathways (right)

different types of dyes as well as on interactions of dye tracers with the soil matrix. Following the soil excavation dye tracer results are reported as photography or field drawings that can then be digitized for numeric analysis (Flury and Wai 2003; Spencer and van Meerveld 2016).

13.7 Soil Water Measurements (Tensiometers, Soil Moisture, etc.)

Several studies use soil water measurements at different depths to determine which depths throughfall and stemflow events progress. In addition, soil water sensors are also installed at different distances to the trunk to evaluate the effect of proximal stem area influences that is more associated with stemflow versus distant stem areas that are then associated with throughfall or free throughfall. Typically, soil moisture sensors as well as soil tensiometers are used (Sansoulet et al. 2008; Li et al. 2008; Liang et al. 2011; Spencer and van Meerveld 2016; Metzger et al. 2017). In comparison with dye experiments soil water sensors allow for time series data, where also the seasonal variability of infiltration and water uptake can be observed. Limitations with respect to stemflow are that the sensors can often not be installed close to the tree due to roots and that preferential flow can often not be observed. Macropore flow monitoring is associated with similar obstacles as the sensors are ideally inserted into an intact soil matrix; given that macropore flow is observed it is often not possible to distinguish it from false observations caused by preferential flow along the sensor.

13.8 Model-Based Experiments

Many studies also include modeling using the in situ monitored data or using generated datasets to focus on theoretical field experiments. The model-based experiments largely focus on soil water transport modeling and generally apply matrix flow through the soil rather than preferential flow paths. Stemflow and throughfall are added as spatial fields () or through stochastic representations of the input. Using a stochastic model approach Guswa and Spence (2012) modeled the effect of throughfall variability on recharge for hemlock and deciduous forests. Based on observed throughfall data Keim et al. (2006) used observed and synthetic throughfall data and used the HYDRUS-2D to model subsurface flows. Other studies applied the finite element model HYDRUS-3D that solves the Richards equation for water flow in different soil layers. Hopp and McDonnell (Hopp and McDonnell 2011) modeled the influence of throughfall on subsurface stormflow generation at the Panola hillslope site including outcrops and soils up to about 1.8 m depth using spatial throughfall patterns from Keim et al. (2005). Coenders-Gerrits et al. (2013) combined the previous modeling study with interpolated throughfall from the Huewelerbach site in Luxembourg to assess the effect of spatially distributed throughfall on soil moisture patterns. Liang et al. (2009) modeled a stemflow-sprinkling experiment. Preferential flow along roots was considered by defining source flux regions around the stem that were then parameterized as a variable source term for each soil layer (Liang et al. 2009).

With respect to modeling, the double funneling concept is largely applied in experimental studies (e.g., Schwärzel et al. 2012), whereas modeling studies still focus on water transport modeling through the soil matrix. Modeled flow through the soil matrix may then include different spatial input fields for throughfall (e.g., Coenders-Gerrits et al. 2013) or higher fluxes at stems through stemflow infiltration areas but with respect to the subsurface revert to matrix flow (Tanaka et al. 1996; Liang et al. 2009). No studies could be found that explicitly include macropore or preferential flow along roots in soil water modeling.

13.9 Observations and Estimates of Throughfall and Stemflow Infiltration and Interflow

Through the use of different experimental setups and methods, several studies show that (i) throughfall and stemflow can bypass shallow soil layers, (ii) one of these fluxes can infiltrate deeper than another, depending on the setting, (iii) they can lead to perched water tables, or (iv) show potential for deep subsurface and even groundwater recharge, and (v) throughfall and stemflow can reach streams through interflow. Although, the above findings are supported by individual studies, a consistent, cross-ecosystem understanding is still lacking due to a paucity of research and the large variety in site characteristics and methods applied.

Spencer and van Meerveld (2016) used blue dye tracers during dry, non-storm conditions and found deep infiltration of stemflow which at their site amounted to only 1% of precipitation. Stemflow was shown to infiltrate deep into the soil; however, it could not be determined whether this deep infiltration was relevant for groundwater recharge. Due to the lateral hydraulic conductivities of the deep soil layers, however, Spencer and van Meerveld (2016) postulated that an interflow pathway to streamwater was more likely than groundwater recharge. Interflow contributions of throughfall to streams has been reported by EMMA studies in various forest types, including various temperate forests in Northeastern USA (Brown et al. 1999; Inamdar and Mitchell 2006, 2007, 2008) and Quebec, Canada (James and Roulet 2006), a Swiss alpine forest (Hagedorn et al. 2000), an evergreen forest in Japan (Katsuyama et al. 2001) and tropical rainforests in small Amazon watersheds (Chaves et al. 2008). These investigations found throughfall contributions to streamwater chemistry were significant, ranging from 30 to 79% of event-based stream exports during foliated canopy conditions. Note that a portion of throughfall contributions to stream water may be attributed to canopy drainage directly into the channel.

Li et al. (2009) also conducted dye tracer experiments under desert shrub vegetation that confirmed deep infiltration patterns. Observed and modeled data for a banana plantation found that the substantially higher drainage volumes of stemflow also led to deeper infiltration (Sansoulet et al. 2008). Deep infiltration of stemflow has been observed beneath crops as well: e.g., potato (Saffigna et al. 1976) and maize (Zheng et al. 2019). Throughfall beneath maize has also been observed to initiate spatially heterogeneous infiltration fronts (Zheng et al. 2019). Metzger et al. (2017), based on an intensive field campaign, showed that the effect of net precipitation on soil moisture is short-lived. Having analyzed soil moisture profiles at stem distances above 1 m this is especially true for throughfall. For stemflow many studies show low soil moisture levels near the stem (Rutter 1963; Buttle et al. 2014; Rashid et al. 2014) and hypothesize that this soil dryness is due to stemflow pathways that seem to surpass the soil matrix very close to the stem (e.g. Schwärzel et al. 2012). Liang et al. (2011) conducted dye tracer experiments distinguishing between throughfall and stemflow by means of different dyes. Results showed deep infiltration from bypass flow occurred for both throughfall and stemflow that bypassed surface soil layers—in fact, the frequency of this bypass flow (presumably along roots) varied little between natural and stemflow-exclusion periods. The study investigated up and downslope regions relative to the trunk. Using soil tensiometers Durocher (1990) observed markedly higher infiltration by soil tensiometers and verified this by tension infiltrometer measurements showing high permeabilities at tree stems (475 mm h^{-1}). A study conducted by Nulsen et al. (1986) on Mallee vegetation in Western Australia using soil moisture probes and dye tracers also show the infiltration of stemflow to deeper soil layers.

Using water and ion fluxes and budgets Chang and Matzner (2000) investigated proximal and distant stem areas. In combination with transpiration data, the study estimated that the total transpiration associated with the proximal stem was only 3.4% at the stand scale, whereas the seepage at the proximal stem area was estimated at over 13%, suggesting transport to streamflow or groundwater. Germer (2013) studied stemflow of palm trees that led to perched water tables below the stem. The perched water table was linked to an impeding soil layer that led to a subsurface saturation. In case of hillslope settings stemflow above impeding layers can also lead to interflow and subsequent streamwater recharge as postulated by Spencer and van Meerveld (2016). Seepage has been derived from large-scale lysimeters at the forest research station in Britz, Germany. In 1974, 100 m^2 lysimeters with a depth of 5 m have been planted with different tree species. Müller and Bolte (2009) report seepage results of about 20% for European beech and 12% for Scots pine. Depending on the stand age and the associated transpiration activity, the study also reports different seepage percentages by age. No differentiation of net precipitation fluxes into stemflow, throughfall and open rainfall were reported. Liu et al. (2015), using water isotopes (δD & δ18O), estimated that throughfall from alpine shrubs could be concentrated enough to account for 33–61% of post-event soil water topically derived contributions to soil water for discrete storms.

With a focus toward aquifer recharge Návar (2011) discussed that in a semi-arid to temperate forest and shrub study in Mexico, any storm event above 15 mm magnitude is likely to contribute to aquifer recharge. With respect to the stemflow infiltration area the study calculated that stemflow infiltrates 2–7 times deeper than rainfall. Bialkowski and Buttle (2015) provide modest estimates of stemflow contributions to soil water recharge, finding identical recharge rates near pine trees without (114–134 mm y^{-1}) and with stemflow (114–135 mm y^{-1}), but a 13% increase in recharge from stemflow near maple trees. Using the chloride mass balance Taniguchi et al. (1996) estimated that the contribution of stemflow to total groundwater recharge ranged from 11 to 19%. Tanaka et al. (1996) corroborated these findings with a modeling study using a cylindrical infiltration model based on the experimental data that produced an estimate of 9–23%. The highest contributions for stemflow have been reported for crops, where maize stemflow has been estimated to increase recharge by 59–82% compared to inter-row areas (van Wesenbeeck and Kachanoski 1988).

Modeling results on hillslopes using observed throughfall fields showed minor influences toward subsurface flow generation and only impacted soil moisture patterns (Coenders-Gerrits et al. 2013). Hopp and McDonnell (2011) also did not find significant effects of throughfall patterns; only the effect of interception losses when using open rainfall was detectable in terms of an overestimation of lateral subsurface stormflow. Regarding soil water recharge, simulations by Guswa and Spence (2012) found that throughfall patterns (with a modest 30% spatial coefficient of variation) could increase recharge rates (mm day^{-1}) by a wide range compared to uniform throughfall patterns, depending on the ratio of total throughfall supply to transpiration. Low throughfall amounts (compared to transpiration) with drip points could increase soil water recharge by 31–129%; however, when throughfall was larger than transpirational water needs, the inclusion of drip points only increased recharge by 5% (Guswa and Spence 2012). Using a variable source term for stemflow in the Richards equation, Liang et al. (2009) showed the importance of including stemflow not only as net precipitation input but also in the soil modeling. Compared to a classic representation of net precipitation their model did not capture the deep infiltration that was seen from stemflow-sprinkler experiments.

13.10 Conclusions

On the one side, stemflow and throughfall routing to deeper soil layers can provide trees with water sources to be tapped during drought conditions. On the other side, however, studies also show that water is likely to be transported further as lateral interflow to streamwater or to groundwater aquifers (Taniguchi et al. 1996; Spencer and van Meerveld 2016). The different experimental studies focus on various regions (root zone, groundwater, or hillslope and streamwater) and, depending on that differentiation, apply different methods that range from water and element fluxes and budgets to color and chemical tracers or lysimeters. Initially, many studies are motivated by the potential of stemflow from trees that albeit being often well below 10% of precipitation, can be a spatially stable point input with high intensities considering the stemflow infiltration area (Aboal et al. 2000; Návar 2011; Carlyle-Moses et al. 2018; Friesen et al. 2018).

The large variety of methods, field sites, as well as species and soil specification do not yet make it feasible to make global assessments of the subsurface flow patterns and depths. Many studies show flow along with root systems and the bypass of upper soil layers. However, whether the water is further transported as lateral flow to rivers or down to groundwater recharge; or whether the infiltrated water is being completely taken up by roots again has only been examined by a few studies. If at all, throughfall seems to be the net precipitation flux with the highest potential to reach streams via interflow (Brown et al. 1999; Hagedorn et al. 2000; Katsuyama et al. 2001; Inamdar and Mitchell 2006; James and Roulet 2006; Inamdar and Mitchell 2007, 2008; Chaves et al. 2008) while stemflow seems to have the highest potential for subsurface recharge (Johnson and Lehmann 2006). Yet, how relevant stemflow is on the global scale is uncertain as, generally, only medium to high stemflow producing tree species are monitored, so there is a bias when considering global relevance. On the other hand, for trees that do produce considerable amounts of stemflow subsurface flow and preferential pathways have been identified and are supported by literature.

Considering the tree species that do show high potential for stemflow-induced subsurface recharge and where soil characteristics hint at the potential for aquifer or streamwater recharge, future studies may include additional monitoring in wells or streams or even sensors to determine and monitor spatial dynamics of the infiltration area at the surface. Often studies are logistically limited to the root zone or relatively shallow depths up to 1 m. The focus on stemflow, of course, is hampered by the requirement of installing sensors close to the tree roots. Established geophysical techniques have recently been applied to estimate root distribution and could potentially be extended to water flux monitoring instead or in combination with few soil water sensors (Mary et al. 2018). Promising techniques include those that combine net precipitation sampling with soil water, streamflow, or groundwater sampling for use in end member mixing approaches (EMMA). EMMA, as such, then allows the partitioning of soil water, streamflow, or groundwater into the main contributing sources, such as open rainfall, throughfall, and stemflow or "old" groundwater (e.g., Inamdar 2011). With regard to modeling, many studies investigate the effect of throughfall patterns on soil moisture but so far none include macropore or preferential pathways in addition to matrix flow that is of high relevance when modeling stemflow.

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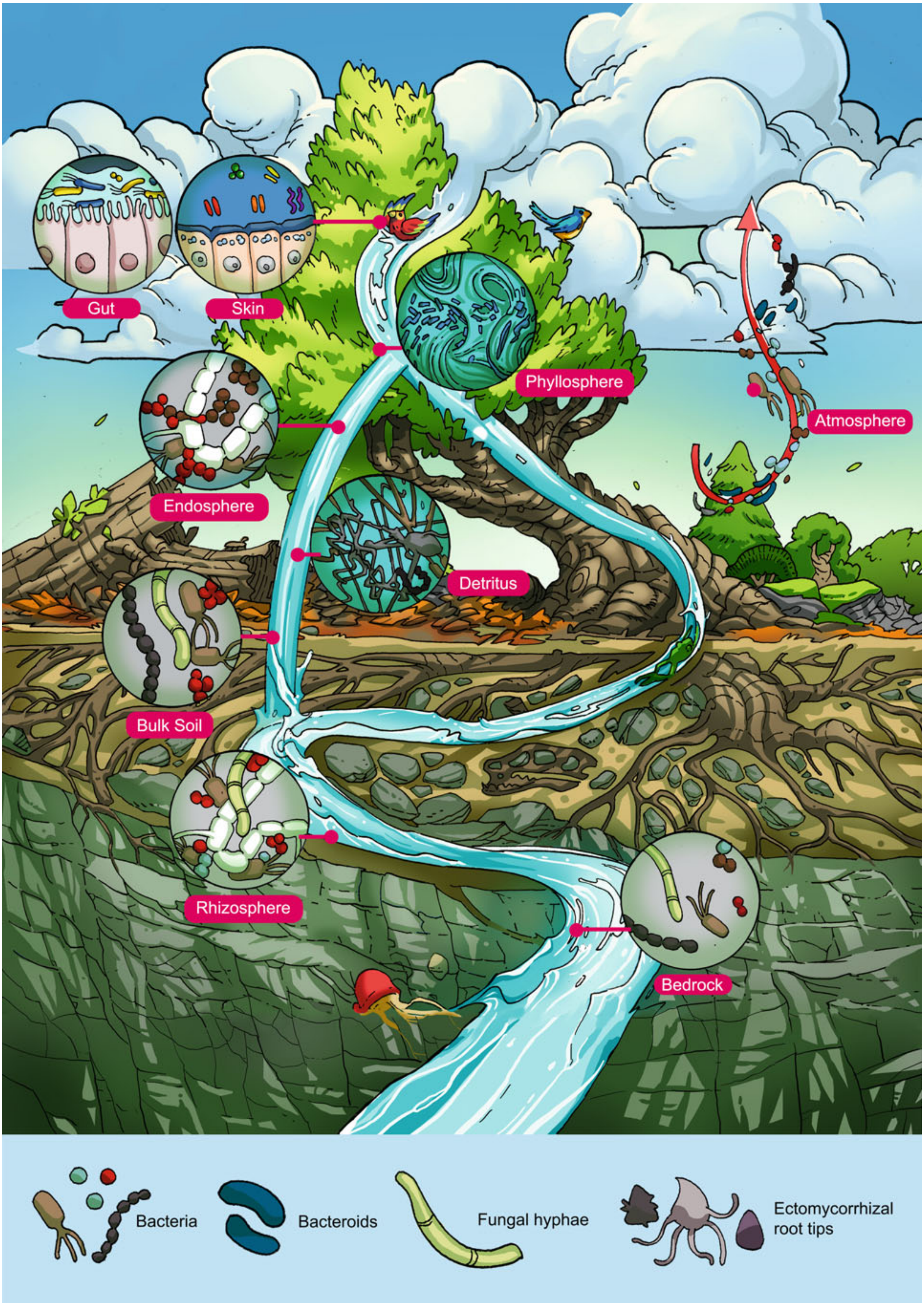
Gut
Skin
Phyllosphere
Atmosphere
Endosphere
Detritus
Bulk Soil
Rhizosphere
Bedrock
Bacteria
Bacteroids
Fungal hyphae
Ectomycorrhizal root tips

Precipitation Partitioning—Hydrologic Highways Between Microbial Communities of the Plant Microbiome?

14

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Abstract

There are multiple distinct habitats for microbiota inhabiting the plant microbiome (phyllosphere, endosphere, litter, rhizosphere) and habitats that act as additional sources (and sinks) of microbes and nutrients for the plant microbiome (atmosphere, pedosphere, bedrock, and fauna). These habitats harbor distinctive microbial communities that differ in structure, composition, function, and spatiotemporal dynamics. Each habitat also differs in the mechanisms that provide "gateways" of exchange of microbes (and microbial products) between two communities, or in their access to "highways" that connect multiple communities. Of the environmental processes driving microbial community exchanges, precipitation events seem to represent the only one highway that can connect all the abovementioned habitats—the "hydrologic highway". When precipitation contacts plants, it is partitioned into interception (water stored on, and evaporated from, plant surfaces), throughfall (water that drips from canopy surfaces and through gaps), and stemflow (water that is drained down the stem). This chapter describes the ways that precipitation partitioning in vegetated ecosystems (into interception, throughfall, and stemflow) may connect microbial communities from the top (atmospheric boundary layer) to the bottom (bedrock face) of the critical zone via these hydrologic highways.

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Throughfall • Stemflow • Ecohydrology • Bacteria • Fungi • Archaea • Plant microbiome

14.1 Introduction

The biogeochemical functioning of vegetated ecosystems depends on soil properties (i.e., mineral parental material, pH, and nutrient availability) and the activities of the biosphere, including plants, macro-(earthworms, insects) and microorganisms (protists, amoebae, fungi, bacteria, and archaea). In recent decades, our ability to explore the abundance, composition, function, and dynamics of soil organisms has achieved an extraordinary level of detail. This is especially the case for microorganisms like bacteria, archaea, and fungi, for which the development of high throughput sequencing methods was a real revolution. This has permitted and motivated research examining combined genomic information associated with all plant-related habitats called the "plant microbiome" (Berg et al. 2014; Pérez-Jaramillo et al. 2018). Across vegetation-dominated ecosystems, there are multiple distinct habitats for microbiota that inhabit the plant microbiome (phyllosphere, endosphere, litter, and rhizosphere) and that serve as sources of immigrants to the plant microbiome (atmosphere, pedosphere, bedrock, and fauna: Fig. 14.1), all of which harbor taxonomically distinctive microbial communities that differ in abundance, function, and spatiotemporal dynamics (Baldrian 2017; Turner et al. 2013). Each habitat also differs in environmental properties that influence the establishment and survival of microbial organisms, including nutrient

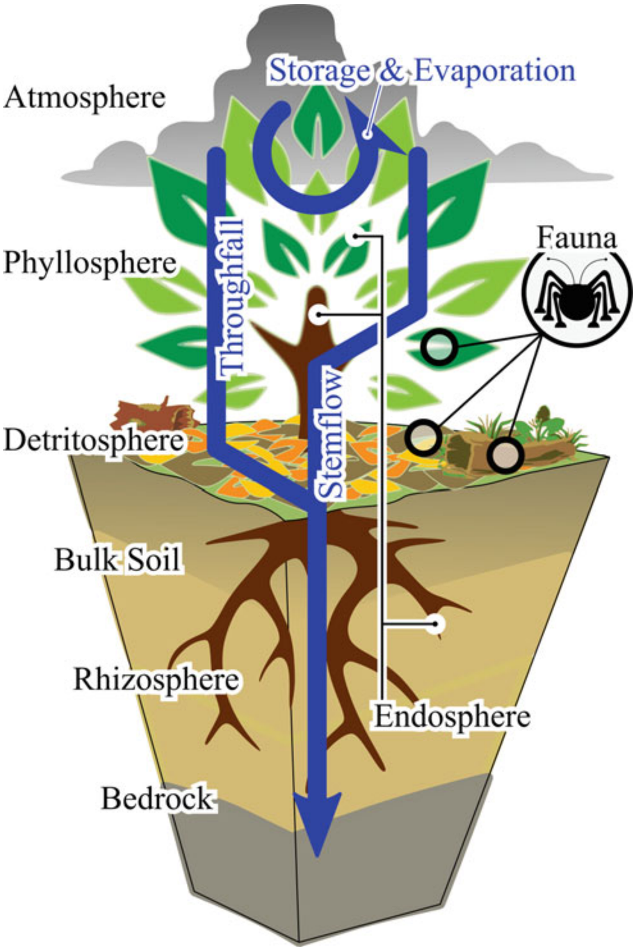

Fig. 14.1 During storms, precipitation is stored or drained throughout the entire critical zone (from the atmospheric boundary layer to bedrock). Along the way, precipitation is partitioned while interacting across all habitats of the plant microbiome and those that serve as sources of immigrants to the plant microbiome

availability, radiation exposure, substrate texture, humidity, etc. Exchanges of microbes and microbial products may occur between two communities at physical or chemical "gateways"—e.g., effectors that mediate rhizo–endosphere interactions (Rovenich et al. 2014). Multiple environmental processes, however, can establish "highways" enabling interaction between multiple communities—e.g., aeolian action aerosolizing microorganisms from the phyllosphere to the atmosphere, which may then enter another habitat, like litter, via deposition (Morris et al. 2014b).

Few environmental processes can connect more than two or three habitats within a mature plant microbiome—as a seed more connections are possible (Nelson 2018). It may be that precipitation events represent the only one that can connect all habitats. Briefly, precipitation contains bioaerosols (Morris et al. 2014a), which interact with leaf and stem surfaces when draining to the litter (Chaps. 4 and 5). Net precipitation fluxes are further partitioned in the litter, being stored, evaporated, and elementally altered by litter decomposition (Chap. 11). Net precipitation then percolates through the pedosphere (Li et al. 2009) and rhizosphere (Johnson and Jost 2011), introducing suspended microbes, and their lysates and exudates, from every preceding habitat. Thus, this "hydrologic highway" may connect the atmospheric microbial community to the very bottom of the critical zone to the bedrock interface, via preferential flow paths through the soil matrix (Backnäs et al. 2012). All along the way, pathogenic and mutualistic microbes within net precipitation will pass gateways to the endosphere—like leaf stomata, stem lenticels, and root hairs. Few studies have examined how net precipitation, water storage, and evaporative dynamics within and from vegetation elements relate to any aspect of microbiota throughout the plant microbiome. Insights from these few studies are further limited by "fingerprinting" methods that permit only coarse comparison of microbial communities, providing no taxonomic information (Moore et al. 2016; Rosier et al. 2015, 2016); yet, more recent methods can yield detailed taxonomic data (Reuter et al. 2015). Therefore, we explicitly acknowledge this chapter's theoretical nature and hope it will inspire future research regarding the influence of precipitation partitioning on the plant microbiome. We begin with an introduction to the microbially relevant aspects of precipitation partitioning, then the following sections describe major known and hypothetical effects of precipitation partitions on the habitat properties and processes of each sphere, including animal-associated microbiomes.

14.1.1 Microbially Relevant Aspects of Precipitation Partitioning

Precipitation interacts with plant canopies, where it is stored (Chap. 2), evaporated (Chap. 3), and redistributed to the surface in a spatially heterogeneous manner (Chap. 6). Precipitation reaches the surface as (i) throughfall consisting of precipitation that falls through gaps and from canopy surfaces and (ii) stemflow consisting of precipitation that is entrained on branches and drained to the stem base (Chap. 4). Throughfall and stemflow are then stored, evaporated, and chemically enriched in the litter layer (Chap. 11). The storage, evaporation, and drainage of precipitation via throughfall and stemflow, despite being rarely considered in plant microbiome research, have clear relevance to microbial ecology. Most obviously, they represent a significant water supply to aboveground microbial communities, like water stored on or in foliage, bark, epiphytic vegetation, tree holes, and litter. Subsurface microbial communities can exploit longer lasting soil water supplies; yet, throughfall and stemflow replenish soil water resources (Guswa and Spence 2012; Návar 2011). Throughfall and stemflow provide water flow that may disrupt microbial communities by washing plant surfaces with hundreds of liters flowing rapidly through the canopy in <0.25 h (Keim and Link 2018; Keim and Skaugset 2004). Net precipitation and stored water contain dissolved nutrients and suspended particulate matter (Chap. 5) that, depending on concentration and chemical constituency, may nourish or stress microbes. Microbiota may rely on dissolved nutrients in net precipitation waters, having been found to consume ~90% of dissolved organic matter transported by throughfall and stemflow within 1–4 days, for example (Howard et al. 2018). Finally, evaporation from wet canopy and litter surfaces exerts a significant influence over humidity dynamics throughout the plant microbiome (Pypker et al. 2017; Van Stan et al. 2017b). Pathogenic disease susceptibility depends on a "triangular interaction" between microbial pathogens, plants, and environmental factors, called the "disease triangle" (Stevens et al. 1960), within which the role of humidity has been well researched (Colhoun 1973; Huber and Gillespie 1992). However, the importance of storms in pathogenic plant–microbe interactions beyond pathogen dispersal has only recently gained attention (Aung et al. 2018); which is surprising considering that conditions during precipitation partitioning may represent a triple threat—open stomata, high humidity, and increased pathogen mobility along within canopy flow paths (Davidson et al. 2008; Garbelotto et al. 2003). Thus, the following sections focus on water storage, evaporation, throughfall, and stemflow as the relevant precipitation partitioning factors interacting to form hydrologic highways between the microbial communities of the plant microbiome.

14.2 Atmosphere

Precipitation connects the microorganisms of the atmosphere with the microbiomes of plants, soil, and water. Given that it is difficult to identify clear distinctions between the component members of each of these different microbial communities, it would be more precise to state that precipitation transports microorganisms between the air, plant surfaces, soil, surface water, and groundwater. For the air over continents, the microorganisms that are aloft originate mostly from vegetation (Carotenuto et al. 2017; Fröhlich-Nowoisky et al. 2016; Lindemann et al. 1982). In urban centers, various anthropogenic features can also be important sources of airborne microbial assemblages whose composition is subsequently influenced by the chemistry of the air and by extreme heat events typical of "urban heat islands" (Fang et al. 2018; Pyrri and Kapsanaki-Gotsi 2017). The various microorganisms that are aerosolized by active or passive mechanisms from land cover are readily lofted into the atmosphere, transported mostly by turbulent wind (and other factors, see Edmonds 1979; Morris et al. 2014b). If microorganisms are lofted out of the planetary boundary layer and into the free atmosphere, they can travel very long distances and eventually mix with microorganisms such as viruses that more typically are emitted from ocean surfaces (Reche et al. 2018). Therefore, the tropospheric air column above any particular continental site will typically contain microorganisms in the boundary layer that are mostly of local origin overlaid with microorganisms that are moved with the air masses that transport clouds in the free atmosphere. For the return trip back to Earth's surface, deposition of these living particles occurs as gravitational settling, molecular diffusion, impacts onto surfaces (like vegetation), or by precipitation through rainout and washout (Edmonds 1979). For example, total "dry" deposition of viral particles has been observed on the order of 10^9 viruses m^{-2} day^{-1} (Reche et al. 2018). Although this quantity is impressive and greater than the number of bacteria dry deposited under the same conditions (Reche et al. 2018), it is likely due to the immensely greater size of the total population of viruses on Earth and hence in the ensemble of its habitats compared to other microorganisms. The various forms of liquid or solid water in the atmosphere—rain, fog, or snow—are very effective downward highways for microorganisms in the atmosphere. The effectiveness of these atmospheric hydrologic highways depends on the capacity of the microorganisms to get on board.

14.2.1 Atmospheric "On-Ramps" to the Hydrologic Highways

There are essentially two main "wet" deposition processes that allow airborne microorganisms to get on board (or become "scavenged" by) the atmospheric hydrologic highways that will bring them downward: rainout and washout. Rainout is the incorporation of microorganisms into raindrops as they form in clouds. In temperate regions of the world, raindrops form via the aggregation of super cooled droplets on an ice crystal. Ice nucleation active bacteria can catalyze the freezing of cloud water at temperatures warmer than most other atmospheric ice nuclei, thereby making initial ice crystals for raindrop formation, and can be considered to actively assure their integration into raindrops (Morris et al. 2013; Stopelli et al. 2017). As the droplets aggregate, any other microorganisms in the cloud water (Amato et al. 2007, 2017; Wei et al. 2017) will be assembled into the forming drops. The growing aggregates are initially solid, and their crystalline form is influenced by the conditions (temperature in particular) under which they form. As they fall, they can melt into raindrops depending on the temperature along the fall. Snowflakes and raindrops can bump into microorganisms in the dry air as they fall, allowing them to incorporate more particles in a second scavenging process called washout. The efficiency of washout in amassing microorganisms into falling precipitation depends on the probability for encounter between the hydrometeors (drops or flakes) and the airborne microbial particles. Encounters with larger particles are more likely than with smaller particles (McDonald 1962) and especially when such particles are not rare in the trajectory of the falling hydrometeor. The importance of particle size is evident in the positive effect of rainfall on bacterial deposition; whereas, there is a lack of influence of rainfall on viral deposition (Reche et al. 2018). Although raindrops clearly scavenge microorganisms as they fall—as illustrated with simulated rainfall using water that was sterile at the beginning of the fall (Hanlon et al. 2017)—scavenging is likely to contribute more to the diversity than to the quantity of microbes in precipitation as direct counts of bacteria in cloud water and in rainfall across a range of studies reveal concentrations ranging from 10^3 to 10^5 cells mL^{-1} for both types of waters (Hu et al. 2018).

The combination of these two wet deposition processes for accessing downward hydrologic highways results in highly diverse mixtures of microorganisms that reflect the range of trajectories and origins that contribute to the falling microbial assemblages. For example, in monsoon rains, the relative abundance of *Pseudomonas* was highest during the southwest monsoon (75%) whereas *Pantoea* was abundant in the northeast monsoon (51.8%) (Akila et al. 2018). Likewise, for rain landing in high mountain "pristine" lakes in Austria, rain from events with Atlantic or continental origins were dominated by Betaproteobacteria, whereas those with Saharan dust storms were dominated by Gammaproteobacteria (Peter et al. 2014). It was shown that *Pseudomonas* is able to generate rain as a result of proteins that enable Gram-negative bacteria to promote nucleation of ice at relatively high temperatures, above −5 °C (Gurian-Sherman and Lindow 1993). These proteins are localized at the outer membrane surface and apparently play a role in the initiation of precipitation (Möhler et al. 2008) and can cause frost damage to many plants after deposition on the canopy. For fungi, for example, rainfall deposits taxa that are not seen during dry deposition, like Agaricomycetes and Sordariomycetes (Woo et al. 2018). For specific microbial species such as *Pseudomonas syringae*, its presence in rain or snowfall collected in France was markedly enhanced by air masses from oceanic or Mediterranean origins that were not subjected to extreme negative temperatures; whereas, *Botrytis cinerea* in the same precipitation samples was not influenced by these parameters (Monteil et al. 2014). The composition of rain in terms of functional groups of microorganisms, and especially those that are ice nucleation active, can also be influenced by the physicochemical conditions of the hydrologic highway. The ice catalyzing bacteria that are active at the warmest temperatures will be the first to fall as rain forms in clouds (Pouzet et al. 2017; Stopelli et al. 2015, 2017) as long as their activity is not damaged by acidic conditions (Attard et al. 2012). Fog droplets also contain microorganisms whose composition is influenced by local sources (Evans et al. 2019). This reflects how fog forms—as condensation of water vapor in the planetary boundary layer. Fog capture and drainage by vegetation can represent a substantial water supply to the surface (Sampurno Bruijnzeel et al. 2006), transporting the microorganisms with them.

14.3 Phyllosphere

The "phyllosphere" refers to all aboveground surfaces of a plant (Ruinen 1956), such as flowers, fruits, branches, stems, epiphytic vegetation, and leaves; however, most microbiological research has focused on leaves. The global leaf surface area alone has been estimated at ~1 billion km^2 and to host 10^{26} bacterial cells (Vorholt 2012). Global phyllosphere surface area and microbial abundance is larger than leaf area alone. An estimate of global bark surface area from summing stem areas from land surface model input data (e.g., Mendoza et al. 2015) yields ~41 million km^2—an area nearly as large as the Asian continent! Epiphytic vegetation is ubiquitous across ecosystems, representing an additional 2–9,865 kg ha^{-1} of biomass (Zotz 2016). Moreover, some plant surfaces can pool and store precipitation, creating sub-habitats in the stem (called dendrotelmata) and on leaves (called phytotelmata).

14.3.1 Leaves

Plant leaves are covered by a cuticle, a polymer of long-chain aliphatic compounds that is embedded with (intracuticular) and overlaid by (epicuticular) soluble waxes (Zeisler-Diehl et al. 2018). Due to the hydrophobic (water repellent) nature of the cuticle, leaf surfaces are often self-cleaning, leading to aerial depositions being washed off during rainfalls (Barthlott and Neinhuis 1997; Neinhuis and Barthlott 1997). The cuticle serves as a barrier to limit the loss of water and solutes from the apoplast to the leaf surface. Notably, the cuticle barrier is heterogeneous and different sites on the leaf surface are more or less susceptible to water and solute loss (Remus-Emsermann et al. 2011; Schlegel et al. 2005). Leaf cuticle characteristics also, in large part, determine how precipitation will be partitioned into interception, throughfall and stemflow (Crockford and Richardson 2000; Holder and Gibbes 2017).

Another unique feature of the phyllosphere is the heavily fluctuating physical conditions: (i) The temperature on the same leaf may fluctuate more than 20 °C within a few hours (Yu et al. 2018). (ii) In temperate conditions, water availability is usually low on leaves due to their exposed nature and hydrophobic properties; even though it has been proposed that leaves may often retain microscopic amounts of water (Burkhardt and Hunsche 2013). However, during rain events, leaves will be flushed by ample amounts of water. (iii) Lastly, most trees and shrubs in temperate environments will shed their leaves once a year.

Physicochemical conditions strongly influence the microbial colonizers of the phyllosphere, which include oomycetes, fungi, and bacteria (Agler et al. 2016). Bacteria dominate this environment and reach up to 10^8 colony-forming units per gram of leaf material and cover about 5% of the leaf under temperate conditions (Remus-Emsermann et al. 2014). Microbial colonizers have different means of reaching the phyllosphere, depending on the plant species and the colonized organs. For annual plants that live close to the ground, such as the model plant *Arabidopsis thaliana*, initial colonizers are recruited during germination of the seed by the surrounding soil microbiota or the air (Bai et al. 2015; Maignien et al. 2014). During this stage, phyllosphere colonizers are selected by the leaf environment and dominate the phyllosphere microbiota thereafter (Maignien et al. 2014). Due to the yearly leaf fall on many plants, this cycle will reoccur every year when leaves reemerge. This is why the species composition of plants' phyllosphere microbiota may differ from year to year, while it remains similar at lower phylogenetic resolutions (Vorholt 2012). The immigrants on freshly emerged leaves either originate from wind distributed soil particles or microbiota of surrounding vegetation where microorganisms were aerosolized (Lymperopoulou et al. 2016) or animal vectors such as foraging insects (Kovach et al. 2000). Once the first leaves are colonized, leaves that are emerging later are most likely colonized by microorganisms from the same plant that are being dislodged by water and move via throughfall and stemflow or that are aerosolized and move with the air turbulences.

On a leaf scale, water droplets often adhere to trichomes, epidermal cell grooves and in the grooves along the curvature of leaves (Wang et al. 2015). On the micrometer scale, which is relevant to bacteria, water relationships are difficult to study and are not well understood (Beattie 2011). At an individual bacterium scale, it was found that bacterial bioreporters for water stress reported heterogeneous distributions of water stress conditions on bean leaves (Axtell and Beattie 2002). At the scale of an individual leaf, fungal infection (by *Erysiphe alphitoides*—the cause of powdery mildew) has been found to alter leaf water storage capacity, which may influence total rainfall interception (Klamerus-Iwan and Witek 2018). Fungal conidia from leaves (as well as bark and atmospheric sources) can be transported to other organs in the phyllosphere (and beyond) by throughfall and stemflow hydrologic highways (Gönczöl and Révay 2004; Magyar et al. 2016).

Phyllosphere microbiota thrives on soluble nutrients leached from the apoplast of leaves to the phyllosphere (Mercier and Lindow 2000; Remus-Emsermann et al. 2011; Ryffel et al. 2016; Shiraishi et al. 2015; Tukey and Mecklenburg 1964). Bacteria may increase the rate by which soluble compounds leach to the leaves by producing surfactants (Knoll and Schreiber 2000; Schreiber et al. 2005) and phytohormones (Ali et al. 2009; Dhandapani et al. 2016). Bacteria will also change the composition and reduce the concentration of nutrients in leachates (Mercier and Lindow 2000). However, thanks to the heterogeneous nature of leaves and the incomplete and segregated colonization by bacteria (Remus-Emsermann and Schlechter 2018) it is unlikely that nutrients will be depleted completely. Leachates are redistributed via throughfall and stemflow within the phyllosphere and are lastly flushed into the litter layer and finally the pedosphere (Bittar et al. 2018).

14.3.2 Accumulation Areas in the Phyllosphere (Bark, Treeholes, and Epiphytes)

Little work focuses on microbiota on non-leaf elements of the phyllosphere; however, many of the particles traveling along canopy hydrologic highways do not reach the ground, but concentrates in canopy "accumulation areas", like bark fissures (Magyar 2008), tree hollows, or dendrotelmata when filled with water (Gönczöl 1976; Gönczöl and Révay 2003; Magyar et al. 2017a; Sridhar et al. 2013), and epiphytes (Karamchand and Sridhar 2009; Sridhar et al. 2006). Much of the trapped organic matter is not microbiota, but leaf litter, twigs, anemochorous seeds and inflorescences (Chauvet et al. 2016) and microlitter (Carroll 1981) that is rich in various nutrients (Schroth et al. 2001), creating a crown humus deposit capable of higher fungal richness than forest floor soil (Cardelús et al. 2009). The accumulation areas store precipitation water for some hours or even weeks, creating aqueous microhabitats, particularly for dendrotelmata in tree holes (Magyar et al. 2017b). Water retention can also be substantial and longer lived in epiphytes (Porada et al. 2018) and bark. Bark, for example, can store up to 700 L tree^{-1} (Van Stan et al. 2016) and experience evaporation rates typically lower, ~8–13%, than those experienced by leaves (Van Stan et al. 2017b). Particles transported by draining precipitation are consumed by saprotrophs, mostly by fungi and, thus, this subsection focuses on fungi; but bacteria, rotifera, amoebae, nematodes, and insect larvae should also be mentioned as "coworkers" in converting such debris into crown humus. In fact, mosquito larvae in stemflow-supplied tree holes (which are important vectors of human and animal pathogens) not only process canopy debris, but can also alter the bacterial and fungal community (Kaufman et al. 2008). From a mechanistic point of view, accumulation areas could be regarded as a sink of airborne particles trapped by plants where the stemflow hydrologic highway powers a self-cleaning system. Accumulation areas in plant canopies have surprisingly complex food webs (Fig. 14.2) where the contribution of fungi is, again, important (Vass and Magyar 2013).

Only a few studies since the 1970s have examined the relationships of fungi with bark, epiphytes and tree holes, and the hydrologic highways connecting them (Gönczöl 1976; Gönczöl and Révay 2003; Karamchand and Sridhar 2008; Kladwang et al. 2003). A recent long-term (5-year) observation of a tree hole in Budapest, Hungary found resident fungal species had various origins but was dominated by spores known to be transported by stemflow and throughfall (Magyar et al. 2017b). Nevertheless, these transported fungi might have low competitive ability in aquatic habitats or serve as food for invertebrates such as insect larvae living in the tree hole (Vass and Magyar 2013). Tree hole fungal community composition varied significantly between years and interannually, likely as a result of changes in the frequency and stochasticity of stemflow and

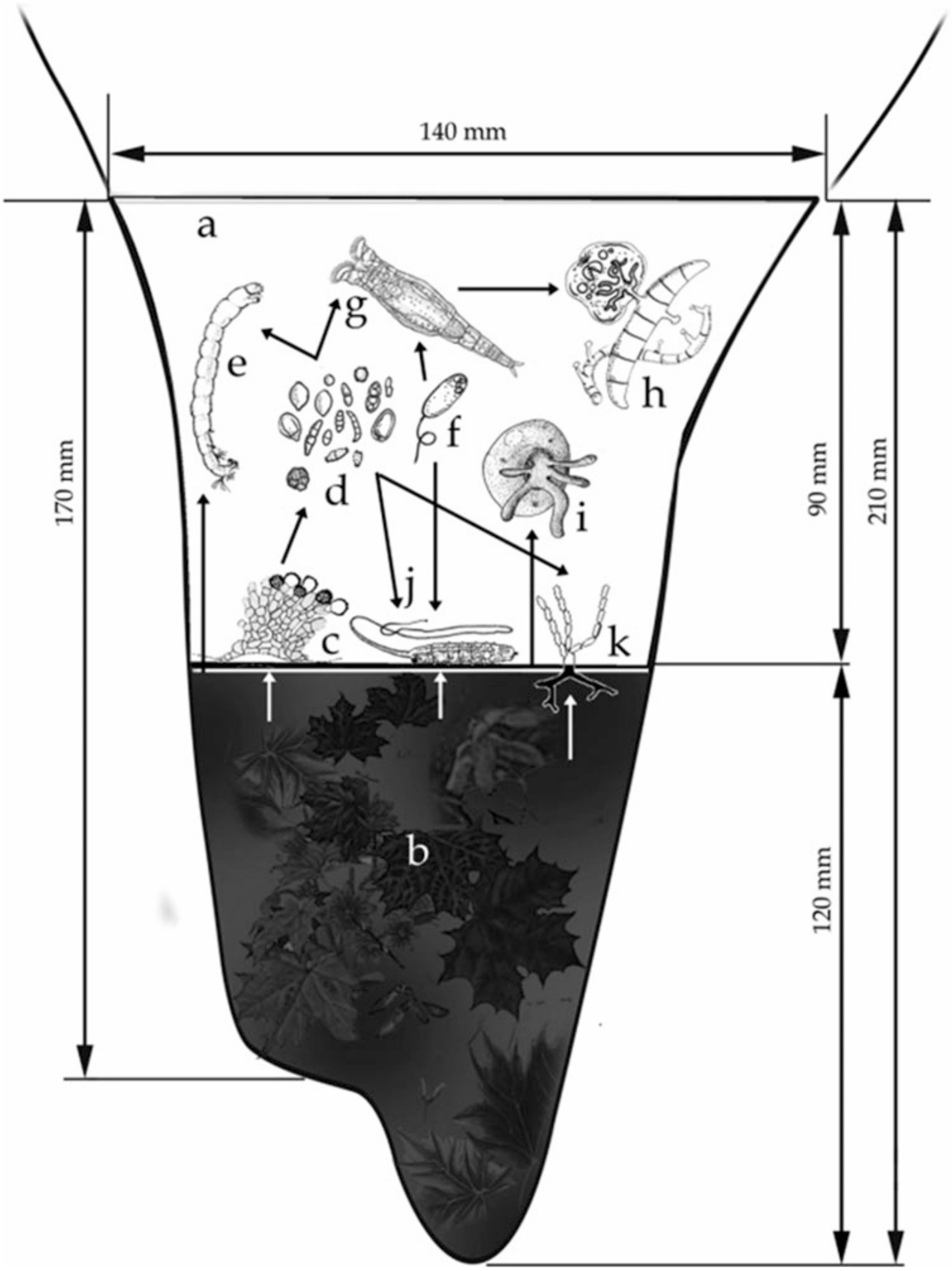

Fig. 14.2 Water-filled tree holes in woody plants support a complex food web beneath **a** the water level, which varies in response to precipitation dynamics. Hydrologic highways during precipitation not only supply moisture, but **b** detritus materials that support, **c** saprophytic fungi, **d** fungal spores, **e** Chironomideae, **f** flagellates, **g** rotifera, **h** *Lecophagus muscicola* (a rotifer-capturing fungi), **i** testate amoebae, **j** larvae of *Eristalomya tenax*, and **k** actinobacteria

throughfall in tandem with variability in the quantity and quality of litter input, as the major energy source in such systems (Magyar et al. 2017b). The length of periods between stemflow events (i.e., age of stagnant water) may be an important factor on fungal species composition of tree hole ecosystems, which merits further studies (Vass and Magyar 2013). Also meritorious of future research is the potential for interactions between fungi, tree holes, and storms to facilitate recolonization of organic matter in the forest floor. Studies of leaf litter in tree holes confirmed them to be permanent habitats of waterborne hyphomycetes (Gönczöl 1976; Gönczöl and Révay 2003). Such tree hole fungi may facilitate recolonization of organic matter when transported by hydrologic highways to the forest floor.

Hydrologic highways on the bark surface follow the bark topography, filling cavities and forming small temporary ponds (dendrotelma) where transported particles are accumulated. Considering large surface area of the bark of some tree species (especially those having complex, multilamellar structure), the number of accumulation areas in fissures and cracks enables storage of a vast number of spores (Magyar 2008). However, further studies are needed to calculate bark surface area of different tree species—see studies like Van Stan et al. (2010) or Sioma et al. (2018)—and its capacity to trap spores. Moreover, the bark itself is a substrate for many fungal species in stemflow. Large colonies of dematiaceous hyphomycetes often occupy deeper parts of bark fissures (Magyar 2008): *Bactrodesmium*, *Camposporium*, *Menispora*, and *Sporidesmium* are common there (Magyar, unpublished). Such large dematiaceous hyphomycete colonies seem to facilitate the deposition of waterborne particles. Waterborne spores of some apparently fungicolous species (*Spermosporella* sp., *Titaea complexa*, etc.) are often seen to anchor and develop on conidiophores and spores of these fungi (Magyar 2008).

Arboreal epiphytic and parasitic vegetation is ubiquitous across ecosystems and can accumulate higher quantities of litter and humus than those lacking such association, e.g., *Borassus* and *Cocos* accommodate orchids and ferns (Ghate and Sridhar 2015). Some epiphytic plants, like "oak-leaf basket fern" (*Drynaria quercifolia*), a dominant fern in Western Ghats and west coast of India, access nutrients through accumulated materials from rainwater drainage along stems (Sridhar et al. 2006). "Tank" forming epiphytic plants (bromeliads) also form miniature detrital ecosystems that may host a variety of microbes transported by precipitation-related hydrologic highways through the canopy (Brouard et al. 2012; Kitching 1971). These reservoirs may also overflow and transport microbes to the litter layer below.

14.4 Detritusphere

The sphere that consists of dead litter on the soil surface and in soil depth (the "detritusphere") is one of the densest microbial habitats in terrestrial ecosystems, and this is especially pronounced in forest litter layers. The detritusphere in forests consists of litter at various decomposition stages, usually from 0 to ~5 years old but also older tree twigs and stems can be present, especially in the bottom part. The detritusphere contains some 3–10 Mg C ha^{-1}, and has a very wide C:N:P ratio. The last fact results from (i) litter origin: the most limiting nutrients (including N, P and base cations) are resorbed to the plant from the leaves before dying (Aerts 1996), and (ii) the first step of its decomposition: intensive leaching of nutrients and base cations from the litter (Chapin et al. 2002). The wide range in C:N:P ratio shows not only a strong N and P limitation but also reflects the high hydrophobicity of the detritusphere in forests. This hydrophobic, N and P limitation represents a direct connection between C and nutrient fluxes, specific microbial communities in the detritusphere, and water fluxes from throughfall and stemflow. In fact, the functioning of microbial communities in the detritusphere is completely dependent on moisture supplied from the plant canopy's redistribution of precipitation as canopies are the "functional interface" between the atmosphere and up to 90% of Earth's terrestrial biomass (Ozanne et al. 2003).

The first step of litter decomposition in the detritusphere is mainly mediated by insects grinding and chewing the cell walls. Therefore, this stage itself is not strongly dependent on throughfall and stemflow moistening the litter, because (i) fresh litter is partly moist (not completely dry), (ii) the litterfall occurs in autumn when precipitation and air moisture are typically high compared to other times of year, and (iii) insects are much less dependent on moisture compared to fungi and especially to bacteria. Because of cell wall destruction, the cytoplasmic compounds—mainly proteinic compounds including various endoenzymes—will be fast leached from the detritusphere to the mineral soil surface. Here, on the soil surface, various pathways of these compounds are common. The low molecular weight organic compounds will be immediately trapped (Fischer et al. 2010) and utilized by microorganisms, mainly by bacteria (van Hees et al. 2005). An important part of released enzymes will be stabilized on mineral surfaces, where their functions for decomposition of organic substrates last for some weeks up to a few months (Schimel and Schaeffer 2012). Mineral N and P released by decomposition of organics will be intensively utilized in this and bottom soil layers. The cations (mainly K^+, Mg^{2+}, Ca^{2+}) released from cells will be leached into deeper soil layers, especially where TF drip points are temporally consistent in supplying substantial water fluxes (Keim et al. 2005) and close to any plant stems producing voluminous stemflow (Van Stan and Gordon 2018). Consequently, the C, nutrients, and enzymes released at the first stage of litter decomposition, and mobilized via throughfall and stemflow, will have strong impacts on the processes and microbial communities in the topsoil and partly in the subsoil.

The second step—decomposition of the remaining cell walls (mainly cellulose and lignified compounds)—is performed mainly by fungi. Fungi release not only hydrolytic enzymes (as bacteria do) but also oxidases and peroxidases. These enzyme groups are very efficient at decomposing high molecular weight compounds under highly oxidative conditions, and this is another direct link to local moisture supply from net precipitation. Close to the stem, stemflow can preferentially infiltrate (Johnson and Lehmann 2006) and the water input can be higher, but the drainage is more intensive as this part of the soil and detritusphere litter is lifted by many roots. So, these areas of the detritusphere have large water inputs and well-oxidated conditions, leading to faster litter decomposition—on this stage—mainly by fungi. Another important advantage of fungi decomposition, especially in the detritusphere, is that fungal hyphae can reach locations without water, like areas between non-densely packed litter. This is huge advantage of fungi compared to bacteria as it allows them to reach substrates even when disconnected from hydrologic highways (in this case, “bridges”), like throughfall and stemflow.

The vertical layering of the detritusphere corresponds not only to the well-known degradation state of the litter but also to litter moisture patterns. Specifically, the water content of the detritusphere increases from top to bottom because of: (i) lower water permeability of the mineral topsoil compared to the detritusphere; (ii) decreasing hydrophobicity and increasing hydrophilic bonds (−COOH, =CO) with the progression of litter decomposition by oxidative enzymes; and (iii) lower transpiration losses from the deeper part of detritusphere. Overall, the vertical (within detritusphere) and horizontal (within the distance from the main trunk) patterns of water flux to the detritusphere (due to the canopy’s redistribution of precipitation into throughfall and stemflow) play significant roles in the decomposition rate of litter, to which insects, fungi, and bacteria successively contribute.

14.5 Rhizosphere

The first few millimeters of soil surrounding roots host a unique microbiome compared to bulk soil (Prescott and Grayston 2013; Richter et al. 2007)—a microbiome that is made unique by plant selection from the more diverse microbial community in the bulk soil (Berendsen et al. 2018; Pieterse et al. 2016). The influx of moisture, nutrients, and microbes from throughfall and stemflow hydrologic highways may influence the rhizosphere microbiome by (i) impacting the soil microbes available for selection by roots, (ii) providing nutrient subsidies in excess of root exudates, and (iii) engendering large spatiotemporal variability of edaphic conditions throughout the root system. Fundamentally, rhizosphere development alters hydrologic processes during storms, compared to the bulk soil, as a result of autogenic environmental factors interacting with the aboveground partitioning of rainfall (Johnson and Jost 2011). Spaces in the soil surrounding roots are lined with root and microbial exudates that typically create hydrophobic margins around “rhizo-pathways” through the subsurface (Hinsinger et al. 2009; Jarvis 2007). During storms, net precipitation fluxes have been observed to enter and flow along these rhizo-pathways (Saffigna et al. 1976; Schwärzel et al. 2012; Spencer and van Meerveld 2016). As a result, the rhizosphere microbiome receives larger precipitation pulses and is bathed in the dissolved and particulate elements, including microbes, carried by throughfall and stemflow (Table 14.1). This is particularly true for the few voluminous stemflow generating trees (Van Stan and Gordon 2018), as they can concentrate substantial water flows at the base of the plant stem. Net precipitation

Table 14.1 Materials suspended and transported by throughfall (TF) and stemflow (SF). Dashes indicate that the element was not measured

Element	Concentration		Citation
	TF	SF	
Total dissolved solids (mg L^{-1})	2–102	38–334	Mahendrappa (1974), Mosello et al. (2002)
Dissolved organic matter (mg C L^{-1})	1–60	7–480	Van Stan and Stubbins (2018)
C:N	9–57	10–37	Van Stan II (2012)
C:S	73–136	29–55	Goller et al. (2006), Schrumpf et al. (2006)
C:P	58–142	25–103	Goller et al. (2006)
Total suspended solids (mg L^{-1})	5–99	8–140	Muoghalu and Oakhuman (2000)
Particulate organic C	1–5	–	le Mellec et al. (2010)
Particulate organic N	0.2–0.9	–	le Mellec et al. (2010)
Bacteria (cells L^{-1})	$2–4 \times 10^8$	$3–7 \times 10^8$	Bittar et al. (2018)
Fungi (conidia L^{-1})	10–16,000	10–13,800	Sridhar and Karamchand (2009)
Macrofauna (individuals L^{-1})	–	0–1,170	Ptatscheck et al. (2018)

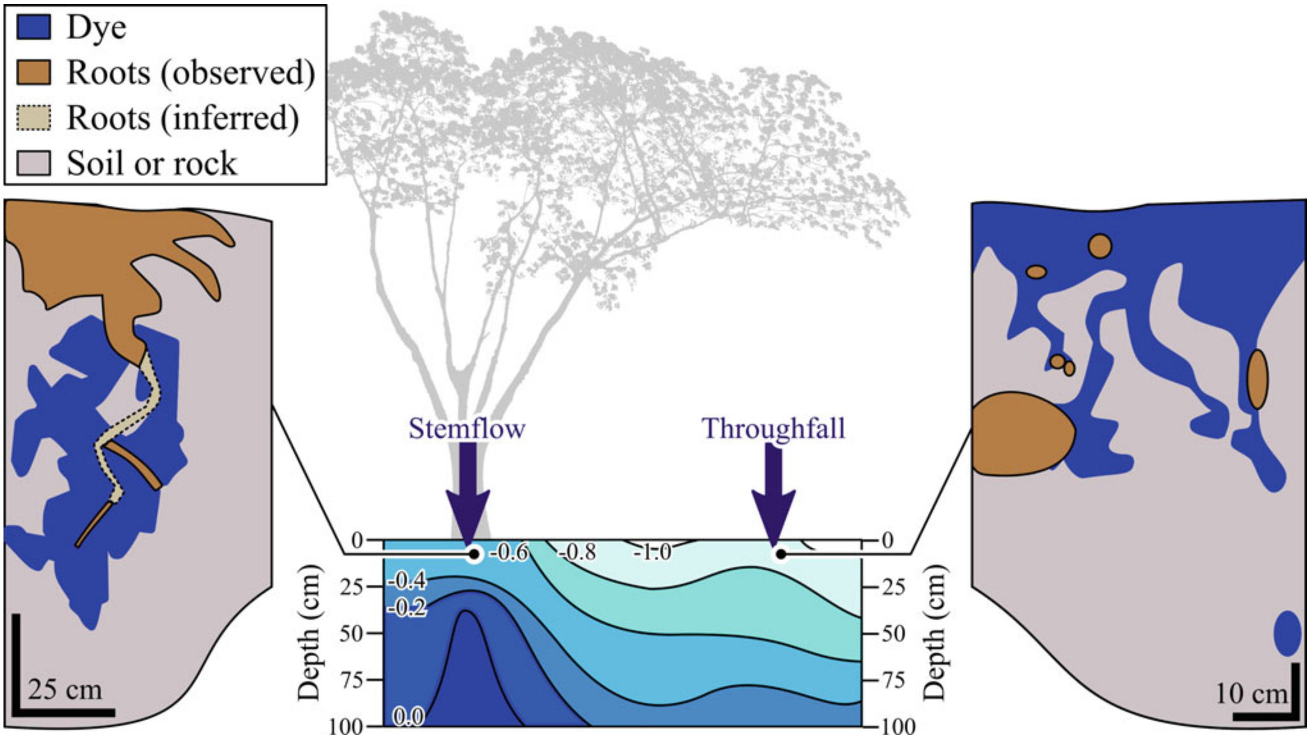

Fig. 14.3 Soilwater potential monitoring and tracer dye mapping have identified spatially variable infiltration pathways linked to throughfall and stemflow. The center profile shows soil moisture patterns become concave beneath stemflow and throughfall drip areas; developed from data reported by Durocher (1990). Profiles on the sides, derived from data reported by Spencer and van Meerveld (2016), show some roots can channel net precipitation (those surrounded by blue dye), while others did not. Could this difference in moisture dynamics (and associated elements) drive significant spatial variability in the rhizosphere microbial community?

effects on soil moisture and chemistry can influence microbial community structure in the bulk soil (Rosier et al. 2015, 2016) and, therefore, may shape the rhizosphere at its beginnings—by shaping the microbial community from which plant roots select their microbial partners.

The greater microbial abundance and activity of the rhizosphere microbial community compared to those of the bulk soil is typically attributed to the abundance and diversity of C- and N-rich root exudates, like carbohydrates, amino acids, and fatty acids (Baldrian 2017; Prescott and Grayston 2013). However, the dissolved organic matter in throughfall, stemflow, and litter leachates is highly concentrated (see Chap. 8) and enhanced with carbohydrates and compounds with N-rich molecular formulae (Stubbins et al. 2017). Previous research on rhizosphere microbiota for model plants and crops indicates that many community members "cannot thrive on plant exudates alone" (Tkacz et al. 2015). So, perhaps the C- and N-rich supply of solutes from net precipitation aid in supporting unique abundance and compositional aspects of the rhizosphere microbial community?

Spatial and temporal dynamics of rhizosphere microbiota are clearly connected with seasonal root dynamics (Shi et al. 2015), plant development (Chaparro et al. 2014), and soil disturbances (Tkacz et al. 2015). However, the amount and elemental composition of throughfall and stemflow also vary by orders of magnitude seasonally (Sadeghi et al. 2018; Van Stan et al. 2012), with plant development (Zheng et al. 2018) and with disturbances (Moore and Jackson 1989). Spatial dynamics in the rhizosphere may, therefore, be related to infiltration of net precipitation, as not all roots provide rhizo-pathways for throughfall and stemflow (Fig. 14.3). Moreover, soils surrounding preferential subsurface flows of net precipitation are further enriched with nutrients as the organic acids carried by net precipitation fluxes can enhance weathering (Backnäs et al. 2012). Thus, soil conditions surrounding roots may vary according to variability in infiltrating net precipitation fluxes. As the amount and elemental composition of net precipitation can vary with storm conditions, most roots may, in reality, fall along a continuum of exposure to throughfall and stemflow—with some rhizo-pathways carrying net precipitation every storm and a few only during larger or more intense events.

14.6 Pedosphere: Soils and Bedrock

Hydrology is a major parameter in soil as it determines many biotic and abiotic processes and soil parameters. The quantities and frequencies of water input to the soil influence the soil solution, as well as its residence time with the different constituents and reactive interfaces existing within the soil (Van Breeman et al. 1982; Chang and Matzner 2000; Coenders-Gerrits et al. 2013). From the topsoil to the deep-soil, water is circulating, connecting different chemical gradients and determining nutrient availability. Indeed, without water, most of the nutrients are immobile and unavailable for the biosphere. The physiological processes engaged by soil microorganisms are thus strongly affected by the water availability (Yan et al. 2015).

14.6.1 Hydrologic Circulation Conditions Nutrient Availability

The hydrologic circulation of chemical elements (protons, hydroxide, nutrients, cations, toxins) and complex molecules (sugars, amino acids, organic and inorganic acids, and chelating compounds) through the critical zone directly affects the dissolution of soil minerals/rocks. When this circulation is perturbed, the dissolution rates are decreased. This is an important point to understand nutrient cycling into the soil. Without water, the quantities of exchangeable cations are limited, and the dissolution of minerals is stopped. When the soil is saturated in water, however, chemicals accumulate in the soil solution and the conditions tend to be anoxic. In other words, soil hydrologic processes, many of which are linked to the infiltration of precipitation via throughfall and stemflow, can condition mineral weathering and nutrient availability (including both organic nutrients and nutritive cations).

14.6.2 Soil Properties and Landcover Determine the Soil and Plant Microbiome

All mineral weathering and nutrient availability processes are, however, impacted by the action of the biosphere and especially of the plants, which modify hydrologic processes at local and regional scales. The presence of vegetation on a soil is known to modify the quantity of precipitation water coming from the atmosphere to the soil, its chemical composition, but also the quantity of water circulating into the soil due to the plant roots' water uptake and routing of throughfall and stemflow. Different plants in similar soils will differentially impact the soil parameters including water, nutrient availability, pH, and microbiome composition (Augusto et al. 2002; Uroz et al. 2016). A common point of these plants is the selection of a complex microbiota at the surface of their root system (rhizosphere microbiota) and inside their tissues (endophytic microbiota), which contribute to the development, health, and nutrition of their host. As noted earlier, the rhizosphere was evidenced in several studies as a reactive interface where specific microorganisms carry out functions beneficial to the host plant. Among these functions, we can point out the mineral weathering ability (i.e., ability to dissolve minerals and rocks), an essential process in which microorganisms contribute to the release of nutritive cations and anions from insoluble forms (i.e., minerals and rocks) and transfer them to the plant. Among the main actors of these two processes are fungi and bacteria (Landweert et al. 2001; Uroz et al. 2009). Notably, mycorrhizal fungi, which form symbiotic association with the plant roots, are able to provide water and nutritious elements (P, cations), due to their ability to forage large volumes of soil. A single symbiotic fungus associated with the tree root system can explore several square meters, representing in this sense a good insurance for the tree host. Regarding the bacteria, the effectiveness and frequency of mineral weathering bacteria in the rhizosphere were shown to vary according to the seasons, potentially in relation to the nutrition status of plants, but also potentially to seasonal hydrologic variability (Collignon et al. 2011). Such changes are not evident in the bulk soil, highlighting an important role of the plant and the environmental parameters (i.e., climate, phenology, and hydrology) in modulating the distribution of soil bacterial communities. In the rhizosphere environment, variations in water availability may allow for the selection of adapted communities. For mycorrhizal fungi, drought periods will favor species such as *Cenococcum geophylum*, which is well known to increase in abundance in low water availability conditions and present functional traits adapted to recover water (Jany et al. 2003; Di Pietro et al. 2007). For bacteria, drought in soil is known to favor Actinobacteria and spore-forming bacteria such as *Firmicutes* and *Bacillus* (Fierer et al. 2003; Hueso et al. 2012; Naylor et al. 2017). Recent development using labeled water (^{18}O) and DNA stable isotope probing has clearly evidenced how bacterial and fungal communities respond to desiccation and rewetting events (Barnard et al. 2013; Engelhardt et al. 2018).

14.6.3 The Mineralosphere Microbiome: Conditioned by Soil Moisture?

Nevertheless, while the tree root zone presents specific features, it is not disconnected from the rest of the soil matrix. Indeed, tree roots and their associated microbiota are connected to the organic matter and the minerals and rocks present in the soil. In shallow soils the root system can be connected to the bedrock, while it depends on the plant species in deep soils. Notably effective mineral weathering bacteria have been reported at the interface between the bedrock and the roots, suggesting that they actively participate in the nutrition of plants. In the context of a nutrient-poor soil, the connection of the plant root to the soil minerals plays an important role, as minerals represent the main source of inorganic nutrients. Indeed, soil minerals and rocks are formed of insoluble forms of base cations (Ca, Mg, and K), microelements (Fe, Al) and other nutrients such as phosphorous. Most of these chemicals are important elements in nutrient-limited soils for the biosphere, both for microorganisms and plants. Besides their nutritional role, minerals, and rocks have themselves been shown to select different microbial communities according to their physicochemical properties (Colin et al. 2017; Uroz et al. 2015). Part of this selection is explained by the intrinsic properties of the minerals, which can contain nutritive or toxic elements in their crystalline structure. These chemicals can attract or repulse specific microbial communities. Another important driving factor of these communities is related to the weather ability of these minerals. Indeed, recent studies found evidence that poorly weatherable minerals were colonized by effective mineral weathering bacterial communities compared to easily weatherable minerals, suggesting the selection of competitive microbes in nutrient-limited conditions (Uroz et al. 2009, 2015; Wilson et al. 2008). However, all these selective events are determined by the environmental conditions (i.e., the extrinsic parameters) and notably by the hydrology. Indeed, in poor water availability conditions—like throughfall "dry" spots where localized precipitation interception is high (Keim et al. 2005), or near stem soils where stemflow production is nearly nonexistent (Van Stan and Gordon 2018)—microbial communities may be modified, allowing to the selection of a part of the microbiome capable of dealing with desiccation (Naylor et al. 2017). Consequently, we may expect a suite of cascade events, which will modulate both the chemistry of the soil solution and the microbial communities and their biotic and abiotic interactions. Investigating this cascade requires work at the frontiers of our current understanding and capabilities. For example, little is known about the water availability of rock-associated microbiota and observations of microbial interaction with rocks and minerals are difficult to distinguish from the rest of the soil interface.

14.7 The Plant Endosphere

The plant endosphere refers to the microbiota colonizing the inner parts of the plant. It has been known for decades that fungi forming arbuscular mycorrhiza can colonize the root cortical cells (e.g., Smith and Read 2010). However, beside arbuscular mycorrhizal fungi, many other fungi can colonize the plant roots (Lê Van et al. 2017; Vandenkoornhuyse et al. 2002; Vannier et al. 2018) along with bacteria (Bulgarelli et al. 2012; Lundberg et al. 2012; Vannier et al. 2018), archaea (Vannier et al. 2018) and microeukaryotes (Sapp et al. 2018). These microorganisms inhabiting plant tissues are called endophytes. All plants are colonized by a complex microbiota (Vandenkoornhuyse et al. 2015) which interact with its host and provide additive ecological functions (Bulgarelli et al. 2013). Because endophytes can play key roles in a plant's ability to quickly adapt to environmental changes, endophytic microbiota are regarded as fundamental to plant environmental responses over both short and longer time-scales (Vannier et al. 2016). The microbial endosphere is less complex than the microbial rhizosphere (e.g., Vandenkoornhuyse et al. 2015), although, for both, soil and litter microorganisms act as microbial "seed banks" from which a plant can actively or passively recruit symbionts to buffer an environmental stress (e.g., Vannier et al. 2016). Endophytes are transmitted horizontally or vertically (Frank et al. 2017). It seems that an ascending migration of endospheric microorganisms from roots to leaves is predominant (Chi et al. 2005) and that precipitation partitioning is considered one of the abiotic major factors facilitating the vertical dispersal of endophytic microbes (Frank et al. 2017). Uncovering the rules of community assembly in the endosphere is a current hot research topic in microbial ecology.

14.7.1 Precipitation Partitioning and the Endosphere “Rules of Assembly”

The endosphere symbiotic community composition and partnership stability are explained by different hypotheses—see Vandenkoornhuyse et al. (2015) for review. The “partner choice” induces immediate fitness benefits for both the host and microbe (Sachs et al. 2004), but requires complex signaling (which is known for only a fraction of microbiota) and is a consequence of coevolution processes. Alternatively or complementarily, the hypothesis of “forced cooperative behavior” by reward/sanction processes (Kiers et al. 2003) allows the filtering of endospheric microorganisms based on cooperation level (Werner et al. 2014) as demonstrated in the case of arbuscular mycorrhiza symbiosis (Kiers et al. 2003). Besides these hypotheses developed to explain the forces at place to build up the plant endosphere composition, the conundrum of assembly rules of the plant microbiota has also been addressed under the biogeography framework, aiming to identify drivers of spatial microbial heterogeneity. In the biogeography framework, several biotic and abiotic factors, including insects, wind, and precipitation are identified as drivers of spatial heterogeneity. The storage and drainage of precipitation via throughfall and stemflow are quite heterogenous between different plant species coexisting in a single environment (e.g., Van Stan et al. 2015). In fact, the role of ecohydrologic processes (of which precipitation partitioning is a part) in the plant endosphere’s rules of assembly has been recently identified as a promising research frontier (Krause et al. 2017).

14.7.2 Heterogeneity of Endospheric Microbiota

Published works that focus on the endospheric microbiota of plants highlight the existence of heterogeneity in the composition of the microbiota between plants of different species coexisting in a given environment (e.g., Lê Van et al. 2017). This heterogeneity in the composition of symbiotic communities may be related to transient associations while other microorganisms may form long-lasting interactions with vertical transmission (Cankar et al. 2005; Vannier et al. 2018) or pseudo-vertical transmission (colonization of the immediate vicinity of the mother plant allowing access to a similar pool of microorganisms) (Wilkinson 1997). If this is true, heterogeneity in endospheric microbiota implies heterogeneity in the reservoir of microorganisms near the host plant (Vandenkoornhuyse et al. 2015) available to be recruited passively (neutral process) or actively (selective process) by the plant. The part of the plant’s selective process of acquisition and/or filtration of microorganisms from the available reservoir can condition differences in spatial structures, while the share of neutral processes explains a stochastic heterogeneity which is, however, dependent on the available microbial reservoir. Thus, what controls the spatiotemporal heterogeneity of the microbial reservoir?

14.7.3 Water Displacement as a Possible Driver of Endospheric Microbiota

Microbial reservoir heterogeneity through time and space is partly explained by biotic interactions, like the type of plants present and microbial predation (micro/mesofauna and microbial viruses), as well as abiotic factors including, wind, moisture, shading, patches of nutrients, and so on (Vandenkoornhuyse et al. 2015). Little attention has been paid so far to the possible effects of microbial dispersion, including dispersion by water. Water displacement can be seen as a driver (or helper) of microorganisms’ migration through various types of soil macropores (“highways” of microbial dispersion, like earthworm burrows; Jarvis 2007) but also through all the other water movements in soils. During plant growth, with the help of their arbuscular mycorrhizal fungi, plants uptake water close to their roots. By doing so, a water depletion area close to the roots is produced inducing passive horizontal fluxes of water to the water-depleted zone. Together with solutes, it can be hypothesized that this phenomenon allows the transfer of microorganisms close to the rhizosphere and allows the enrichment of the microbial reservoir from which the plant can recruit microorganisms. An additional hypothesis is an existing network of small galleries formed by fungal hypha grazers, like collembola. Because a dense mycorrhiza hyphal network linked to roots exists, it can be suggested that hyphal grazers might engineer an oriented network of little galleries replacing the former hypha, allowing an easier microbial dispersion together with water displacement to roots. Under this framework, microbial heterogeneity is expected since dispersion is expected to be stochastic and everything could not be everywhere.

Although these hypotheses sound possible, as far as we know there is no experimental evidence supporting the idea that the plant endosphere composition could be, at least in part, the consequence of microbial dispersion mediated by water displacements. If, similarly as solutes, this microbial dispersion by water movements is possible, so is dispersion of microbial viruses. The understanding of the impact of viruses in the control of soil microbial community composition is clearly hypothesized (Kimura et al. 2008; Williamson et al. 2017); however, their significance in the plant microbiota endosphere is unknown.

14.7.4 Pathogens and the Endosphere: Storms as a Triple Threat in the Disease Triangle

Processes in precipitation partitioning are considered one of the major factors facilitating the dispersal of endophytic microbes—although the exact terms for precipitation interception, throughfall and stemflow are rarely used in this literature. It has long been recognized that rain can disperse microbes from infected plants to surrounding plants (Walker and Patel 1964). Raindrops generate bioaerosols, which allow the spreading of microbes from soil to plants at distance (Joung et al. 2017). Moreover, heavy precipitation may damage plant surfaces (Baker and Hunt 1986), creating entryways for phyllosphere and rhizosphere microbes to gain access into the apoplast. Together, precipitation partitioning not only facilitates the dispersal of endophytic microbes but also create opportunities for microbes to enter new host plants. In addition, heavy precipitation may temporarily alter the microenvironment around plants and change endophytic community structure. Most endophytes are beneficial or harmless to plants; however, pathogenic microbes can also reside within host plants without causing disease (Bacon and White 2000; Strobel 2018). Environmental conditions are another set of major constraining factors for disease outbreaks—and water is a key trigger for pathogenic microbes to promptly proliferate in the apoplast. The interplay between pathogen, host, and environment, known as the "disease triangle", has been long established as crucial for understanding disease outbreak (Stevens et al. 1960). For example, a field study identified more endophytic fungi during the rainy season, when these hydrologic highways are naturally more active, for two tree species, *Tectona grandis* and *Samanea sama* (Chareprasert et al. 2006). The study of the life cycle of *Pseudomonas savastanoi* pv. *phaseolicol*a, a causal agent of bean halo blight, showed that rain magnitude and intensity largely contribute to the proliferation of the bacteria and disease outbreak (Hollaway et al. 2007; Marques and Samson 2016). In a controlled environment, water availability in the atmosphere, and thus higher relative humidity, greatly facilitates the proliferation of a bacterial pathogen of tomato, *Pseudomonas syringae* strain DC3000, in a host plant *Arabidopsis* (Xin et al. 2016). In addition to a dispersal pathway, the resulting high humidity from rainwater storage and evaporation provide more accessible water source for endophytic microbes to proliferate. High humidity from precipitation interception also suppresses the function and activity of resistance genes and downstream signaling events (Aung et al. 2018), which may allow opportunistic microbes to become pathogenic. As a result, conditions during precipitation partitioning represent an environmental "triple threat" in the disease triangle: (i) throughfall and stemflow provide dispersal pathways while the high humidity from intercepted precipitation (ii) facilities pathogen proliferation and (iii) can enable opportunistic microbes to become pathogenic. Together, the effects of precipitation partitioning can create drastic changes in the endophytic community and promote disease outbreak in plants.

14.8 Animal-Associated Microbiomes

The forest canopy is the habitat of multiple species of amphibians, reptiles, mammals, and birds. This habitat accumulates organic matter derived mainly from leaf litter, feces, and other faunal remains. These residues are in turn, the nutrient source of thousands of arthropod species that have also found a niche at the top of plant canopies (Nadkarni 1994). As all other animals, canopy animals harbor symbiotic communities in their guts and their skins, which play vital roles in their growth and health, including immune system development, gut nutrition, and pathogen defense (Hacquard et al. 2015; Hooper et al. 2012). In addition, when animals die, they become a nutrient source for a diverse array of heterotrophic microbes. Thus, the canopy is also the habitat of microorganisms that play a part in ecosystem nutrient cycling (Nadkarni 1994).

Most of the animal-associated microbiome studies in wildlife have focused on describing bacterial diversity and determining the abiotic and biotic factors that influence these symbiotic microbiomes (Hayakawa et al. 2018; Jiménez and

Sommer 2017; Kohl et al. 2017). In many cases, the ultimate purpose of these studies relies on the need to integrate the role of symbiotic microbiomes to implement conservation strategies for threatened animals, such as primates and amphibians (McKenzie et al. 2018; West et al. 2019). However, to date, there has been no work aiming to evaluate how these animal-associated microbiomes contribute to other microbial communities in the ecosystem. Moreover, it is unknown how hydrologic highways like stemflow and throughfall contribute to the transfer or movement of animal-associated microbial communities to plant and soil microbiomes. Below we will exemplify how animal-associated microbes could contribute to microbial communities that are transferred through the various hydrologic highways to plant and soil microbiomes.

The amphibian skin microbiome is known to play an important defense role against pathogens, since many of its bacterial members are known to produce antifungal metabolites (Harris et al. 2009; Woodhams et al. 2015). Recent studies have shown that the composition of the skin microbiome of many amphibians is highly enriched in bacterial taxa that are not common in their surrounding environments, e.g., leaves, soil, and leaf litter (Fitzpatrick and Allison 2014; Rebollar et al. 2016; Walke et al. 2014). However, environmental bacteria are of great importance since these serve as a reservoir to maintain skin bacterial diversity (Antwis et al. 2014; Loudon et al. 2014). In addition, changes in precipitation throughout the seasons have been associated with changes in the composition of skin microbial communities in frogs (Familiar López et al. 2017; Longo et al. 2015; Longo and Zamudio 2017). This leads to two hypotheses (non-mutually exclusive) on how changes in precipitation affect skin bacteria. Changes in precipitation regimes (which lead to changes in stemflow and throughfall volumes) could modify bacterial reservoirs by transferring (or isolating) microbial communities across canopy strata, in turn affecting the diversity and function of skin microbiomes. An alternative (perhaps complementary) mechanism is that skin bacteria are directly washed away from their hosts by rain. In this way, skin bacteria would be transferred to new environments and hosts (i.e., plant surfaces, soil) through the hydrologic highways.

Although skin microbiomes might be important contributors of the bacterial pool in forests, these have a far lower bacterial density in contrast with gut microbiomes (Sender et al. 2016). Studies on gut microbiome of insects, birds, lizards, and primates have shown that diet is one of the most important factors shaping these symbiotic communities (Clayton et al. 2018; Kohl et al. 2017; Lucas et al. 2017; Waite and Taylor 2015). This would mean there is a constant flow of bacteria from the environment (available food) to animal guts and vice versa (Colston 2017; Shukla et al. 2018; Trevelline et al. 2018). We could hypothesize that changes in stemflow and throughfall produce changes in environmental reservoirs, which would then be linked to changes in gut microbiomes. Likewise, feces can contribute to the bacterial pool present in the canopy, where stemflow and throughfall would transport gut bacteria through different strata and hosts. Animal carcasses can serve as an additional source of bacteria, since they provide an important nutrient source for environmental bacteria and necrophagous insects (Shukla et al. 2018).

In summary, animal-associated microbiomes may be transferred from the canopy to other plant and soil habitats in the ecosystem by changes in net precipitation fluxes. However, it remains to be determined whether skin or gut bacteria, along with their associated functions (i.e., antifungal capacities), can be successfully transferred across habitats (i.e., colonize and proliferate). Many key questions about the role of precipitation partitioning in the microbial community dynamics need to be explored, i.e., what proportion of animal symbiotic bacteria is present in hydrologic highways? What ecological functions are these bacteria playing in different habitats or hosts?

14.9 Conclusions

We note that every section discussing interactions between precipitation-related hydrologic highways (interception, throughfall, and stemflow) and each habitat in, and surrounding, the plant microbiome found little-to-no research on the topic. However, current theory indicates that future research is merited throughout the critical zone. Most work on interception, throughfall, and stemflow has been rooted in hydrologic (Newtonian) research traditions, which often contrasts with ecological (Darwinian) research traditions. Resolving differences between these scientific world views has been a challenge for many integrated research areas (Harte 2002) and has been particularly problematic for the subdiscipline within which

Fig. 14.4 Manipulation experiments are needed to explicitly address research questions at the intersection of precipitation partitioning processes and the plant microbiome. This photo is an example stemflow collar outfitted to redirect flow to an area typically receiving throughfall (credit: John T. Van Stan II). A video of SF redirection from this system is provided in the supplemental materials [https://youtu.be/AKhRV6Q7hGM]

most precipitation partitioning research is executed—ecohydrology (Harman and Troch 2014; Newman 2006). A result of most work on throughfall, stemflow, and interception being more hydrology oriented is that few studies have included manipulation experiments. However, manipulation experiments involving the removal or relocation of throughfall and stemflow will be necessary to explicitly address most questions about how net precipitation water and elemental fluxes connect and influence habitat properties and processes across the plant microbiome. Experiments based on the use of isotopically labeled water as presented in the pedosphere section would also represent a way to bridge the different compartments connected by these hydrologic highways. Thus, we suggest future research design and deploy ways of removing and relocating hydrologic highways during storms (for example, see Fig. 14.4). We again explicitly acknowledge the theoretical nature of this chapter and hope that this discussion will inspire future research regarding the influence of storms on the plant microbiome.

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15 Valuing Urban Tree Impacts on Precipitation Partitioning

David J. Nowak, Robert Coville, Theodore Endreny, Reza Abdi, and John T. Van Stan, II

Abstract

Trees impact surface stormwater runoff, soil moisture, streamflow, water quality, and air temperatures by intercepting precipitation (rain and snow), enhancing soil water infiltration, shading surfaces, and evapotranspiring water. These impacts affect human health and well-being. Many of these tree impacts remain to be more accurately quantified and valued, particularly related to water quality aspects such as mass (e.g., sediments), chemical (e.g., nutrients, metals, pesticides), biological (e.g., pathogens, microbes), and thermal loads. Urban trees can help mitigate many of the negative hydrologic effects created by the relatively large amount of impervious surfaces in cities. Urban tree impacts are generally positive but can create negative outcomes if improperly managed (e.g., leaves or branches clogging drains or streams). Although more and better valuation of tree impacts is needed, studies to date value tree effects on reducing runoff into water bodies in the range of millions of dollars per year at the city or watershed scale.

Keywords

Rainfall interception • Throughfall • Stemflow • Stormwater • Hydrology • Urban forest • Urban forestry

15.1 Introduction

One of the more important benefits that trees provide in urban settings relates to their hydrological functions, which impact surface stormwater runoff, soil moisture, streamflow, water quality, and air temperatures. Trees affect hydrological processes primarily through three main precipitation partitioning mechanisms: canopy interception, soil water infiltration, and evapotranspiration, which includes evaporation from leaf and soil surfaces and transpiration of soil moisture through leaves. Trees also affect water quality by generally decreasing the concentration and amount of nutrients and pollutants reaching a water body. Air temperatures can be reduced by trees returning precipitation to the atmosphere via evapotranspiration (ET).

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With ET, some of the net radiation that would otherwise warm air temperature is directed to evaporating water when water is available (latent heat). Further, warm air passes its heat to the evaporating water, which also reduces the temperature of the air (sensible heat).

The impact of trees can vary within an urban environment depending upon the extent of impervious surfaces and variations in urban forest structure and management. Impervious surfaces limit the infiltration of water into soils, and due to their slopes and relative smoothness can accelerate runoff speed, increasing peak flows reaching streams through pipe or gutter networks. Urban forest structure affects rainwater storage, evaporation, and transpiration through variations in the number of trees, species composition, and leaf area. Likewise, urban forest management can affect local tree composition, density and leaf area through such actions as tree planting, removals, and pruning.

The purpose of this chapter is to discuss how urban trees and impervious surfaces combine to affect streamflow, soil moisture, and water quality, as well as air temperature; review economic impacts of changes in streamflow and water quality; and summarize how tree processes can affect these economic impacts and which impacts need to be valued. By understanding tree impacts on hydrology and their wide-ranging broader impacts, better management plans can devise uses for trees and forests to improve water quality, reduce negative economic impacts, and promote human health and well-being.

15.2 Tree Impacts on Hydrology (Evapotranspiration, Streamflow, and Soil Moisture)

Trees affect streamflow rates primarily through: (a) rain and snowfall interception, which captures precipitation in the tree canopy on leaf and stem surfaces and prevents, slows, and reduces precipitation reaching the ground; (b) enhancing soil water infiltration via tree root impacts, which reduces total and peak runoff and recharges unsaturated and saturated soils pores used to support plants and baseflow to rivers; and (c) evapotranspiration, which cools air temperatures and regenerates water storage space in the canopy and in soils for future precipitation. These processes are part of a natural hydrologic cycle. While these processes generally increase baseflow in streams and reduce peak streamflow events (e.g., flooding), unmanaged trees can also increase flooding if branches or leaves clog drains or dam streams.

15.2.1 Rainfall and Snow Interception, Throughfall and Stemflow

Tree canopies intercept precipitation in the form of snow and rain, on leaves and branch surfaces, thereby affecting runoff volumes and delaying the onset of peak stream flows. Trees have a specific leaf water holding capacity ranging from 0.07 to 0.6 mm, with an average of 0.25 mm, and an average branch water holding capacity of 0.15 mm (Wallace et al. 2013; van Dijk 2010). The snow storage capacity of leaves can be much greater, maximizing around 40 mm under favorable conditions, like high-density maritime snow on evergreen forests (Storck et al. 2002).

The leaf rain or snow water holding capacity is multiplied by the tree canopy leaf area index to get the total depth of canopy interception at any time. During a precipitation event, some of this water can evaporate, some can be blown off, and some can drip off and become throughfall or flow down the branches and trunk as stemflow. The effect of stemflow in concentrating rainfall from the relatively large canopy area to the relatively small trunk area is quantified as a funneling ratio; a funneling ratio of 10 implies 10 mm of rainfall depth arrives as stemflow for each 1 mm of rainfall measured above the canopy. Schooling and Carlyle-Moses (2015) report average funneling ratios of 17.7 for single leader trees, and 20.2 for multi-leader trees. Single leader trees have a dominant main stem trunk or leader, while a multi-leader tree has two or more leaders converging at the base of the tree, with each leader intersected by feeder branches (Schooling and Carlyle-Moses 2015).

The depth of the canopy water storage capacity often exceeds the depth of precipitation for many low intensity and short duration precipitation events. The water storage capacity of tree bark and the plants living on the canopy (i.e., epiphytes and parasites) can be substantial: 0.2–5.9 mm (Liu 1998; Pypker et al. 2011) and 0.4–16.6 mm (Jarvis 2000; Van Stan and Pypker 2015), respectively. Together, leaves, bark, and epiphytes can result in canopy water storage capacities up to 19 mm (Porada et al. 2018). For more information on water storage capacity of vegetation elements and their influencing factors during rainfall and snow, the reader is referred to Chap. 2.

Urban tree canopy interception may be different from that of natural forests because of differing microclimates and tree architecture (Fig. 15.1). Compared with rural forests, urban forests typically have fewer trees per unit area, larger average tree stem diameters, greater species diversity with different phenological patterns, and greater spatial variation in canopy

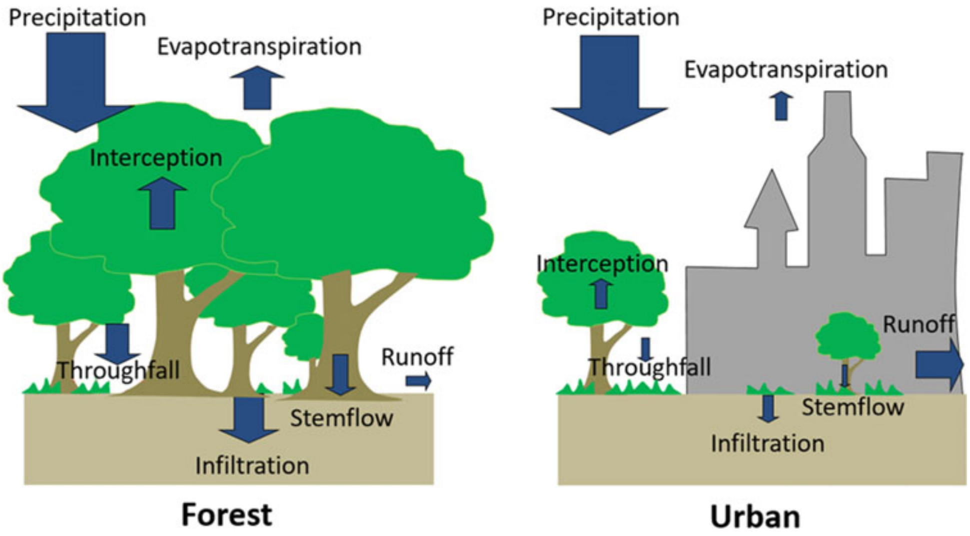

Fig. 15.1 Schematic of hydrologic process differences between a forest and urban area. Due to reduced tree cover and increased impervious surfaces, urban areas typically have reduced evapotranspiration, interception, throughfall, stemflow and infiltration, and increased runoff, relative to forested areas

cover (McPherson 1998). Urban forest structure is influenced by a mix of varying management actions (e.g., tree planting, pruning), natural regeneration and other natural (e.g., storms) and anthropogenic (e.g., development) forces that create forest change (Nowak 2012, 2017).

15.2.2 Soil Water Infiltration

Precipitation reaching the ground beneath canopies can enter soils in a natural hydrologic cycle. Terrain micro-topography and tree organic matter can pool and slow water movement on the soil, and tree root growth and decomposition in soils can increase water infiltration rates into soils and reduce surface runoff. Infiltration rates vary through time and are fastest when soils are dry due to suction of water into the pores via capillary action, and then progressively decrease to the slowest rate, which is typically limited by the soil saturated hydraulic conductivity. The soil saturated hydraulic conductivity varies with soil texture, structure, and compaction, with an estimated value of 2.99 cm hr^{-1} for loamy sands and 0.05 cm hr^{-1} for silty clays with standard compaction based on numerous observations from across the United States (Rawls et al. 1983). Tree roots also create soil macropores that can accelerate infiltration through soil pores, further reducing runoff and recharging deeper soil water (Aubertin 1971). Forests can be used as buffers around water bodies to naturally filter and infiltrate runoff. Thus, forest buffers can not only reduce the quantity of urban runoff but also reduce pollutants carried with urban runoff through physical, chemical, and biological processes in the soil. Greater detail on the relationship between soil moisture patterns and throughfall and stemflow can be found in Chap. 13.

15.2.3 Evapotranspiration

Land cover strongly affects evapotranspiration (ET). ET is a measure of the amount of water evaporated from surfaces or transpired (evaporation of liquid water in the plant) through leaf stomata. Globally, two-thirds of precipitation is evapotranspired, returned to the atmosphere through evaporation and transpiration (Hornberger et al. 1998). Evapotranspiration, on average, annually accounts for 484 mm, nearly 60% of the 800 mm that falls on average as precipitation over the global land area (Chin 2013). Over oceans, evaporation accounts for more than total precipitation, with additional water provided by river runoff to the ocean. The combined flux of evaporation and transpiration from trees is lower than the evaporation from an open water surface, due to resistances to vapor flux in tree stomata and the canopy air. Soil pores and the overlaying air typically have even greater resistances to vapor flux, and hence have lower rates of ET than trees. Given that ET from soils is at a lower rate than ET from trees, removal of forest cover can increase streamflow as a result of reduced ET, as well as lost attenuation through interception.

When water is not limited by storage, rates of ET are a function of tree leaf area index and stomatal conductance, as well as atmospheric variables such as vapor pressure gradient, wind speed, pressure, and radiation. Generally evergreen trees have the highest actual ET, due to year-round ET, followed by deciduous trees, shrubs, and grasses, with differences diminished in areas with low mean annual precipitation (Matheussen et al. 2000). Evapotranspiration changes the phase of water from liquid to gas and reduces local air temperatures (Akbari et al. 1992). A comparison of different evapotranspiration components in forest ecosystems and their dynamics/controls is provided in Chap. 3.

15.3 Tree Impacts on Stormwater Quality

Precipitation partitioning by plants not only affect water flows, but also water quality. Important tree-based processes that can improve stormwater quality include: (a) soil filtration of particles/sediments and adsorption of chemicals that can reduce the transport of substances such as plant and animal wastes, nutrients, pesticides, petroleum products, metals, and other compounds that can cause water quality problems (Clark 1985; Neary et al. 1988); (b) nutrient assimilation by plants which can reduce excess nutrients (e.g., nitrogen, phosphorous) reaching the stream and degrade water quality (e.g., eutrophication) (Dupont 1992; US EPA 1995); (c) slowing the movement of metals and other contaminants (e.g., pathogens, pesticides) to surface waters, thereby increasing the opportunity for the contaminants to become buried in sediments, adsorbed into clays or organic matter, or transformed by microbial and chemical processes (Johnston et al. 1984; Young et al. 1980; MacKay 1992); (d) degradation or volatilization of chemicals by microorganisms (Winogradoff 2002); and (e) shading surfaces and reducing air temperatures, which reduces thermal loads on shaded objects and can reduce the heating of river water, thereby mitigating biological activity that can degrade water quality (e.g., eutrophication) (Yang et al. 2008).

15.3.1 Sediments

Sediments are considered the largest pollutant by mass in surface waters and are primarily transported by surface runoff. Sediment refers to soil particles that enter receiving waters from eroding land, including plowed fields, logging sites, urban construction, and eroding stream banks (US EPA 1995). Trees can also increase sediments in surface runoff due to stemflow funneling water from the canopy to the base of the tree. The magnitude of this stemflow initiated erosion depends upon tree architecture, rainfall intensity, and soil cover/conditions (e.g., Herwitz 1986; Keen et al. 2010). To reduce the likelihood of stemflow initiated soil erosion in urban areas, Schooling et al. (2015) recommend maintaining high infiltration capacities at the base of trees, or maintaining micro-topography that retains soils rather than conveying them to receiving waters.

In addition to mineral soil particles, eroding sediments may transport other substances such as plant and animal wastes, nutrients, pesticides, petroleum products, metals, and other compounds that can cause water quality problems (Clark 1985; Neary et al. 1988). Sedimentation of receiving waters can have negative impacts on water quality and aquatic habitat. In a study of upper Chattahoochee River Basin, GA, the greatest suspended sediment yields were from urban areas, compared with forested and agricultural lands (Faye et al. 1980). In Virginia, forestry practices contributed little sediment; agriculture was an important source of sediment, and urban development contributed the most sediment (as well as other pollutants) (Jones and Holmes 1985).

Studies indicate that forest riparian buffers can effectively trap sediment when runoff is spread across the area and not concentrated in a rill or gully, ranging from removal of 60–90% of the sediment (Cooper et al. 1987; Daniels and Gilliam 1996). Along the Little River in Georgia, riparian forests have accumulated between 350 and 529 tonnes ha^{-1} of sediment annually over the last 100 years (Lowrance et al. 1986). Based on this finding, a hectare of riparian forest can protect between 39 and 112 ha, using national average erosion rates between 4.7 and 9 tonnes ha^{-1} of sediment annually. Many factors influence the ability of the buffer to remove sediments from land runoff, including the sediment size and loads, slope, type and density of riparian vegetation, presence or absence of a surface litter layer, soil structure, surface and subsurface drainage patterns, and frequency and intensity of storm events (Osborne and Kovacic 1993).

15.3.2 Nutrients

Nutrients are essential elements for aquatic ecosystems, but in excess amounts, they can lead to many changes in the aquatic environment and reduce the quality of water (Dupont 1992). Urban runoff can transport chemicals that lead to nutrient enrichment in rivers (Long and Dymond 2014; Allan and Castillo 2007). Lawn and crop fertilizers, sewage, and manure are major sources of nutrients in surface waters. Industrial sources and atmospheric deposition also contribute significant amounts of nutrients (Guldin 1989). One of the most significant impacts of nutrients on streams is accelerated eutrophication, the excessive growth of algae and other aquatic plants in response to high levels of nutrient enrichment (US EPA 1995). When this growth dies, its decomposition will lower the oxygen level in the water column and can lead to loss of target water species and uses. In addition, some forms of nutrients can be directly toxic to humans and other animals (Chen et al. 1994; Evanylo 1994). In general, the highest nitrogen and phosphorus yields typically occur in highly agricultural and urbanized watersheds, and lowest nutrient yields occur in streams of forested watersheds (e.g., Spruill et al. 1998; Hampson et al. 2000). Riparian forests have been found to be effective filters for nutrients, including nitrogen, phosphorus, calcium, potassium, sulfur, and magnesium (Lowrance et al. 1984a, b).

Riparian forests have been shown to reduce between 48 and 95% of nitrogen from stormwater runoff (Lowrance et al. 1984b; Peterjohn and Correll 1984; Jordan et al. 1993; Snyder et al. 1995). In urban areas, such forests and their soils can include vegetation bordering flow paths along drainage paths or other intermittent channels. The processes by which soils remove nitrates include denitrification, uptake by vegetation and soil microbes, and retention in riparian soils (Beare et al. 1994; Evanylo 1994). Trees can take up large quantities of nitrogen as they produce roots, leaves, and stems, with a fraction, returned to the soil as plant materials decay. For example, scientists in Maryland estimated that deciduous riparian forests took up 77.4 kg ha^{-1} of nitrogen annually, and returned 61.7 kg ha^{-1} (80%) each year in the litter (Peterjohn and Correll 1984). Nevertheless, Correll (1997) suggested that vegetative uptake is still a very important mechanism for removing nitrate from riparian systems, because vegetation (especially trees) removes nitrates from deep in the ground, converts the nitrate to organic nitrogen in plant material, then deposits the plant materials on the surface of the ground where the nitrogen can be mineralized and denitrified by soil microbes.

Riparian areas can be important sinks for phosphorus; however, they are generally less effective in removing phosphorus than either sediment or nitrogen (Parsons et al. 1994). Removal of phosphorus by riparian stands range from 30 to 80% (Cooper et al. 1987; Lowrance et al. 1984b; Peterjohn and Correll 1984). Some phosphorus may be taken up and used by vegetation and soil microbes, and like nitrogen, much of this phosphorus is eventually returned to the soil. For example, researchers estimated that less than 3% of the phosphate entering a floodplain forest in eastern North Carolina was taken up and converted to woody tissue, while scientists in Maryland reported a deciduous riparian forest buffer annually took up 9.9 kg ha^{-1} of phosphorus but returned 7.8 kg ha^{-1} (80%) as litter (Brinson et al. 1984; Peterjohn and Correll 1984). In some riparian areas, small amounts of phosphorus (0.06–2.4 kg ha^{-1}) may be stored as peat annually (Walbridge and Struthers 1993). Through leaf and branch drop into streams, trees add nutrients to streams and provide food and habitat for various aquatic organisms (Allan and Castillo 2007).

15.3.3 Metals

Riparian areas may slow the movement of metals and other contaminants to surface waters and increase the opportunity for the contaminants to become buried in the sediments, adsorbed into clays or organic matter, or transformed by microbial and chemical processes (Johnston et al. 1984). Urban runoff can increase the concentration of contaminants such as copper (Cu), zinc (Zn) (Strecker 1998), nitrogen (N), phosphorus (P), degradable carbon (Dong et al. 2013), and dissolved salts (Merikhpour and Jalali 2013). The fate of metals in riparian areas is not well understood. However, scientists in Virginia have found significant amounts of lead, chromium, copper, nickel, zinc, cadmium, and tin buried in the sediments of the floodplain along the Chickahominy River downstream of Richmond (Hupp et al. 1993). Analysis of the woody tissue of trees reveals that these compounds are also taken up by the trees. Therefore, sediment deposition and uptake by woody vegetation may help mitigate heavy metals in riparian areas.

15.3.4 Pathogens and Other Microbes

Pathogens such as waterborne bacteria, viruses, and protozoa are the source of many diseases that infect humans, livestock, and other animals (Chesters and Schierow 1985; Palmateer 1992). There is relatively little information on the role of riparian buffers on pathogens. In one study, strips of corn, oats, orchardgrass, and sorghum/sudangrass were all effective in reducing bacterial levels by nearly 70% (Young et al. 1980). They estimated a vegetation buffer 36 m wide would be required to reduce total coliform bacteria to levels acceptable for human recreational use. Other researchers have demonstrated the ability of grass sod filter strips to trap bacteria from dairy cow manure under laboratory conditions (Larsen et al. 1994). They found that even a narrow (0.61 m) strip successfully removed 83% of the fecal coliform bacteria, while a 2.1 m filter strip removed nearly 95%. Further information on the microbial communities hosted on habitats throughout the plant microbiome and how they may be connected and transported during storms can be found in Chap. 14.

15.3.5 Pesticides

Pesticides are a common issue in urban areas with a wide array of insecticides, repellents, herbicides, fungicides, disinfectants, and rodenticides used in urban pest management programs (Racke 1993). Pesticides were frequently present in streams and, to a lesser extent, groundwater, particularly in areas with substantial agricultural and/or urban land use. Pesticide concentrations exceeding human health benchmarks are more likely for streams with agricultural or urban watersheds, which account for ~12 and 1%, respectively, of public water supply intakes on streams (Gilliom 2007).

Few studies have been conducted that examine the fate of pesticides in riparian areas. However, where the proper conditions exist, riparian forest buffers have the potential to remove and detoxify pesticides in runoff. Probably the most important process is the breakdown of organic chemicals by soil microorganisms (MacKay 1992). Scientists have observed that soil microorganisms adapt to the presence of a pesticide and begin to metabolize it as an energy source (Fausey et al. 1995). As it is metabolized, the pesticide is broken down into various intermediate compounds, and ultimately carbon dioxide. In addition, most pesticides have a high affinity for clay and organic matter and may be removed from the soil water as they are bound to soil particles. Once bound, pesticides are often difficult to desorb from the soil (Clapp et al. 1995). Pesticides are often designed to degrade in soils in an effort to limit their adverse impacts when released in the environment (Kah et al. 2007).

15.3.6 Stream and Air Temperatures

Changes in both chemical and thermal properties of the water reaching rivers affect local water quality (Everard and Moggridge 2012; Herb et al. 2008; Somers et al. 2013). Trees have a substantial influence on incoming solar radiation and can reduce it by over 90% (Heisler 1986). Some of the radiation absorbed by tree canopies leads to the evaporation and transpiration of water from leaves. This evapotranspiration cools tree leaves and the surrounding air. Along with evapotranspirational cooling, tree shade can help cool the local environment by reducing the solar heating of some below-canopy surfaces (e.g., streams, buildings, parking lots). Together these evapotranspiration and shading effects can reduce air temperatures by as much as 5 °C (Akbari et al. 1992). Reduced air temperatures will contribute to reduced stream temperatures, given that air temperature leads to sensible heating of water (Mohseni et al. 1998). Shallower river water heats more rapidly due to lower thermal inertia and larger surface area to volume ratios. Infiltration will generally increase baseflow, and baseflow typically has a temperature equal to the average annual air temperature, which then cools the river during the warm season (Loheide and Gorelick 2006).

As runoff passes over impervious surfaces, the water is often warmed, creating thermal pollution within receiving water bodies. This thermal pollution changes aquatic ecology by directly and indirectly affecting living organisms (Gitay et al. 2002). The combination of nutrient enrichment and elevated water temperatures in rivers are precursors to harmful algal blooms (Erdner et al. 2008) and can lead to accelerated eutrophication (Rigosi et al. 2014; Lürling et al. 2017; Yang et al. 2008). After the algae bloom dies, its organic matter undergoes microbial decomposition, which can severely deplete the dissolved oxygen (DO) (Peperzak 2003) and lead to biomass-related hypoxia and anoxia, also known as dead zones (Chislock et al. 2013; Pang et al. 2017). In addition, the maximum or saturated DO is reduced by increased water temperature (Coutant 1985), which limits habitat zones for aquatic organisms.

15.4 Urban Impervious Cover Impacts on Water Volume and Quality

Conventional urban development dramatically increases the amount of stormwater runoff generated by the landscape (Chow and Yen 1976; Boyd et al. 1994; Beach 2002). The principal causes of this effect are impervious surfaces, primarily streets, parking lots, and buildings (Leopold 1968; Schueler 1994); and compaction of the soil due to construction activities (Hamilton and Waddington 1999; Pitt et al. 2003). Instead of infiltrating into the ground, precipitation, including rainfall and snowmelt, is converted quickly to surface runoff and is rapidly delivered to receiving waters via sewers and other man-made channels.

Impervious cover and compaction of soils in urban areas impede infiltration rates (Hamilton and Waddington 1999; Pitt and Lantrip 2000) and transform more precipitation into stormwater runoff. Increased stormwater runoff leads to reduced deeper percolation and consequently lower water table levels (Lerner 2002) and lowers stream baseflow regimes (Faulkner et al. 2000). Lower baseflow adversely impacts drinking water supplies, aquatic habitat, water temperature, navigation, and recreation. Increased stormwater runoff can increase surface flushing of pollutants to receiving waters, diminishing the chance for biogeochemical transformation. When stormwater is treated in engineered retention or detention basins, rather than infiltrated through forested areas, pollutants tend to experience less sorption with soils and are more likely to degrade subsurface water quality (Thomas 2000; Fischer et al. 2003).

According to US General Accounting Office (2001), when natural ground cover is present over the entire site, infiltration is higher and on average 10% of precipitation runs off the land into nearby creeks, rivers, and lakes. In contrast, when a site has 75% impervious cover that is not all directly connected to receiving waters, on average 55% of the precipitation runs off into receiving waters. Runoff from parking lots and other paved areas is estimated as 98% of storm event precipitation (USDA NRCS 1986). The impervious surfaces in a typical city block may generate nine times more runoff than a woodland area of the same size (US EPA 1996). Urban impervious cover in the conterminous United States averages 26.6% (Nowak and Greenfield 2018). Runoff from urban land cover collects pollutants from the land surface and poses a threat to receiving waters. Trees over impervious surfaces can help reduce these negative consequences by intercepting rainfall and reducing the amount of rainwater reaching impervious surfaces.

15.5 Cumulative Effects of Urban Trees on Stream Flows and Runoff

Relatively little research has been conducted on the effects of urban trees on stream flows and runoff compared to non-urban forest areas. In Tucson, Arizona, increasing tree canopy cover from 21% (existing) to 35 and 50% was projected to reduce mean annual runoff by 2 and 4%, respectively (Lormand 1988). In Austin, Texas, it was estimated that the existing trees reduce the potential runoff volume by 3.2 million m^3, or 7% of a 14 cm, 5-year storm (Walton 1997).

In Baltimore, Maryland, an increase in tree cover over pervious surfaces, from 12 to 24%, together with an increase in tree cover over impervious surfaces, from 5 to 20%, decreased peak flow by 12%, while increasing baseflow and only reducing annual streamflow by 3%. By contrast, reducing tree cover over pervious areas from 12 to 6% and replacing it with impervious surfaces connected to streams lead to a 30% increase in peak flow (Wang et al. 2008). The trend and relative magnitude of these tree effects on runoff is consistent with other model findings.

15.6 Economic Impacts of Hydrologic Changes

The removal of trees typically leads to increased stormwater runoff, potentially increasing localized and extensive flooding in urban areas. The economic impacts of flooding can be substantial. The costs/impacts associated with urban flooding include: wet structures with mold and potential increase in respiratory problems (Pind et al. 2017), potentially lower property values (Snyder 2013), stream bank erosion (e.g., Hammer 1972), degraded water quality, and reduced health of aquatic ecosystems (e.g., Brookes 1988). In Cook County, Illinois alone, total claims paid for urban flooding incidents over five years (2007–2011) were more than $773 million (CNT 2014). In addition to larger peak flows, increased stormwater can also lead to instability in drainage systems and reduced recharge of groundwater (Herricks 1995; Thorne 1998; FISRWG 1999). Instability in the drainage system can rapidly erode stream banks, damage streamside vegetation, and widen stream channels (Hammer 1972). Instability combined with reduced groundwater recharge results in lower water depths during non-storm periods, higher than normal water levels during wet weather periods, increased sediment loads, and higher water temperatures (Brookes 1988). As described earlier, trees can reduce stormwater runoff in many ways and help reduce these impacts.

Over a third of our nation's streams, lakes, and estuaries are impaired by some form of water pollution (US EPA 1998). Pollutants can enter surface waters from point sources, such as single-source industrial discharges and wastewater treatment plants. However, most pollutants result from nonpoint source (NPS) pollution activities, including runoff from agricultural lands, urban areas, construction and industrial sites, and failed septic tanks. These activities can introduce harmful amounts of sediments, nutrients, bacteria, organic wastes, chemicals, and metals into surface waters (WEF/ASCE 1998). Damage to streams, lakes, and estuaries from nonpoint source pollution was estimated to be about $7 to $9 billion a year in the mid-1980s (Ribaudo 1986), with urban NPS runoff a leading cause of receiving water pollution (US General Accounting Office 2001). Nutrient pollution alone can lead to problems such as accelerated eutrophication or harmful algal blooms, creating millions of dollars in costs associated with impacts on tourism and recreation, property values, human health, drinking water treatment, and pollution mitigation (US EPA 2015).

Substantial economic value is derived from reducing river temperature (Seedang et al. 2008), increasing DO (Rabotyagov et al. 2014), avoiding harmful algal blooms (Anderson et al. 2000; Hoagland et al. 2002), and slowing eutrophication (Dodds et al. 2009; Pretty et al. 2003). The estimated annual damage costs of freshwater eutrophication are approximately $2.2 billion in the US (Dodds et al. 2009) and $105–160 million in England and Wales (Pretty et al. 2003). The loss in economic welfare from recreational fishing due to lowering DO levels in the Patuxent River, Maryland is between $100,000 and $300,000 per year (Lipton and Hicks 2003). The estimated economic impact of harmful algal bloom in the United States is approximately $0.5 billion (Anderson et al. 2000). About 45% of this value is from impacts on public health costs. To help

Table 15.1 Summary of general tree effects, hydrologic services provided and associated hydrologic impacts. Services and impacts of trees are denoted as generally increasing (+) or decreasing (−). The impacts could be assigned economic values based on their effects on human and aquatic health, recreation and tourism, groundwater supplies, sedimentation removal, property values, insurance rates, etc

Tree Effects	Services	Impacts
Evapotranspiration	Air temperature (–)	Aquatic life (+)
Interception	Aquatic food and habitat (+)	Base streamflow (+)
Litter deposition	Chemical[a]/biological[b] degradation (+)	Dissolved oxygen (+)
Root growth	Chemical[a] removal/uptake (+)	Erosion (–)
Shade	Chemical[a] transport (–)	Eutrophication (–)
	Infiltration (+)	Flooding (∓)
	Nutrients (uptake, litter) (∓)	Groundwater recharge (+)
	Runoff (–)	Treatment costs (–)
	Stream temperature (–)	Water pollution (–)
	Water uptake (+)	

[a] Metals, nutrients, pesticides, sediment
[b] Pathogens

Table 15.2 Estimated monetary values of urban tree effects on reducing runoff into streams

City	Value type	$/gallon avoided	Value/year	References
Austin, TX	Local[a]	0.27	$230 million	Walton (1997)
Plaster Creek subwatershed, Grand Rapids, MI	Local[b]	1.25	$52.7 million	Plan-It Geo (2015)
Core city subwatersheds, Grand Rapids, MI	Local[b]	1.25	$36.5 million	Plan-It Geo (2015)
Houston, TX	Average[c]	0.009	$11.6 million*	Nowak et al. (2017a)
Wakarusa River watershed, Lawrence, KS	Average[c]	0.009	$5.9 million	Nowak et al. (2014)
New York, NY	Average[c]	0.009	$4.6 million	Nowak et al. (2018)
Austin, TX	Average[c]	0.009	$4.3 million*	Nowak et al. (2016a)
Blue River watershed, Kansas City, KS/MO	Average[c]	0.009	$4.2 million*	Nowak et al. (2013a)
Cobbs Creek watershed, Philadelphia, PA	Average[c]	0.009	$3.0 million*	Nowak et al. (2016b)
Don Watershed, Toronto, ON	Average[c]	0.009	$2.2 million*	Nowak et al. (2013b)
First St. subwatershed, Grand Rapids, MI	Local[b]	1.25	$2.0 million	Plan-It Geo (2015)

[a] Stormwater retention pond costs
[b] Stormwater mitigation and environmental impact costs
[c] U.S. average stormwater control and treatment costs from several cities
*Value not given in publication, but reported here assuming $0.009 per gallon

mitigate damage from urban runoff, the US Clean Water Act (US EPA 2013) sets a total maximum daily load (TMDL) for rivers receiving urban runoff, which defines quantitative thresholds for the concentrations and fluxes of thermal and material pollutant sources (Seedang et al. 2008; US EPA 2007).

15.7 Valuing Tree Impacts on Hydrology

To value tree impacts on hydrology, the tree effects (e.g., interception, ET, and avoided runoff) first need to be quantified. Once the effects are quantified, these effects can be related to services and impacts (e.g., reduced pollution and improved human health) and then the impacts valued (Table 15.1). Various models exist to quantify tree impacts on hydrology and water quality (Coville et al. 2019), but the valuation of these impacts is limited. Once the flow or provision of the good or service (e.g., reduced pollution) is quantified, various market and non-market valuation methods can be applied to characterize their value. Methods of non-market valuation can be pecuniary or non-pecuniary (e.g., number of human lives saved). This valuation includes various procedures such as market prices, contingent valuation surveys, replacement or substitute costs, hedonic regression, and damage costs avoided (Nowak et al. 2017b). Some studies estimate the value of reduced runoff due to trees in cities is on the order of millions of dollars per year (Table 15.2).

For the most part, the economic valuation of tree effects on the myriad of hydrologic impacts remains to be evaluated as many of these impacts are not quantified. Once the impact of trees is more fully quantified, the total economic impact related to human and aquatic health, recreation and tourism, groundwater supplies, sedimentation removal, property values, and insurance rates, etc., can be evaluated. However, care must be exercised to avoid double-counting of benefits and costs. More research is needed to quantify the many tree and forest hydrologic impacts and values. This research can lead to better, more informed, and cost-effective management decisions to improve water quality, enhance groundwater recharge, and reduce flooding. These improvements can ultimately enhance human and aquatic health and well-being for current and future generations.

15.8 Valuing Total Tree Impacts and Costs

While this chapter is focused on urban tree impacts on hydrology, urban trees provide numerous other benefits and costs. To understand the true value and costs of vegetation, all the benefits and costs need to be understood and quantified. Other benefits provided by these trees include reducing building energy use and atmospheric carbon dioxide (CO_2), improving air quality, reducing ultraviolet radiation, creating wildlife habitats and esthetically pleasing environments, enhancing human health and social well-being, and lowering noise levels (Nowak and Dwyer 2007). Although national effects of urban trees on hydrology in the United States have not been analyzed, the national urban forest values from other benefits are estimated as $18.3 billion per year; $5.4 billion from air pollution removal, $5.4 billion from reduced building energy use, $4.8 billion from carbon sequestration, and $2.7 billion from avoided pollutant emissions (Nowak and Greenfield 2018). This estimate is conservative as it only addresses four benefits out of a myriad of potential benefits from trees.

Urban forests also have various costs associated with tree planting, maintenance and removal, and other indirect costs related issues such as allergies from tree pollen, chemical emissions from trees, and maintenance activities that contribute to air pollution, invasive plants altering local biodiversity, and increased tax rates due to increased property values (e.g., Roy et al. 2012; Lyytimaki 2017). Trees can also increase waste disposal, infrastructure repair, water consumption, and building energy use in the winter due to tree shade.

Studies suggest that benefits from urban street trees are on the order of 1.4–5.8 times greater than costs (McPherson et al. 2005, 2016). However, these estimates are likely conservative as many benefits remain to be quantified. While the direct management costs of street trees are generally known, these costs are often higher than other urban trees that require less direct individual tree management and maintenance (e.g., trees in natural forest stands). Thus, management costs can vary widely in urban areas. The benefits can also vary depending upon the number of healthy trees, species, sizes, and location. These changes in management costs and benefits will alter the cost-benefit ratios in urban areas. The overall urban forest likely has higher benefit-cost ratios than found for street trees due to often lower costs per tree and numerous benefits that remain to be quantified. More research is needed to better understand local variations in tree costs and benefits to help sustain optimal forest structures to enhance human health, well-being, and ecosystem sustainability.

15.9 Conclusions

Tree canopies can profoundly alter the amount, patterning, timing, and quality of precipitation reaching the ground and streams. Tree precipitation partitioning processes alter all subsequent hydrological processes, including many that hold market and non-market value, like stormwater runoff, soil moisture, peak streamflow, water quality, and air temperatures. The interception of precipitation by tree canopies, in particular, can help mitigate the hydrologic consequences of increased impervious cover in urban environments. This reduction of runoff to water bodies provides pecuniary benefits, being valued at $2–200 million US dollars per year at various scales, and, more importantly, non-pecuniary benefits like improved human health and well-being. Of course, urban trees have inherent costs (for installation and maintenance) to maintain these benefits and minimize negative hydrologic outcomes (e.g., clogging of stormwater management systems). As trees provide multiple benefits that go well beyond hydrologic benefits, net total benefits typically exceed total costs. Many theoretical and methodological unknowns remain that impact our ability to comprehensively quantify and value urban tree hydrologic benefits and costs, including the: (i) dynamics of suspended, dissolved, and thermal stormwater qualities; (ii) influence of stemflow and throughfall drip points on runoff versus infiltration in urban settings, and associated water quality; and (iii) relationship between variability in precipitation partitioning processes and societal processes beyond stormwater management, like recreation/tourism, property values, etc. Improved understanding of the costs and benefits of trees facilitates informed and cost-effective water resource management using nature-based solutions, that can enhance human well-being and ecosystem sustainability for current and future generations.

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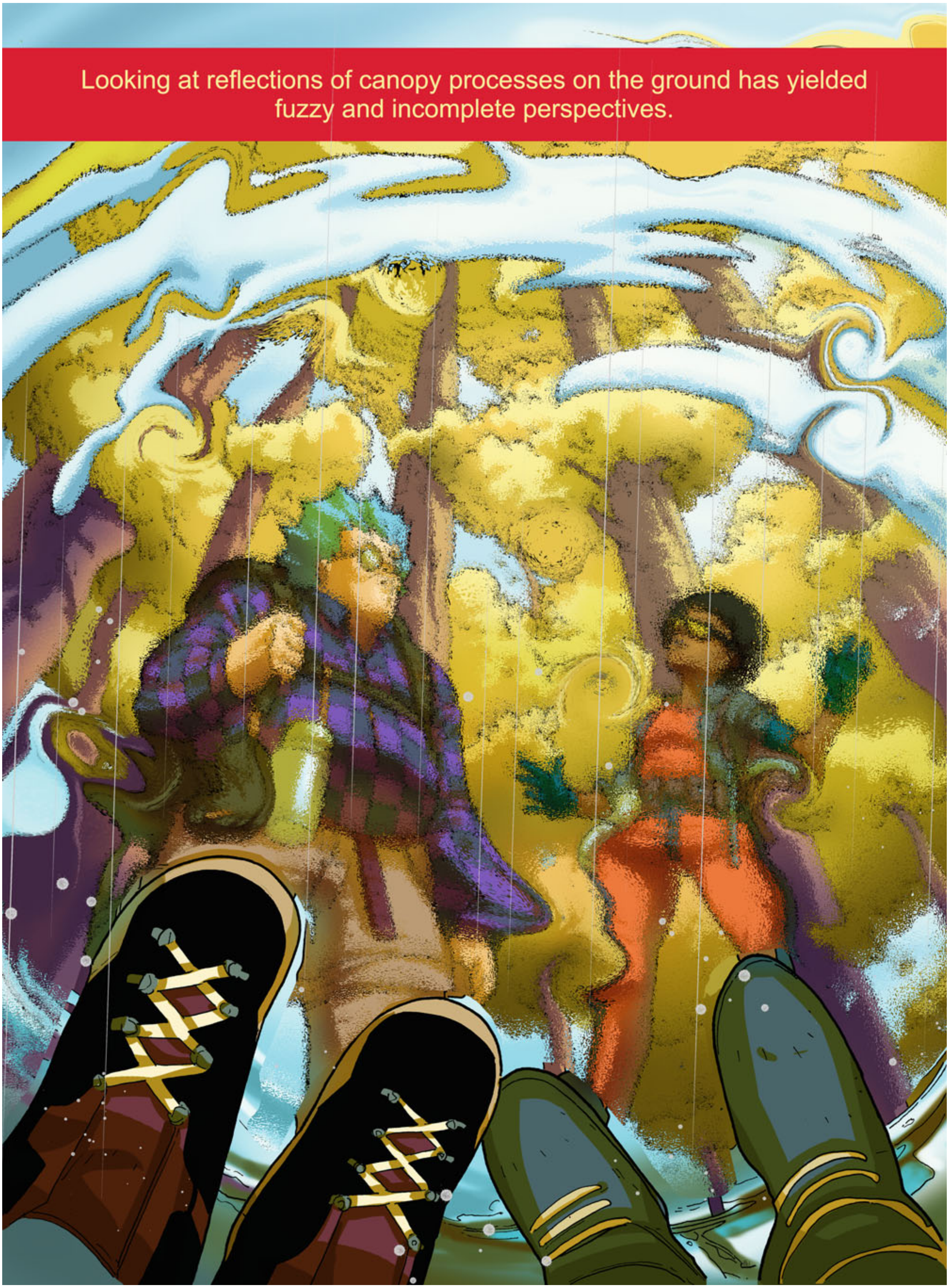
Looking at reflections of canopy processes on the ground has yielded fuzzy and incomplete perspectives.



Key Questions on the Evaporation and Transport of Intercepted Precipitation

16

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Abstract

The interception of precipitation by vegetation has important consequences for climate and water resources. Although canopy interception has been studied for centuries, many fundamental unknowns remain. We present persistent questions that reflect challenges in measuring, representing, and understanding how terrestrial ecosystems intercept, partition, and transport precipitation—down to soils or back to the atmosphere. In summary of this book, we outline future needs and simultaneously provide a primer for those interested in precipitation interception processes.

Keywords

Precipitation • Vegetation • Throughfall • Stemflow • Evaporation • Hydrology • Interception

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16.1 Why Are Interception Losses so High?

Despite the impressive number of observational studies on precipitation, throughfall, and stemflow that have empirically constrained the magnitude of interception losses, and despite generally useful physically based models of interception, there are basic holes in our understanding that prevent robust predictive modeling. Acceptable performance of interception models depends on calibration and likely compensating errors in modeling approximations (Klaassen et al. 1998; Vrugt et al. 2003), and the micrometeorology of canopy interception at the plot scale remains incompletely described. Both the details of partitioning processes by different canopy elements and the micrometeorology of canopy interception at the plot scale remain incompletely understood, hindering our ability to extrapolate model results to climates and ecosystems with low availability of calibration data, including future conditions.

The evaporation of intercepted water has mostly been quantified as the difference between precipitation measured in the open versus precipitation measured under canopies (Chap. 4)—a practice that has persisted since the mid-1800s (Chap. 1). While many might suppose that evaporation mainly occurs at the end of precipitation events (and thus the total amount of evaporated water is equal to that which is stored on the canopy at the end of a rain event), analyses have revealed interception loss totals that exceed apparent storage (Carlyle-Moses and Gash 2011). For example, one particularly intensive study demonstrated total evaporation increasing with gross rainfall amount on an event basis (Marin et al. 2000). Increased evaporation in larger events suggests that more evaporation occurs during events and that losses are not just evaporation of the storage after an event ends.

Energy budget approaches have sometimes failed to explain inferred within-event evaporation, or have arrived at conflicting conclusions. Stewart (1977) and others (Pearce et al. 1980) remarked on how wet canopy evaporation rates seem to exceed the evaporation rates that most conventional models would lead us to expect during such humid, low-energy conditions. Debates have ensued regarding appropriate modeling and scaling practices (Monteith 1977; Shuttleworth and Calder 1979; Shuttleworth 1989; Klaassen et al. 1998). While it is generally accepted that advective heat from higher in the atmosphere or laterally from warmer or drier sources is responsible for high evaporation rates (e.g., of magnitudes several times higher than expected rates; Schellekens et al. 2000), there are still open questions regarding when, where, and how water evaporates to yield such high losses. Identifying sources of heat depends in part on identifying the exact location of evaporation. For example, one hypothesis is that evaporation occurs from tree surfaces, and stored heat in trees may be a key, under-appreciated factor (van Dijk et al. 2015). Indeed, evaporation rates from bark surfaces often account for 5–20% of total wet canopy evaporation (Van Stan et al. 2017b). An alternative hypothesis is that evaporation is mostly by small drops splashing from canopy surfaces and then evaporating as they fall (Dunin et al. 1988; Murakami 2006; Dunkerley 2009). Regardless, direct measurements of the evaporation process are difficult to obtain with high precision and thus there is considerable uncertainty in expected wet canopy evaporation rates. For example, the potential evaporation rate under 96% humidity is four times larger than it is at 99% humidity (ignoring the contribution of radiation to available energy), but most humidity sensors perform poorly when distinguishing small differences (e.g., Colbo and Weller 2009; Mesas-Carrascosa et al. 2015). Instrumental precision is also a barrier to the most sophisticated approaches to measuring evaporation, such as eddy covariance, which performs poorly in wet conditions (e.g., during rainfall; Foken 2008). Isotope tracers have only revealed coarse details about when evaporation occurs (Cayuela et al. 2018b). Thus, the actual evaporation processes that contribute to interception losses remain poorly understood.

Although most of this research has focused on the evaporation of liquid precipitation from canopies, the interception effects on sublimation and condensation are also poorly understood. Just as for rainfall, energy budgets perform poorly in explaining snow interception losses (Hedstrom and Pomeroy 1998) for which they need to simultaneously explain melting, evaporation, and sublimation (Molotch et al. 2007).

16.2 How Do Intercepted Waters Move Through Canopies?

The products of canopy interception are often categorized as throughfall or stemflow (i.e., binary), but throughfall and stemflow amount and chemistry are immensely heterogeneous in space and time (Hoppe 1896; Kittredge et al. 1941; Herwitz 1987; Staelens et al. 2006; Levia et al. 2011b; Nanko et al. 2016). These variations in chemistry and amount imply spatiotemporally varying flow generation mechanisms, yet these mechanisms are mostly unknown—especially at the canopy scale. If we can discern how incoming precipitation displaces, mixes with, or bypasses interactions with water and other components of the canopy, we can better understand why throughfall and stemflow composition vary.

Hydraulic residence time analyses have found mean transit times of about 10–20 min for low-intensity rainfall on complex canopies of coniferous forests (Keim and Skaugset 2004; Keim and Link 2018). These observations offer some insights on the bulk attenuation of flows through a canopy but do not identify mechanisms or pathways of flow. Some fine-scale investigation has resulted in detailed descriptions of small portions of flow paths (e.g., Herwitz 1987), and signatures of some components of flow paths are visible in drop-size distributions of throughfall (Nanko et al. 2013, 2016), but these observations are difficult to generalize and develop into a coherent conceptual model at the canopy scale. Identification of transport paths and particle velocities remains elusive.

Water isotope (or other) tracers have the potential support quantifying canopy-scale residence times and mixing dynamics (Ikawa et al. 2011; Cayuela et al. 2018b). In one field experiment (Allen et al. 2014), stable isotopes in throughfall revealed punctuated points under the canopy that reflect substantial contributions of long-residence time water that persist in the canopy across events, and thereby presumably also mixing with stored canopy waters (see discussion by Allen et al. 2017a, b). However, this observation has only been made in one study of a forest with high storage, heavy epiphyte loads, and low available energy, which would tend to promote long-residence time water in the canopy. Allen et al. (2014) also found that canopy effects on spatial variability in isotopic composition of throughfall did not persist, as strongly across events as did spatial variability in amount of throughfall, suggesting that flow paths vary across events or, more likely, that mixing with pre-event or atmospheric water varies across events. Most isotope analyses to date have not been targeted at understanding flow processes and have not yielded data useful for these analyses.

The interaction of droplets with plant surfaces must follow general physical rules but many considerations are needed to predict how those rules manifest in different flow processes. Parameters that describe physical surface properties (e.g., droplet angle and free surface energy) are controlled by the surface condition and other traits (Holder 2007). For example, rainwater penetrates damp wood, whereas dry wood or bark is hydrophobic (Błońska et al. 2018). For leaves, hydrophobicity is not only a function of plant biology (e.g., species, age, developmental stage) but also of environment. For example, droplets will roll off of leaves coated in aromatic hydrocarbons with minimal surface interaction (Klamerus-Iwan et al. 2018), whereas water seeps across leaf surfaces coated in hydrophilic mycelium of oak mildew (Klamerus-Iwan and Witek 2018). These factors not only control storage capacity but also how droplets adhere to and flow across leaf surfaces (and hypothetically transport dry-deposited constituents). Frameworks for implementing these physical models remain limited; however, and thus we have a poor understanding of how heterogeneity in net precipitation chemistry arises from canopy processes.

Heterogeneity in the chemical composition of net precipitation must relate to variations in chemical sources, how those sources interact with intercepted waters, and how flow paths deliver water to the ground; however, these connections are poorly understood. Spatial and temporal variability of throughfall chemical constituents are considerably greater than variations in water amount because dry deposition and biological processes (including consumer recycling and redistribution) also affect heterogeneities within the canopy (Puckett 1990; Draaijers et al. 1997; Beard et al. 2002; le Mellec et al. 2011). Solute exports have been frequently investigated for the most conspicuous canopy components, including leaves (Lovett and Lindberg 1984), bark (Levia and Frost 2003), and epiphytes (Van Stan and Pypker 2015). However, few studies have quantified the source dynamics, including how residing solutes are flushed by incoming precipitation. Van Stan and Gordon (2018) suggest that stemflow quantity is inversely related to solute concentration, which would indicate supply limitations and that the higher stemflow amounts diluted solute concentrations. Similar observations have been compiled specifically for dissolved organic matter in stemflow, where DOC concentration decreases with stemflow production for most tree species (Van Stan and Stubbins 2018), although DOC concentration can also increase in concentration with stemflow production for trees which host rich epibiota and protosoils (e.g., in southern live oaks; Van Stan et al. 2017c). However, it remains unknown whether stemflow displaces, mixes with, or bypasses water that are absorbed into bark matrix or epiphytes that are presumably more enriched in solutes. Investigating these processes in more detail could prove key to better understanding canopy flow processes.

16.3 How Do Interception Storage Capacities Differ Among Ecosystems?

Canopy storage remains one of the most elusive quantities in canopy interception (Chap. 2). Canopy storage estimates can contrast substantially depending on whether they are based on whole-canopy measurements, top-down inference from throughfall-precipitation differences, or bottom-up scaling of direct storage measurements (Hancock and Crowther 1979; Klaassen et al. 1998; Llorens and Gallart 2000; Vrugt et al. 2003). By the top-down approach, storages are inferred from the differences between throughfall and open-precipitation across a range of event sizes (Leyton et al. 1967) or overtime for individual events (Link et al. 2004). Direct measurements of interception capacity involve measuring, for example, branch storage and then scaling them up to the whole-canopy level (Herwitz 1985; Keim et al. 2006), stem-compression or deflection measurements (Huang et al. 2005; Friesen et al. 2015), ground-based sensing such as gamma ray (Olszyczka and Crowther 1981), or microwave attenuation (Bouten et al. 1991). Direct measurements often exceed top-down measurements, especially if bark storages are accounted for (Klaassen et al. 1998).

Bottom-up estimated storages should also account for the presence of epiphytes, which can (in extreme cases) increase storages by as much as 16 mm (Jarvis 2000; Hölscher et al. 2004; Pypker et al. 2006; Porada et al. 2018). Unlike lianas, epiphytes are disconnected from soil water and nutrient sources and thus present a wide range of adaptations for capturing and storing atmospheric water, i.e., for maximizing interception (see Chap. 9). They should, therefore, augment canopy-storage capacity disproportionally to their biomass. On the other hand, due to the long-residence time of water in specialized structures (e.g., bromeliad tanks and moss tissue) compared to surfaces like bare bark and leaves, the active storage capacity of epiphytes is *probably* small, especially in continuously wet environments (Hölscher et al. 2004; Tobón et al. 2010); however, little relevant data exists, while the realized storage increases by epiphytes are accounted when inferring stand-level interception losses from throughfall-precipitation differences, it is not clear what proportion of total canopy storage and interception are accounted for by epiphytes. Furthermore, the lack of knowledge at the stand scale makes it difficult to assess the role of epiphytes for interception at the global scale. Few studies quantify the potentially large contribution of epiphytes to global canopy storage and rainfall interception (see Porada et al. 2018 for nonvascular epiphytes). Vascular epiphytes and lianas are rarely considered, but they may have substantial effects too, e.g., lianas in the tropics can add 1.3–5.3 $m^2\ m^{-2}$ to leaf area (Gerwing and Farias 2000). To advance modeling approaches in this direction, more systematic measurements are needed.

Model representations of storage often involve defining storage “buckets,” and parameterizing their filling and draining characteristics (Muzylo et al. 2009). Nearly all interception models include at least one canopy storage bucket, whereas some include multiple buckets such as bark (Gash et al. 1999) and litter, or multiple elements or layers within canopies (e.g., Davie and Durocher 1997; Lhomme and Montes 2014), each with potentially distinct sizes and filling and draining dynamics. However, estimates of these storage sizes and how they interact are often poorly constrained by data, which inhibits development of physically based models needed to predict interception losses without empirical calibration.

These idiosyncrasies in apparent storage, plus the fact that storage is the key calibration variable in most interception models, create a grand challenge: we cannot predict interception losses at sites without data. Thus, when faced with the need to scale to regional or global estimates—to assess the relevance of precipitation partitioning to the hydrological cycle, on groundwater recharge, or on soil chemistry—relatively simple relationships must be applied that often only rely on leaf area index (LAI) (e.g., Miralles et al. 2010; Murray 2014; Samaniego et al. 2010). This choice has been made despite the fact that plant morphology and environmental conditions strongly affect storage capacity per leaf area (e.g., Keim et al. 2006; Klamerus-Iwan and Błońska 2018; Xiao and McPherson 2016), so that woody surface area and biomass sometimes appear to be better predictors of storage than leaf area (e.g., Li et al. 2016). The result is that large-scale estimates of canopy interception evaporation are, at present, based on extrapolating rough correlations to estimate a parameter that is conceptually poorly constrained and almost impossible to measure in practice.

Many studies have examined the relationships of throughfall, stemflow and/or interception to single tree properties besides leaf area and diameter, like bark texture or branch angle (e.g., (Levia and Germer 2015; Van Stan et al. 2016; Fathizadeh et al. 2017; Cayuela et al. 2018a); however, comparative, larger-scale field studies have not always identified strong predictive parameters in LAI, diameter, or tree height (Dietz et al. 2006; Zimmermann et al. 2013). The question remains whether current technologies, such as high resolution satellite data or ground and airborne LiDAR data can shed light on parameters beyond leaf area and diameter for regional precipitation partitioning assessment (Roth et al. 2007; Baptista et al. 2018), or, whether most tree properties can be explained by allometric relationships and are, therefore, strongly cross-correlated.

Contrary to both of those lines of approach is the common finding that throughfall and stemflow measurements are a linear function of storm size, explaining >95% of the variation in event-scale partitioning across forest types (see Chap. 4), implying that storage may not even be a useful model parameter. Similar results are found by Gerrits et al. (2009), who found that their model was most sensitive to the rainfall pattern and that the actual interception storage capacity is less dominant. Such observations prompt the question: do the fine-scale, interacting, nonlinear processes between multiple canopy structural and meteorological variables “organize” at coarser scales into a well-behaved linear relationship with storm size and are these relationships unique to different plant functional types?

Lastly, while it is well-known that storage relates to vegetation structure and is not an intrinsic characteristic of landscape, the progression of storage with forest succession is rarely considered. The structural complexities that affect canopy storage and rainfall partitioning (Nadkarni and Sumera 2004; Deguchi et al. 2006; Barbier et al. 2009; Friesen et al. 2015) are not fixed, but instead vary as stands develop or undergo disturbances (Cisneros Vaca et al. 2018). Succession and disturbance can involve restructuring forests to have new species or changes in productivity (Lohbeck et al. 2014; Arroyo-Rodríguez et al. 2017), or simply a reallocation of biomass to substantially fewer stems with small changes to productivity (Allen et al. 2019). Epiphytes may also establish over time (Pypker et al. 2005), adding to storages. Although succession cycles may be coarsely predictable from physiographic data (Guariguata and Ostertag 2001), those predictions are unlikely to reflect the progression of storage capacity. For example, similarly characterized Tropical Dry forests of the same successional stage (e.g., early, intermediate, or late) can differ substantially in rainfall partitioning (Calvo-Alvarado et al. 2018). Thus, it remains unclear how successional patterns and the survey data used to characterize those patterns can be used to predict the success of canopy interception.

16.4 Are Interception Losses Always Lost (and How Do They Feedback with Microclimate)?

As intercepted water evaporate, hypothetically they partly continue to reside in the canopy space, modifying the local microclimate. To date, we have a relatively poor understanding of the trajectory of vapor sourced from interception and how it may continue to interact with the forest. The above canopy and below canopy airspaces can be highly decoupled (e.g., Froelich and Schmid 2006), which means that vapor may simply add to the forest's humidity, but rather than exiting vertically, the vapor may reside or disperse laterally; while empirical evidence suggests that smaller storages such as leaves dry relatively quickly, larger storages such as deadwood (Błońska et al. 2018) and forest-floor litter (Gerrits et al. 2010) can contribute substantially more vapor (e.g., 6–43% of throughfall can evaporate from the forest floor; Van Stan et al. 2017a). If a forest floor is regularly rewetted, exchanges likely match those observed in the sub-canopy space of flooded forests, where evaporation rates approach potential maxima and maintain high humidity (Allen et al. 2016, 2017b). Similarly, epiphytic mosses and lichens and vascular epiphytes with water storage structures can contribute to prolonged canopy humidity through both evaporation and transpiration (Stanton et al. 2014). However, it is important not only to understand how much liquid water is lost but whether that so-called "lost" vapor continues to play a role in the ecosystem.

While we know that vapor can recirculate under canopies (Berkelhammer et al. 2013), directly measuring the fate of evaporated water is challenging. The wet conditions associated with interception loss also are often concomitant with stable boundary layers and lateral transport, which impede most micrometeorological flux measurement techniques. Air movements and environmental gradients in forest canopies are challenging to classify or model (Alekseychik et al. 2013; Flerchinger et al. 2015; Hiscox et al. 2015; Schilperoort et al. 2018), and thus we have little understanding of vapor exchanges in humid conditions.

Regardless of measurement challenges, modifications to humidity have ecological implications. Humidity is a dominant control over stomatal aperture and thus gas exchange and photosynthesis rates (Ball et al. 1987; Berry and Goldsmith 2019). Additionally, for epiphytic organisms like lichens and mosses, slower drying in humid air may offer crucial benefits for the amount of time they can actively photosynthesize (see Chap. 9). High humidity conditions can also allow the formation of radiation fog and condensation, returning liquid water to the canopy (Bruijnzeel et al. 2006). Hypothetically, condensation may be crucial for transporting dry-deposited nutrients downward during dry seasons. By focusing on throughfall and stemflow sampling during storm events, we may overlook important fluxes of water (and nutrients) via condensation-driven throughfall and stemflow (e.g., Shure and Lewis 1973). However, wetness and humidity can also be considered undesirable for leaves, especially with respect to pathogens (Dawson and Goldsmith 2018), the dispersal of which may be facilitated by canopy flows (Chap. 14; Swiecki and Bernhardt 2016). This issue has been studied extensively in agricultural crops (Huber and Gillespie 1992) but much less in natural ecosystems. Thus, the effects of interception on microclimate and plant growing conditions, from an ecological and an evolutionary perspective, are relevant but not sufficiently considered questions.

At much larger scales, rainfall recycling has been documented (van der Ent et al. 2014). For example, precipitation and river isotope ratios in the Amazon basin suggest that rainfall is composed of large fractions of water from terrestrial evaporation (Gat and Matsui 1991); interception is a likely source of that vapor. Follow up work further emphasized that intercepted vapors may have a disproportionately large role in the fraction of terrestrial evaporation that supplies rainfall (Victoria et al. 1991). However, the extent to which rainfall recycling depends on ecosystem's interception capacity remains unknown.

16.5 Do Interception Effects Matter?

Of course, interception matters to water balances because interception losses are a major evaporation flux (and thus land cover has major effects on water yields; Bruijnzeel 2004). However, perhaps some of the most important questions about the effects of canopy interception pertain to what other, related processes it influences. Some of these questions pertain to scale, some to nonlinear or threshold triggering of subsequent hydrological processes, and some to the consequences for related physical and biological cycles such as biogeochemistry, energy budgets, or ecological relationships. However, many other (often assumed) influences remain poorly understood. Some of the important areas of discussion relate to interception effects on soil chemistry, carbon accounting, surface erosion, rainfall–runoff responses, and plant-available water, and how these effects propagate through landscapes and ecosystems. While there have been many potential impacts identified, how important are they?

16.5.1 Soil Chemistry and Biogeochemistry

It remains unclear how the effects of interception on precipitation input chemistry affect litter decomposition. Factors known to influence decomposition and nutrient dynamics of plant litter include litter moisture content, pH, addition of inorganic nutrients, and the content of polyphenols and carbohydrates (Berg and McClaugherty 2014), which are also influenced by interception. However, to date, few studies have been conducted to isolate the effects of interception or substances leached from the canopy. Throughfall exclusion experiments show altered soil microbiological activity (Chap. 11), but chemical effects are confounded by changes in hydrology. Manipulations of nitrate and ammonia concentrations in throughfall have inconsistently affected decomposition, which prompts two alternative hypotheses (see Qualls and Haines 1992): that polyphenols or humic substances in throughfall inhibit decomposers, or that sugar and other carbohydrates in throughfall increase decomposition via a priming effect. It remains difficult to disentangle the effects of litter moisture content, nutrient leaching, and, in particular, the organic substances in throughfall. Stemflow's interaction with litter decomposition has not been investigated; however, the previously described patterns in stemflow (and concentrated throughfall drip points) prompt the hypothesis that soil chemistry and microbial activities are affected by pathways of solute delivery (e.g., stemflow creates potential hot spots of microbial activity). It also remains unclear how plants respond to nutrient additions in soils and whether direct rainfall inputs would yield substantially different soil and plant responses.

16.5.2 Carbon Accounting

Throughfall and stemflow can become significantly enriched in dissolved organic carbon (DOC), with concentrations increasing by 1–2 orders of magnitude compared to rainwater (Van Stan and Stubbins 2018). Understory plant canopies can further interact with the already enriched throughfall and contribute an additional supply of organic material to the forest floor. Although evidence is scarce, it suggests that 2–10 g-C m^{-2} $year^{-1}$ leach from canopies as DOC (Gray 1997) as water further transits downward, highlighting the potential contribution of plant understory to C fluxes from the crown of trees to soils. However, DOC has not been systematically measured, and doing so requires understanding that throughfall and stemflow chemistry are highly variable at multiple spatial and temporal scales. In addition, a handful of studies suggest that all tree-derived organics are not uniform, but rather vary systematically between throughfall and stemflow and between tree species (Chap. 8). Chemical information may thus prove useful to ascertain the sources, but also the fate of DOC in the environment: tree-derived DOC is readily available to microbes (with 30–75% consumed over a few days; Howard et al. 2018) and contains chemical compounds that are typically considered bioavailable (Wickland et al. 2007). This suggests that tree-sourced DOC may have cascading consequences downslope. Thus, future questions not only relate to carbon balance but also how that enrichment influences ecosystems.

16.5.3 Erosion

Throughfall's erosional potential has received moderate research attention because droplets are larger and more spatially concentrated (Levia et al. 2017), although litter cover strongly reduces this form of erosion (Geddes and Dunkerley 1999). The role of stemflow as a geomorphic agent has rarely been examined because stemflow is commonly assumed, with little observational data, to preferentially infiltrate at the stem. Although there is little data on both preferential infiltration and erosion by stemflow, the data appear to favor stemflow's geomorphic potential (Chap. 12). One study found that, in Macadamia orchards, stemflow as high as 28% of rainfall eroded nearly 4 t ha^{-1} y^{-1} (Keen et al. 2010). It has also been hypothesized that canopy effects on infiltration rates may reduce erosion by decreasing the occurrence of shallow landslides (Keim and Skaugset 2003).

16.5.4 Rainfall–Runoff Responses

Interception modifies the amount, intensity, and spatial distribution of throughfall but the consequences of those changes for infiltration are poorly understood. Both field data and models suggest that spatial patterns in throughfall are not retained in soil moisture and do not affect runoff generation (Hopp and McDonnell 2011; Bachmair and Weiler 2012; Metzger et al. 2017), perhaps because of variability in rooting, soils, and topography overwhelm infiltration patterns (Guswa and Spence 2012). However, these conclusions are based on few data and even less theory, and there are exceptions. Given that interception can cause preferential infiltration in soils (e.g., Li et al. 2013; Schwärzel et al. 2012; Spencer and van Meerveld 2016), also reproducible in physical models (Liang et al. 2009), this preferential infiltration in soils could result in more rapid runoff responses (e.g., Bui and Box 1992; Charlier et al. 2009), especially where below-soil active storage is minimal.

16.5.5 Plant-Available Water and Nutrients

Although canopy interception mostly reduces the amount of water reaching soils, it has been argued that tree crowns funnel water to roots and thus can augment plant-available water (Li et al. 2009; Liang et al. 2011). Funneling ratios are used to quantify the localized augmentation of precipitation: the volume of stemflow divided by the product of rainfall depth times stem basal area; values over 1.0 indicate localized augmentation. Funneling ratios can be large (e.g., 7–26; Carlyle-Moses and Price 2007; Levia et al. 2011a, b), implying that substantially more precipitation may enter the soils surrounding stems. However, others have argued that funneling ratios are mostly small, and thus may not substantially increase tree-available water (Van Stan and Gordon 2018). Furthermore, to understand whether stemflow augments plant-available water, we must also know whether stemflow preferentially provides water to zones of uptake, for example, bypassing shallow soils (so-called “double funneling”; Johnson and Lehmann 2006). While studies have used tracers to demonstrate that stemflow influences infiltration and soil moisture patterns around stems in certain conditions (e.g., Schwärzel et al. 2012; Spencer and van Meerveld 2016), supporting observations are limited and not generalizable. Although the benefits of stemflow to trees are often asserted, it remains an open question whether or not stemflow augments plant-available water.

16.6 Conclusion

In summary, open question on the mechanisms, quantities, and effects of precipitation interception by vegetation persist. As tools and datasets continue to develop, new opportunities will arise. The questions that challenge us have progressed substantially from those of 120 years ago: “*I would be quite satisfied if we could just accurately calculate the loss that forest soils and springs suffer by precipitation interception on canopies. Whether it is exactly 51% or 59%, I do not care. Today, we do not even know if it is 20% or 80%.*” ~*C.E. Ney* (1894; *translated from German*). However, our current challenges are also reminiscent of the concerns that existed many decades ago: “*the processes involved do not seem to have been carefully analyzed, and, as a result, many of the experimental data are not in a form permitting interpretation of the results to the best advantage*” ~*Robert E. Horton* (1919) or, “*In spite of the many rainfall interception experiments which have been conducted in the past 78 years, further more complete and carefully planned research is needed.*” ~*C. L. Wicht* (1941). We hope that the questions discussed here serve to support more directed efforts toward advancing the understanding of the role of canopy interception in hydrologic and biogeochemical cycles.

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