



Review

A review and evaluation of forest canopy epiphyte roles in the partitioning and chemical alteration of precipitation



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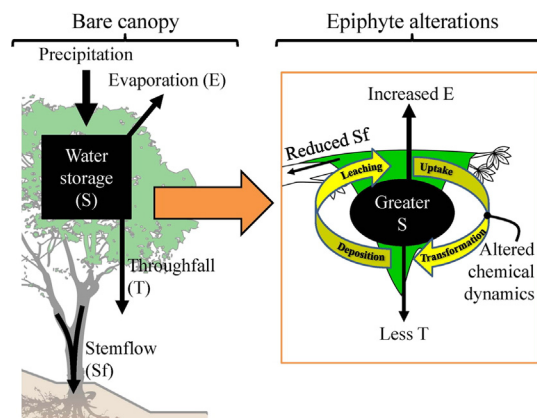
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HIGHLIGHTS

- Reviews >100 studies on epiphyte effects on throughfall, stemflow, & interception
- Identifies shared hydro-biogeochemical impacts on precipitation across epiphyte types
- Synthesizes methods used for characterizing water & chemical impacts of epiphytes
- Discusses important knowledge gaps for epiphyte impacts on canopy hydro-biogeochemical processes
- Highlights innovative methods for addressing identified knowledge gaps

GRAPHICAL ABSTRACT



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ABSTRACT

Interactions between precipitation and forest canopy elements (bark, leaves, and epiphytes) control the quantity, spatiotemporal patterning, and the chemical concentration, character and constituency of precipitation to soils. Canopy epiphytes exert a range of hydrological and biogeochemical effects due to their diversity of morphological traits and nutrient acquisition mechanisms. We reviewed and evaluated the state of knowledge regarding epiphyte interactions with precipitation partitioning (into interception loss, throughfall, and stemflow) and the chemical alteration of net precipitation fluxes (throughfall and stemflow). As epiphyte species are quite diverse, this review categorized findings by common paraphyletic groups: lichens, bryophytes, and vascular epiphytes. Of these groups, vascular epiphytes have received the least attention and lichens the most. In general, epiphytes decrease throughfall and stemflow and increase interception loss. Epiphytes alter the spatiotemporal pattern of throughfall and increase overall latent heat fluxes from the canopy. Epiphytes alter biogeochemical processes by impacting the transfer of solutes through the canopy; however, the change in solute concentration varies with epiphyte type and chemical species. We discuss several important knowledge gaps across all epiphyte groups. We also explore innovative methods that currently exist to confront these knowledge gaps and past techniques applied to gain our current understanding. Future research addressing the listed deficiencies will improve our knowledge of epiphyte roles in water and biogeochemical processes coupled within forest canopies—processes crucial to supporting microbe, plant, vertebrate and invertebrate communities within individual epiphytes, epiphyte assemblages, host trees, and even the forest ecosystem as a whole.

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1. Introduction

Material and energy exchange at the Earth's surface is drastically altered by the presence of forest canopy cover. Canopy structures that control this exchange (leaves, branches, bark, epiphytes, etc.) differentially alter the amount, spatiotemporal patterning, and solute concentration of precipitation reaching the surface (Levia et al., 2011; Pypker et al., 2011). Precipitation over forest canopies is either intercepted and evaporated, or reaches the surface below via gaps and drips (throughfall, Levia and Frost, 2006) and concentrated flow down the tree trunk (stemflow, Levia and Frost, 2003). The sum of precipitation that reached the ground (as throughfall and stemflow) is called net precipitation. Amount, type, spatiotemporal configuration, and composition of canopy elements control the proportion of precipitation partitioned into interception or net precipitation, as well as the solute concentration and spatiotemporal patterning of net precipitation at the forest floor (Pypker et al., 2011). Of the various canopy surface types, epiphyte cover arguably has received less attention from the precipitation partitioning research community (Levia and Frost, 2003, 2006). This is surprising as epiphytes are ubiquitous across forest types (e.g., Hölscher et al., 2004; Husk et al., 2004; Zotz, 2005; Pypker et al., 2006a; Hauck, 2009; Lundström et al., 2013; Van Stan et al., 2015), and their coverage, patterns, and forms can significantly alter canopy structural attributes, by (1) closing canopy gaps and connecting edges across, and branches within, individual trees (Fig. 1a), (2) filling voids in branch crotches and tree holes (Fig. 1b), (3) increasing area of "stable" above-ground biomass structures (Fig. 1c), and (4) ultimately changing the vertical biomass distribution of the host forest (Fig. 1d). This, in conjunction with epiphytes' diversity and uniqueness of nutrient acquisition mechanisms (e.g., Pittendrigh, 1948; Madison, 1977; Martin, 1994), illustrates the need for work to evaluate epiphyte impacts on canopy precipitation partitioning and its solute dynamics.

Consistent across most epiphyte types is the ability to store large amounts of water (Penfound and Deiler, 1947; Biebl, 1964; Martin and Schmitt, 1989; Martin, 1994; Pypker et al., 2006a; Martorell and Ezcurra, 2007), which elevates a forest's canopy water storage capacity and, as a result, interception loss (Table 1). This enhanced water storage is coupled with greater wet canopy surface area in epiphyte-covered forests, which can further increase interception losses through larger evaporative surface area and rates (Table 1). Since water storage and evaporation depend on atmospheric motion, epiphyte influences over interception loss magnitudes and processes will also vary depending on how coverage alters air circulation (Clark et al., 1998, 2005; Freiberg, 2001; Fleischbein et al., 2005; Pypker et al., 2005, 2006b; Martorell and Ezcurra, 2007; Villegas et al., 2008). Epiphytes alter the interchange between throughfall and stemflow by preventing drainage along leaf and branch pathways, disrupting or diverting water drainage along epiphyte drainage pathways (e.g., Fig. 1a–c shows epiphyte impediments to branch flow) and closing free throughfall gaps (as

shown in Fig. 1a). Solute flux and character of throughfall and stemflow is affected by epiphytes' myriad of nutrient acquisition mechanisms and unique leaching behavior (Schlesinger and Marks, 1977; Carroll, 1980; Reiners and Olson, 1984; Veneklaas, 1990; Coxson, 1991; Farmer et al., 1991; Knops et al., 1991, 1996; Prussia and Killingbeck, 1991; Coxson et al., 1992; Cappellato et al., 1993; Godoy et al., 2001; Levia, 2002; Liu et al., 2002; Husk et al., 2004; Oyarzún et al., 2004; Dezzio and Chacón, 2006; Turner et al., 2007; Zimmermann et al., 2007; Winkler and Zotz, 2009; Hauck, 2010; Van Stan et al., 2015). Net precipitation chemistry is further modified by enhanced dry deposition and aerosol transformation on epiphyte surfaces (Denison, 1979; Coxson, 1991; Knops et al., 1991; Rodrigo et al., 1999; Aubert et al., 2002; Hietz et al., 2002; Gaige et al., 2007; Inselsbacher et al., 2007; Umana and Wanek, 2010; Woods et al., 2012), and the decomposition of bark, leaf and stem litter trapped in epiphytes (Benzing, 1990; Richardson et al., 2000; Hietz et al., 2002; Turner et al., 2007; Woods et al., 2012).

Clearly substantial work has been accomplished regarding forest epiphyte roles in the partitioning of precipitation and alteration of canopy-derived solute flux to subcanopy soils, yet the authors are unaware of any comprehensive reviews summarizing and evaluating the current state of understanding to recommend future directions. Thus, the goal of this paper is to perform a review and evaluation of >100 studies by: (1) discussing measurement methods and (2) findings relating epiphyte type and abundance to canopy precipitation partitions (interception, throughfall, stemflow), and net precipitation chemistry; (3) relating broad ecophysiological mechanisms of common epiphyte types (lichens, bryophytes, and vascular – primarily bromeliads) to dissolved ion and organic matter enrichment or depletion in throughfall and stemflow; and (4) suggesting future directions for investigation of forest canopy epiphyte roles in the partitioning and solute alteration of precipitation. Our epiphyte grouping scheme (lichens, bryophytes, and vascular) was based on the studies to date, which did not allow more detailed phylogenetic comparison. Specifically, the broad grouping of "lichen" and "bryophyte" studies in this review was due to very few papers having reported detailed phylogenetic information on the epiphytes impacting precipitation partitioning processes. The bias toward one vascular epiphyte family, Bromeliaceae, is simply because this family is highly represented in interception, throughfall and stemflow literature. With the exception of one study (Awasthi et al., 1995), the authors are not aware of any studies investigating the impact on precipitation partitioning by the remaining common vascular epiphyte families (Orchidaceae, Cactaceae, Ericaceae, Araceae, Apocynaceae, Gesneriaceae, Melastomataceae, Polypodiaceae, and Rubiaceae). Thus, generalizations regarding vascular epiphyte impacts on precipitation partitioning from the current state of research are limited taxonomically and, therefore, geographically (mostly neotropical). Please also note that this review does not address previous literature regarding throughfall and stemflow impacts on

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