

Throughfall and stemflow are major hydrologic highways for particulate traffic through tree canopies

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For one-third of Earth's land surface, precipitation passes through tree canopies (as throughfall or stemflow) before entering watersheds. Over a century of research has described fluxes of water and solutes along these “hydrologic highways”, yet little is known about their “traffic” – that is, the organisms and nonliving particulates frequently discarded from water samples after filtration in the lab. A comprehensive understanding of the composition of sub-canopy precipitation is necessary to estimate the total nutrient and pollutant inputs to watersheds for redistribution downstream, as well as to systematically investigate precipitation effects on organismal exchanges along the atmosphere–plant–soil continuum. Here, we review current concepts and research showing that the hydrologic highways from tree canopies to soil carry ecologically relevant quantities of biologic (viruses, microbes, microfauna, and meiofauna) and abiotic particulates. Their fate may have important consequences for the biogeochemistry and biodiversity of terrestrial systems.

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Storms and condensation connect residents and resources in plant canopies to the soil surface via “hydrologic highways” consisting of (1) throughfall, water that falls through gaps between branches, leaves, and epiphytes, and drips from canopy surfaces; and (2) stemflow, water that travels down plant stems (Figure 1). As most precipitation falling over trees contacts the canopy before reaching the soil surface, the physicochemical and particulate composition of water exiting the

canopy can be markedly different from the rainwater entering from above. Throughfall and stemflow integrate the products of biological, physical, and chemical processes occurring in the canopy, which results in the transport of diverse travelers (ie unicellular-to-multicellular organisms; eg Chauvet *et al.* 2016; Bittar *et al.* 2018; Ptatscheck *et al.* 2018) and vehicles (eg dust particles, excretions from canopy fauna; Lequy *et al.* 2014; Arango *et al.* 2019) to the below-canopy environment.

Discussion of the ecological roles of canopy hydrologic highways begins at the origins of botanical science (Van Stan and Friesen 2020). Beyond the water and weather controlling throughfall and stemflow, research has predominantly focused on these highways' dissolved fraction – requiring filtration of water samples to 0.2–0.4 μm and detouring the travelers (ie organisms) and vehicles (ie nonliving particulates) to the trash when sample filters are subsequently discarded. As such, the organisms and nonliving particulates delivered to the soil surface via throughfall and stemflow remain “hidden” within sub-canopy precipitation. Current theoretical concepts and recent data indicate that the traffic within these hydrologic highways is biogeochemically and ecologically important, and therefore merits a closer look. Indeed, basic knowledge (eg mass flux, community composition and function) of the organisms and nonliving particulates within all water fluxes (or aquatic habitats) has been fundamental for describing their ecological and environmental context, and for understanding such functions as nutrient and pollutant cycling.

Here, we synthesize current knowledge and conceptualizations about the traffic that uses these hydrologic highways through tree canopies. We describe (1) the origins and characteristics of known living and nonliving particulates in tree canopies, (2) their mobility in canopy-to-soil hydrologic

In a nutshell:

- Precipitation initiates flow paths (“hydrologic highways”) through tree canopies that scour particulate-covered surfaces
- Current theory and observations indicate that the traffic (biotic and abiotic particulates) that moves along these hydrologic highways affects the flux and compositional diversity of materials transported to soils during precipitation
- Particulate motion and transport within branchflows (the intra-plant hydrologic highway) controls throughfall and stemflow particulate flux but is poorly understood
- Variability in the particulate traffic riding these hydrologic highways is relevant to the dispersal of microbiota and macrobiota in tree-dominated ecosystems

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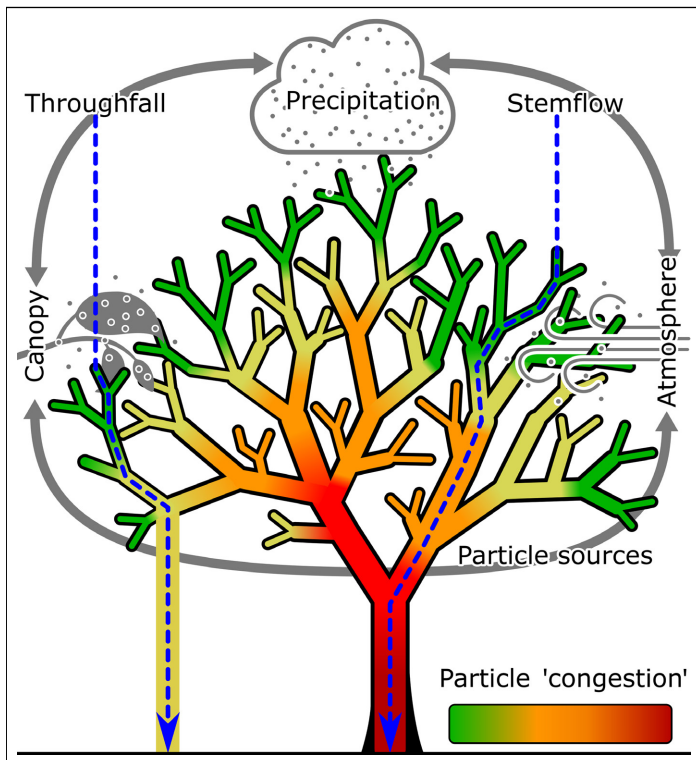


Figure 1. Throughfall and stemflow “hydrologic highways” in tree-dominated ecosystems. These highways transport particulates derived from atmospheric wet, dry, and cloud deposition, as well as from in-canopy processing. As water flows through plant canopies, the mass (“congestion”) of particulates increases as particulates are scoured from leaf, bark, and other canopy surfaces.

highways, (3) unexplored factors affecting mobilization via throughfall and stemflow, and (4) the possible fates and functions of organismal and particulate mass fluxes at the end of these hydrologic highways.

■ Onramps for particulates to access hydrologic highways

Water that flows from tree canopies to the ground – including rain, snow, fog, and dew water – contains a large and diverse suite of organisms and nonliving particulates that vary in size by at least four orders of magnitude (Figure 2). The primary source of nonliving particulates, such as dust, black carbon (C), radioactive particles, and microplastics, is the atmosphere. Mineral dust, one of the most abundant particles in the atmosphere by mass (Boucher *et al.* 2013), is swept up into the atmosphere by strong winds in regions with no or low vegetation cover and/or erodible soils. In contrast, black C is a minor but climatically and ecologically important constituent of the atmosphere produced as a result of incomplete fossil-fuel and biomass combustion. In addition, nuclear weapons testing, nuclear fuel cycles, and nuclear accidents have released radioactive particles (<1–2000 μm) into the atmosphere; all of these particles can be captured by tree

surfaces (Kato *et al.* 2012). Although to date rarely quantified in air, natural and synthetic microplastics (plastic particles with the longest dimension <5 mm) enter the atmosphere via shedding or drying, industrial processing, or photo-oxidative degradation (Gasperi *et al.* 2018).

Nonliving particulates derived from organisms (eg excretions), plus microorganisms, comprise ~20% of the atmosphere’s load (by mass or count) of suspended particulates between 0.2 μm and 50 μm in diameter (Morris *et al.* 2011). Given their widespread global distribution and potential effects on ecosystems and climate, microbial aerosols are receiving considerable scientific attention (Reche *et al.* 2018; Evans *et al.* 2019). These microorganisms are emitted from diverse sources through shedding of plant and animal parts (eg leaf fragments), soil erosion, bursting of bubbles at the water surface, and wave–shore interactions (Evans *et al.* 2019). Microfauna (~0.45 μm to ~100 μm in diameter) and meiofauna (~100 μm to ~2000 μm in diameter), albeit often overlooked, are transported through the atmosphere as well and have been found to colonize leaves, bark, epiphytic plants, and in-canopy water impoundments, such as phytotelmata (leaf cavities that fill with water) and dendrotelmata (holes in tree stems that fill with water) (reviewed in Ponette-González *et al.* 2020). Regardless of source, organisms and nonliving particulates can travel in atmospheric waters, with prevailing winds, and/or adhered to other particulates before deposition to tree canopies via wet, fog, dew, and dry deposition (Weathers and Ewing 2013).

Tree canopies represent another major source of particulates to throughfall and stemflow waters, with producers, consumers, and decomposers contributing directly and indirectly to total particulate mass. For example, abrasion of canopy surfaces by wind, rain, hail, and other branches and leaves, and pollen and seed production can generate large quantities of particulate organic matter (POM) for transport in water. In systems with high levels of herbivory or roosting (eg urban trees), consumers produce POM through litter fragmentation, leaf damage, excretions (Arango *et al.* 2019), and death (ie cadavers). Leaf surfaces, which can be colonized by bacterial and fungal decomposers well before the initiation of senescence (Fonte and Schowalter 2004), and temporally persistent bark surfaces that efficiently capture biological particulates (Ponette-González *et al.* 2020), provide a source of bacterial cells and fungal spores to precipitation. As such, when water reaches tree canopies, there is an abundant and diverse, living and nonliving, and modified particulate load ready to ride (or resist) the hydrologic highways that manifest as throughfall and stemflow.

■ Do we stay or do we go? Mobility of canopy travelers and vehicles

Particulates deposited to or derived from tree canopies have three immediate fates: “move” (mobilization), “stick” (retention), or “change” (in-canopy processing) (Weathers and

Ewing 2013). Between storms, physicochemical and biological processes act to shape the composition and amount of canopy travelers and vehicles (Figure 3). Resuspension, for example, a process influenced by tree species, wind speed, time, and their interactions (Xie *et al.* 2018), contributes to a reduction in canopy particulate load. Nonliving particulates (eg C-rich particles) may also be transformed into living particulates through bacterial consumption (Vacher *et al.* 2016). Finally, microbial community composition and activity in the phyllosphere (the aboveground portion of a plant available for colonization by microorganisms) are sensitive to climatic stressors (eg drought, warming), pesticide applications, and air pollution (reviewed in Vacher *et al.* 2016). Indeed, tree canopies represent a collection of dynamic and ever-changing surfaces and sources of particulates.

Canopy retention includes particulates that reside on canopy surfaces as well as those that adhere to or become embedded in leaf waxes (Rindy *et al.* 2019). In the case of nonliving particulates, retention is affected by physicochemical properties, namely chemical composition and size (Figure 3). Observational and experimental studies show that once deposited, fine particulates are more likely to “stick and stay” than larger particulates by virtue of their high surface-to-volume ratios (Wang *et al.* 2018) and low resuspension rates (Xie *et al.* 2018). Particulates also have diverse surface compositions and coatings, which influence the nature and strength of interactions between particulates and surfaces. An example can be found in measurements conducted 5 months after the Fukushima Daiichi nuclear power plant accident in Japan in 2011, where >60% of the radiocesium but only 25% of the radioiodine deposited in a nearby forest was retained in the canopy (Kato *et al.* 2012). Therefore, only a portion of nonliving particulates becomes traffic on hydrologic highways through the canopy.

Similarly, not all canopy organisms will ride the hydrologic highways of throughfall and stemflow. Many adaptations exist to resist being swept along by branchflows or battered off by the impact of rainfall and throughfall droplets. Phyllosphere microbial communities, for instance, may aggregate in micro-depressions or generate biofilms to remain attached or stuck to surfaces (analogous to a car pulling into a highway rest stop; Flemming and Wuertz 2019). Seeds of epiphytic plants have evolved adaptations that improve canopy retention; for instance, the seed wall of *Chiloschista* spp orchids extends into helical tendrils after contact with water to secure the seed to the tree bark (Barthlott *et al.* 2014). The mobility of some phyllosphere bacterial taxa in hydrologic highways may be a function of ecological interactions, such that some bacteria gain entrance into protective aggregates or biofilms while others do not (Teachey *et al.* 2018).

Of course, the scouring capability of these hydrologic highways, particularly during long or intense rainfall, may overcome adaptations designed to prevent organisms from being swept away by branchflows into heavy traffic. Conversely,

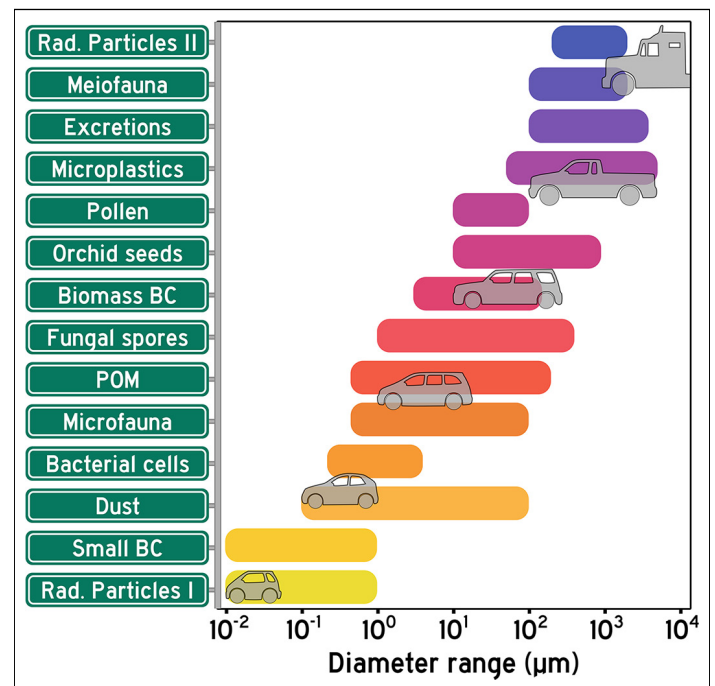


Figure 2. Diameter size (μm) of various particle types (living and nonliving) measured in throughfall and stemflow waters. Diameter sizes range by four orders of magnitude. In some cases, parameters are bounded by the limit of filtration or the reported observation per notes in WebTable 1. Rad particles = radioactive particles; BC = black carbon; POM = particulate organic matter. Summary of size diameter range boundaries and references can be found in WebTable 1.

pathogenic microbial organisms have been found to use in-canopy flow paths to initiate downstream infections in plant leaves or to infect other organisms in the canopy (see Ponette-González *et al.* 2020). Other generally nonpathogenic microbes, including star-like fungal spores (Chauvet *et al.* 2016), have adaptations that may support dispersal out of the canopy via branchflows (or into canopy depressions, like tree holes).

As a result of pre-storm conditions, physicochemical factors, and organismal adaptations, some proportion of particulates washes from canopies to the soil in throughfall and stemflow (Cayuela *et al.* 2019). Research simulating the mobilization of nonliving particulates with rainfall indicates that 30–86% of particulates <2.5 μm can be washed from canopy surfaces (Chen *et al.* 2017). Mobilization is, however, a complex process, with the likelihood that particulates will be mobilized dependent on atmospheric factors, canopy and particle characteristics, and accumulated particulate mass (Figure 3). Both in controlled experiments and field settings, particulates >2.5 μm represent the largest proportion of particulate mass collected in rinse, throughfall, and stemflow waters (Cayuela *et al.* 2019). Furthermore, most particulates are washed from trees within the first 15 minutes of rainfall, with higher intensity storms being more effective at initiating particulate movement and removal from plant surfaces due to the larger diameter and kinetic energy of rainfall drops (Xu *et al.* 2017).

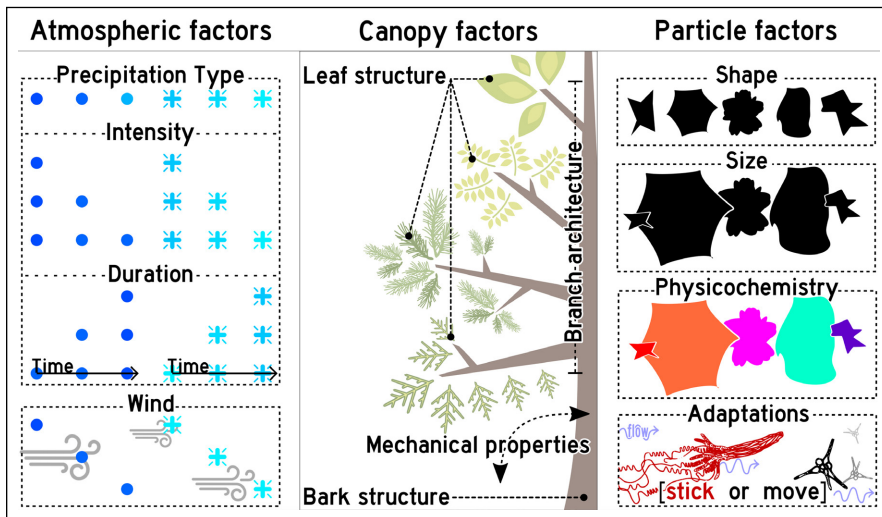


Figure 3. Conceptual summary of the major physical controls on particulate transport in throughfall and stemflow. These include multiple atmospheric factors associated with storms, canopy structural factors, and the physicochemical and biological properties of particulates.

■ If we go, how does the traffic flow? Particulate motion and transport modes

In addition to the studies reviewed above, our knowledge of particulate transport in hydrologic highways stems from a need to predict the onset and volume of particulates delivered by pressure- or gravity-driven flows along low-sloping natural (eg river channels) and engineered (eg sewer pipes) surfaces. These flows differ markedly from the canopy hydrologic highways that drain along the outside and underside of branches, while being buffeted by droplets and winds. Describing particulate motion and transport modes within branchflows is necessary to understand the mechanisms controlling throughfall and stemflow particulate flux, as a large portion of throughfall consists of “released” water or water that has traveled along branches to “drip points” (Figure 1). Branchflows also contribute substantial organismal and elemental fluxes to tree-hole ecosystems (Chauvet *et al.* 2016), which may subsequently overflow to become throughfall or stemflow.

Current theory regarding the onset of particulate motion, transport mode, and flux of particulates within hydrologic highways states that the force required to mobilize a stationary particle is chiefly a function of gravity and the friction angle between the particle and pocket where it rests (Wiberg and Smith 1987). If flow conditions initiate particle motion, the mode of transport changes with increasing flow velocity: from creep, to short hops, to suspension in vigorous flows. As branchflow depths are shallow (only a few millimeters) and the canopy environment is highly complex and dynamic, the types and roles of forces applied to particulates, as well as the transport modes of this well-established framework, are literally “turned upside-down” (Figure 4).

Because particles on a branch are parked in bark “garages” that could be at any orientation, gravitational forces may act as a resisting or driving force to initial motion (Figure 4).

Particulate traffic that leaves the “garage” and travels in branchflows or stemflows appears small, 10^{-2} – 10^4 μm (Figure 2), but occupies a large fraction of flow depth (10^2 – 10^4 μm), which should influence flow structure – similar to boulder transport by flash floods. Meanwhile, droplet impacts may repeatedly pound this hydrologic highway, mobilizing particulates, altering flow properties and particulate transport rates, and ejecting vehicles and travelers from the highway (Beuselinck *et al.* 2002). Canopy flows and associated particulate motion may be partially forced by winds shearing the transporting air–water interface and swaying the canopy structures on which the highways flow. The shallow branchflows may cause particulates to interact with the air–water interface at various orientations, and therefore the forces associated with particulate emersion and immersion due to surface

tension (Figure 4, a and c) must be considered (Chatterjee *et al.* 2012). Due to variation in particle composition and shape, the rate at which suspended particles will gravitationally settle will fluctuate (Figure 4b). However, bark and particle surfaces may have some amount of fringing biofilm (Fang *et al.* 2017), which can increase thresholds for “getting out of the garage” above physical cohesion alone (Malarkey *et al.* 2015).

These concepts make up a portion of the roadmap for future studies needed to better understand the “modes” of particulate transport (eg creep, saltation, suspension), as well as how these transport modes and volumetric particulate fluxes correspond to competition between driving and resisting forces at the particle scale (hypothesized in Figure 4). Such efforts may eventually culminate in a predictive unified model of fluid and particle routing through canopy hydrologic highways.

■ What happens at our destination? Fate and function of organismal and mass fluxes

The hydrologic highways that develop through tree canopies guide both water and particulates to localized destinations at the soil surface. Throughfall drip and stemflow input areas may be 10–100 times more spatially and chemically concentrated (in solutes) than open precipitation (Ponette-González *et al.* 2016; Van Stan and Allen 2020). Annual stemflow fluxes can be especially magnified, as the canopies can concentrate draining precipitation waters to 10^{-2} – 10^1 m^2 of soil surface surrounding trees (Van Stan and Allen 2020). Overall, annualized flux estimates for organisms and non-living particulates in throughfall and stemflow are scarce, but such estimates as do exist suggest that ecologically and biogeochemically relevant amounts of particulates flow along these hydrologic highways (Figure 5). As an example from

a temperate deciduous forest, throughfall can supply >120 kg ha⁻¹ yr⁻¹ of particulates to the soil surface (Lequy *et al.* 2014). Fine throughfall particulate (0.45–500 μm) flux alone can comprise 11–15% and 14–21% of total (dissolved, particulate, and litterfall flux) annual C and nitrogen (N) fluxes, respectively (Lamersdorf and Blank 1995). Throughfall particulates may influence other nutrient cycles as well (Figure 5): 24–47 kg ha⁻¹ yr⁻¹ of mineral dust (Lequy *et al.* 2014), 7 kg ha⁻¹ yr⁻¹ of radioactive particles when present (Kato *et al.* 2012), and 1 kg ha⁻¹ yr⁻¹ of black C (Figure 5) have been delivered via hydrologic highways from canopy to forest floor in these temperate forest sites. The only estimate known to the authors for annual stemflow particulate flux is for the 0.45–500 μm size fraction (1.5–2.4 kg ha⁻¹ yr⁻¹) (Cayuela *et al.* 2019). The coarse particle contribution to annual stemflow particulate flux is currently unknown (Figure 5).

Although much of what (particulate elemental composition) flows along hydrological highways has yet to be quantified, more observations exist on who (organismal composition) is present and how much of each there is, albeit most of the data derive from studies of stemflow versus throughfall (Figure 5). For example, the free, suspended bacterial flux along both hydrologic highways in an oak-cedar forest in coastal Georgia (10¹³–10¹⁶ cells ha⁻¹ yr⁻¹) (Bittar *et al.* 2018) appears modest compared to the bacterial flux within soils and from fallen leaves (10⁸–10⁹ cells g⁻¹) (Girvan *et al.* 2003; Remus-Emsermann *et al.* 2014); however, this estimate does not include bacterial cells residing on suspended particulates. At this same coastal Georgia study site, bacterial community composition in throughfall and stemflow was similar and included taxa known to influence litter degradation and soil nutrient cycling (Teachey *et al.* 2018) (see also Chauvet *et al.* [2016] for data on fungi at other sites). Therefore, the fungal and bacterial travelers suspended within hydrologic highways may exert considerable biogeochemical influences at the surface if they can establish in the litter or soil.

No studies to date report meiofauna or macrofauna flux or community composition for throughfall. The first analysis (to our knowledge) of multicellular fauna in stemflow was published only recently (Ptatscheck *et al.* 2018), and indicates that 10⁶ of these organisms can be delivered to near-stem soils each year (Figure 5). These results not only suggest an annual flux of ecologically relevant magnitude (2.5 × 10⁴–1.2 × 10⁶ individuals tree⁻¹ yr⁻¹, depending on the organism) compared to mean annual abundances in forest soils (3 × 10⁴–1 × 10⁶ individuals m⁻² yr⁻¹) but also show that stemflow-transported meiofauna include bacterial- and hyphal feeders (eg nematodes) capable of surviving in soil environments. If throughfall meiofaunal fluxes are of similar magnitude (throughfall annual per ha fluxes are generally many times larger than stemflow; Figure 5), then organisms flowing from tree canopies to the surface may play an important role in the biodiversity and biogeochemistry of forest litter and soils.

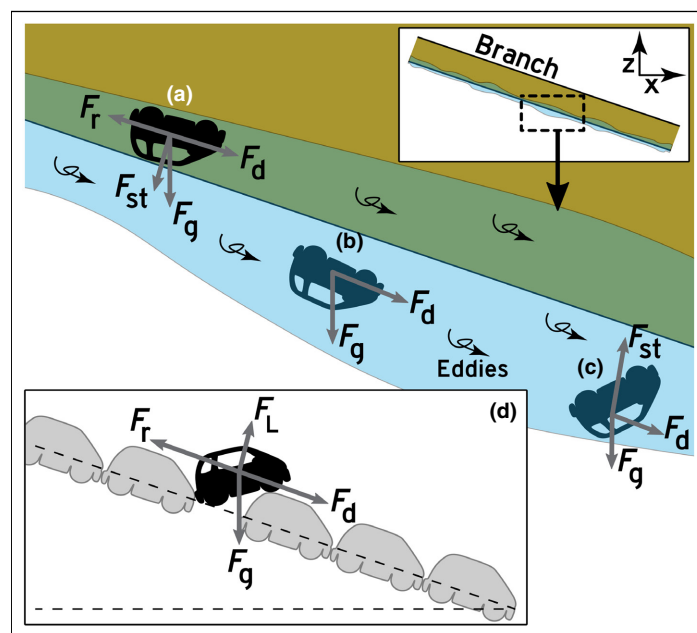


Figure 4. A conceptual diagram showing three hypothetical particulate states in a hydrologic highway along a branch. (a) A particle “parked” on the bark. When at rest, a particle is subjected to a resisting force (F_r) associated with possible physical and biofilm cohesion, a gravitational settling force (F_g), a surface tension that keeps the particle from emerging from flow (F_{st}), and a drag force (F_d) that is exerted on the particle by the passing water flow. (b) Once a particle has exited its bark “garage” and entered the hydrologic highway, it is subjected to F_g and F_d . (c) As the particle approaches the highway edge, the air–water interface may act as a “guard rail”, where F_{st} helps counter F_g to keep particulate traffic in the branchflow and moving down-branch due to F_d . (d) A comparison of the hypothetical forces on a particle in the better-researched streambed hydrologic highway, including the lofting force (F_L) per Wiberg and Smith (1987).

Conclusions

Hydrologic highways connect the atmosphere to soils. Organisms and nonliving particulates (the traffic) flow, likely in large quantities, to the main highway via onramps (atmosphere, leaves, branches, epiphytes, and so forth), such that the composition of traffic beneath tree canopies bears little resemblance to that present at the start of the highway. Overall, we know relatively little about the organisms and nonliving particulates (and even less about emerging pollutants and particulates, such as microplastics) transported by these hydrologic highways. Vegetation controls on particulate fluxes and the dynamics of particulate retention and mobilization warrant further research, especially in the context of global environmental change (eg novel pollutant emission, agriculture, urbanization). In addition, current theoretical concepts of particulate transport from natural and engineered systems must be turned “upside down” before they can be applied to particulate transport in throughfall and stemflow. We contend that substantial amounts of living and nonliving particulates can be transported to the soils

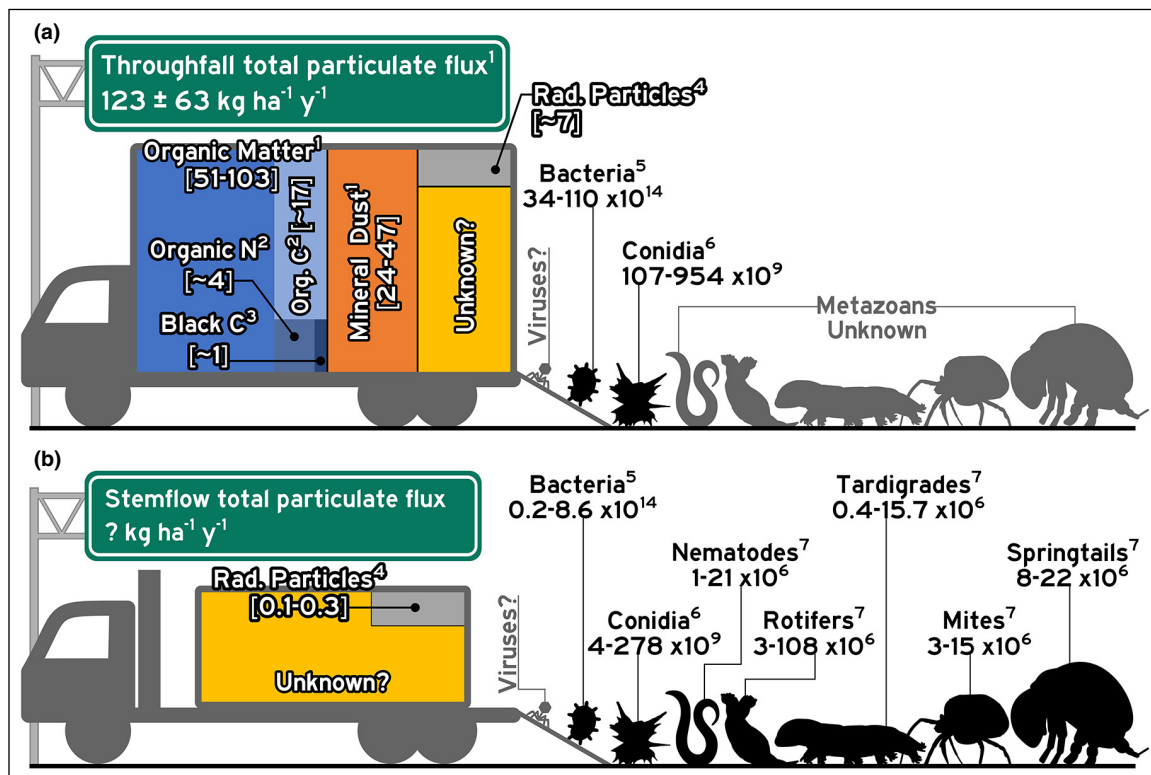


Figure 5. Estimated (a) throughfall and (b) stemflow total nonliving particulate mass flux (depicted as vehicles) and organismal fluxes. Organisms in black have published flux values, whereas the organisms in gray have no published flux values to date, to the authors' knowledge. Superscripted numbers associated with particle types and organism names refer to relevant studies, which are listed in WebTable 2.

via these hydrologic highways, and that the composition of this traffic and its role in biogeochemical function is a largely unexplored frontier at the interface of atmosphere–terrestrial ecosystem dynamics.

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■ Supporting Information

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