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ECOSYSTEMS

Medium, Vector, and Connector: Fog and the Maintenance of Ecosystems

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ABSTRACT

Fog and low-lying cloud (fog) play a significant role in the maintenance of ecosystems, from desert to alpine and from coastal to inland systems. Our central thesis is that fog provides ecosystems with critical water and nutrient subsidies, and also delivers pollutants, that often control ecosystem function. Fog is a medium, vector, and connector. In this mini-review, we synthesize recent research advances that reveal the diverse ways that fog shapes ecosystem processes. Crown wetting, elemental deposition, and light scattering and absorption are fundamental mechanisms by which fog has been shown to influence water fluxes, productivity, and decomposition in hyper-arid to ever-wet regions. These impacts are ultimately mediated by the structure and composition of biological systems that allow fog capture and utilization of resource subsidies. Climate change, and changes in land use, ocean circulation, and atmospheric pollution are simultaneously altering the nature of fog itself, and the architecture of the ecosystems adapted to capture it. The coupling between atmosphere and biosphere in fog-enshrouded areas raises new questions about past and future fog-dominated ecosystems, and their maintenance and diversity, in the face of global change.

Key words: cloud; water; elements; light; productivity; decomposition; ocean-land interactions; microbes; global change.

HIGHLIGHTS

- Fog subsidizes ecosystems and modulates their light climate
- Fog influences ecosystem processes: water flux, productivity, decomposition, and elemental cycling
- Fog is dynamic, encompassing and connecting ocean, atmosphere, and terrestrial system interactions

INTRODUCTION

Fog and low-lying cloud (hereafter fog) immerse and influence ecosystems across the globe (Weathers 1999). Ground fogs are common in valley bottoms and envelop low-lying systems, advection fogs inundate coastal forests and hyper-arid deserts along nearshore-coastal upwelling zones, and mountain-mists are a constant occur-

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rence in tropical and temperate montane cloud forests in the new and old worlds alike. The small horizontally driven droplets of liquid water that enshroud and impact animal and plant surfaces and deliver water and nutrients have long been considered to be fundamentally important to these fog-dominated ecosystems (for example, Kerfoot 1968), but how does fog contribute to ecosystem function (Weathers 1999)?

Although the answer to this question is still incomplete, scientific interest in and inquiries into fog date back centuries. Perhaps most notable in regard to fog and pollution is nineteenth century London, when smoke pollution from widespread, coal-based heating and coal-powered industries coupled with cool temperatures contributed to high fog—or more appropriately named ''smog''—frequency, raising concerns about the public health of urban residents (Weathers and Lovett 1998; Thornes and Metherell 2003). Studies examining fog chemistry and fog-vegetation interactions followed not long after, and by the early to mid-1900s ecologists and geographers had begun to estimate the amount of fog drip under individual trees or across wide areas of the landscape using simple observations and rudimentary collectors (for example, Marloth 1903, 1905; Means 1927). Along the U.S. California coast, scientists aptly noted the influence of tree height and topography on fog water deposition to soil as well as the spatial overlap between redwood communities and the fog belt (Oberlander 1956; Parsons 1960). Meanwhile, investigations of air pollution impact on forest vegetation in North America and Europe prompted research on the chemistry of fog and its potential role in biogeochemical cycling (for example, Schlesinger and Reiners 1974; Dollard and others 1983; Munger and others 1983; Fuzzi and others 1985; Schemenauer 1986; Weathers and others 1986). At this time, fog was also garnering attention among tropical ecologists, some of whom suggested that fog was possibly the most salient factor affecting the structure and function of high-elevation tropical forests (Grubb and Whitmore 1966; Baynton 1968).

Subsequent decades witnessed increased efforts to assess the relative significance of fog as a hydrological input to ecosystems (for example, Ingraham and Matthews 1988, 1995; Cavelier and Goldstein 1989; Bruijnzeel and Proctor 1995; Dawson 1998; Ewing and others 2009; Lehnert and others 2018), as a vector of nutrient and pollutant deposition (for example, Weathers and others 1988, Weathers and Likens 1997; Collett and others 1998, Heath and Huebert 1999; Weathers and others 2000; Baumgardner and others 2003; Ponette-González and others 2010a; Desyaterik and others 2013; Templer and others 2015; Weiss-Penzias and others 2016), and as a water source for plants, plant communities, and even beetles, during otherwise rainless periods (for example, Seely 1979; Dawson 1998; Burgess and Dawson 2004; Corbin and others 2005; Seely and others 2005; Ewing and others 2009; Fischer and others 2009; Limm and others 2009; Simonin and others 2009; Matimati and others 2012; Warren-Rhodes and others 2013; Baguskas and others 2014).

Fog has since been shown to modulate several plant (for example, Burgess and Dawson 2004; Del-Val and others 2006; Gutiérrez and others 2008; Goldsmith and others 2013; Alvarado-Barrientos and others 2014; Gotsch and others 2014) and, less frequently, ecosystem functions (Ewing and others 2009; Carbone and others 2013; Templer and others 2015; Fischer and others 2016). Here, we provide a framework for conceptualizing the mechanisms for fog-ecosystem interactions. Our central thesis is that water, elemental, and biological inputs from fog can subsidize inputs from rainfall—or represent the entire annual hydrologic, labile elemental, and/or biological flux to a system. Further, fog modulates heat, water, and radiative interactions between atmosphere and terrestrial systems. Much of the literature points to fog's direct hydrological inputs as most important in controlling ecosystem processes; here, we suggest that energy and hydrological modulation—meaning an impact that can improve both overall water balance from primary inputs of water and secondary benefits to the organisms that receive the inputs—are likely to be equally important. Perhaps the most important influence fog has on terrestrial ecosystems is how it impacts the strength and manner of coupling between the atmosphere, vegetation, and the soil processes known to drive ecosystem functions, such as water flux, productivity (Nyaga and others 2015; Templer and others 2015), element cycling, and decomposition (for example, Jacobson and others 2015; Figure 1).

We explore our conceptual framework by first synthesizing studies on the role of fog as a medium and vector. We then review recent research on the diverse ways that fog impacts processes from plants to ecosystems. We conclude by identifying frontiers where research is now needed to better understand fog's role as a connector among atmospheric-ocean-terrestrial systems. Finally, we speculate on how global change will alter the availability, nature, or capture of this ephemeral resource and, in turn, fog-ecosystem interactions.

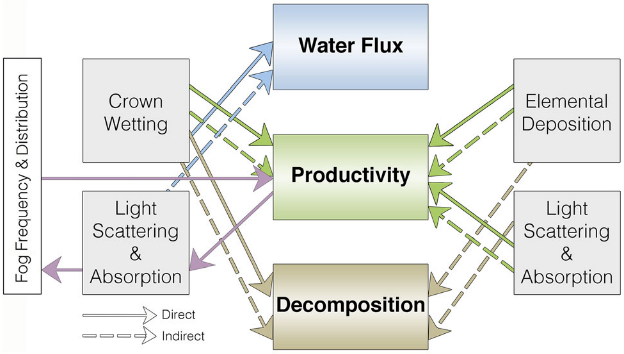

Figure 1. Mechanisms—crown wetting, elemental deposition, light scattering, and absorption—by which fog can directly (solid arrows) and indirectly (dashed arrows) influence major ecosystem functions, including water flux, productivity, and decomposition. Purple arrows indicate feedback effects (Color figure online).

Fog as Medium and Vector

Fog serves as a medium and vector, delivering, supplying, and regulating the flow of critical limiting resources—water, elements, and light—to ecosystems. Fog influences the ''top'' (forest canopy or tree crowns) and ''bottom'' (soils and rhizosphere) of ecosystems when droplets advected by wind envelop and collide with plant surfaces, evaporate back to the atmosphere, are directly absorbed into tissues or areal soils or, alternatively, coalesce and fall to the ground.

Water

Estimates of fog water inputs to the top of vegetation canopies vary widely within and across ecosystem types due to differences in climatic and meteorological factors as well as measurement methods (Dollard and Unsworth 1983), ranging from 11% to 83% of total (rain + fog) annual precipitation (Figure 2; Supplemental Material). The relative importance of fog increases as water becomes more limiting to plant performance and growth as well as to critical ecosystem functions. At subtropical sites with extreme aridity, including northern Chile, western South Africa, and the Namib Desert, fog moisture comprises a median of 83% of the total above-canopy water input (Figure 2), although inputs may display high interannual variability due to large-scale climatic oscillations (ENSO; del Río and others 2018). There are also many ecosystems, including those with a Mediterranean climate, or those located at the edge of the tropics, where fog represents either the primary source, for example, about 100% (Hildebrandt and others 2007; Lehnert and others 2018), or a significant proportion, from approximately 25–35% (Dawson 1998), of the above-canopy dry-season water input.

Measurements of below-canopy fog fluxes show that the amount of fog water deposited to soils is strongly affected not only by climatic and meteorological conditions but also by vegetation and three-dimensional canopy structure (Nadkarni and Sumera 2004; Ewing and others 2009; Ponette-González and others 2010b, 2014; Chung and others 2017). As fog water falls from the canopy toward the soil surface, leaves, branches, mosses, and epiphytes, intercept, retain, and even absorb fog droplets. As a result, the soil of ecosystems with a high degree of vertical stratification (vegetation layering), such as tropical and temperate montane forests, may receive less than half the inputs deposited to the top of the ecosystem (Figure 2). In subtropical forests and woodlands characterized by less vertical complexity, such as those found on the Island of Madeira in Portugal, atmosphere-to-canopy inputs and canopy-to-soil fog fluxes can be of similar magnitude (Prada and others 2009). For comparison, in tropical and temperate montane and lowland forest, throughfall is about 80%, whereas stemflow is 2–6% of rainfall (Ponette-González and others 2016). Leaf- and crown-scale physiological research across a wide range of tropical (Goldsmith and others 2013), temperate (Berry and others 2014; Emery 2016; Baguskas and others 2017), and desert (Hill and others 2015; Yan and others 2015) plants demonstrates that direct absorption of water into leaves and stems is more widespread than botanists originally had thought and has physiological impacts, such as improved water status, that until recently were not appreciated.

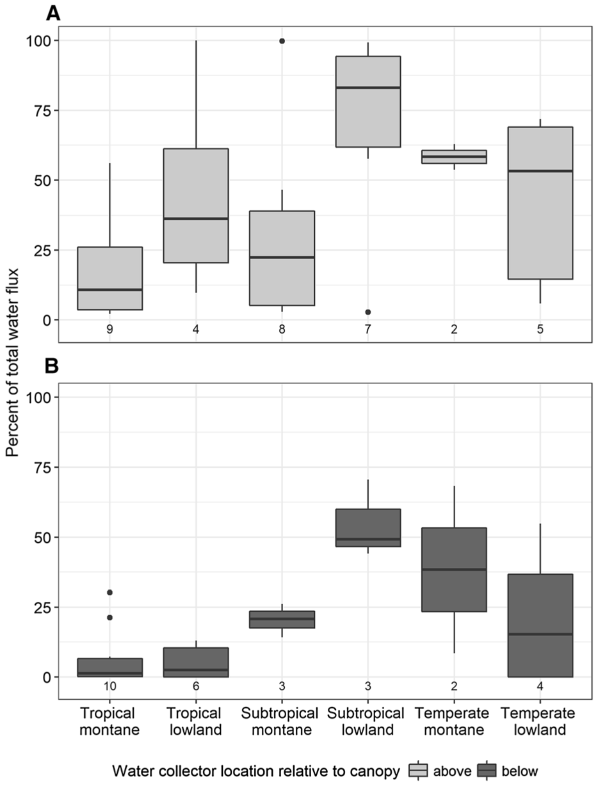

Figure 2. Fog water inputs to montane (≥ 1000 m) and lowland (< 1000 m) forest, woodland, grassland, and desert ecosystems in tropical (0–23.5°), subtropical (23.5–35°), and temperate (35–66°) regions where fog was measured for nine months or more. **A** Fog water fluxes to artificial collectors installed above vegetation canopies or in clearings and displayed as a percentage of total annual water input (rainfall + fog precipitation). **B** Fog water fluxes to forest soils as a percentage of total annual water input (rainfall + fog drip). Boxplots represent interquartile ranges (25th and 75th percentiles), horizontal bars denote median values, and whiskers sample minimum and maximum values. See Supplemental Material for a list of studies included.

Elements

Along with water, fog transports nutrients and pollutants incorporated into droplets during fog formation and/or washout (that is, the collision of particles with moving fog droplets). Sampling conducted around the world shows that chemical concentrations are often higher in fog as compared with rain (Weathers and others 1988; Figure 3) often due to the smaller size (Bator and Collett 1997) and lower liquid water content of fog droplets (Lovett and others 1982; Anderson and others 1999). In southern Chile (Weathers and Likens 1997; Weathers and others 2000), Hawai'i (Carrillo and others 2002), and Japan (Aikawa and others 2006) concentrations of nitrate (NO_3^-), ammonium (NH_4^+), and calcium (Ca^{2+}) in fog have been shown to be enhanced by more than 50-fold over those in rainwater. Further, Weathers and others (2000) have documented high concentrations of labile phosphorus (as phosphate) in coastal fog. Fog water also has distinct regional signatures that reflect the origin and trajectory of air masses (Gioda and others 2011, 2013). In coastal, near-coastal, and marine environments, such as Puerto Rico (Weathers and others 1988; Asbury and others 1994), Chiloé Island (Weathers and others 2000; Weathers Unpublished Data), and Hawai'i (Carrillo and others 2002), sea salt ions (sodium (Na^+) and chloride (Cl^-)) are the most prevalent in fog water, whereas in urban and industrial environments in the USA and Europe fog droplets often have low pH due to sulfuric and nitric acids (for example, Waldman and others 1982; Weathers and others 1986; Thalmann and others 2002; Aleksic and others 2009). In agricultural and arid areas, such as in southern China (Liu and others 2005) and Congo (Lacaux and others 1992), biomass burning and dust emissions contribute to high concentrations of NH_4^+, potassium (K^+), Ca^{2+}, and magnesium (Mg^{2+}) in fog.

That fog-borne chemistry is often more concentrated than rain means that fog can be a significant pathway of atmospheric deposition to ecosystems. For example, in the Appalachian Mountains, where fog frequencies are high during the summer season (June–September), fog is estimated to contribute 80–90%, 70–87%, and 90–95% of total (wet + dry + fog) SO_4^{2-}, H^+, and NH_4^+ deposition, respectively (Baumgardner and others 2003). Even when fog water inputs are quantitatively insignificant compared to rain, fog can be a major vector of nutrient and pollutant inputs to ecosystems (Weathers and others 2000; Ewing and others 2009; Nyaga and others 2015; Vandecar and others 2015)—a little fog can go a long way. The fate of these chemical inputs ultimately depends on the form in which the element is deposited as well as biological demand. Biologically active ions, such as NH_4^+, may be taken up by or leached from plant canopies (Templer and others 2015) depending on nutrient status, while biologically conservative ions including SO_4^{2-} and Na^+ are typically washed from the canopy and transferred to soils in throughfall (Weathers and others 2006).

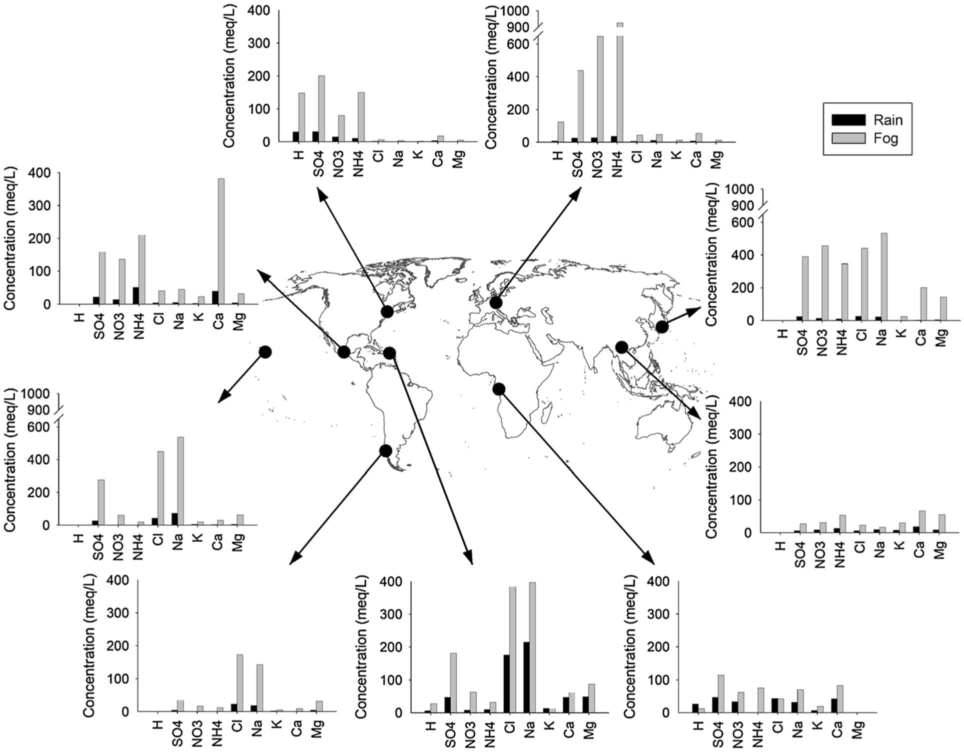

Figure 3. Chemical concentrations (µeq/L) of paired rain and fog water samples collected at sites influenced by natural (volcanic, marine, dust) and anthropogenic (agricultural, industrial, and urban) emissions sources. From top left clockwise, data from: Báez and others (1997), Aleksic and others (2009), Thalmann and others (2002), Liu and others (2005), Aikawa and others (2006), Lacaux and others (1992), Asbury and others (1994), Weathers (Unpublished Data), Carillo and others (2002).

Light

Fog presence also alters the light climate of ecosystems. Under foggy conditions, total shortwave radiation can be reduced by as much as 75% (Ritter and others 2009). Because of the resultant reduction in energy at the surface, the presence of fog also decreases upward longwave fluxes (Klemm and others 2006). Downwelling longwave radiation, however, can be enhanced by up to 15% (Brant and others Unpublished Data). In addition, fog increases the proportion of diffuse to direct radiation, modifying the intensity, duration, and quality of light reaching vegetation canopies. Enhanced diffuse radiation reduces peaks in maximum sunlight and dampens temporal variations in the supply of photosynthetically active radiation (PAR; Johnson and Smith 2006), but this also leads to greater PAR penetration into deep forest canopies (Still and others 2009) that in turn can enhance photosynthesis of lower canopy leaves and understory plants (Gu and others 2003; Santiago and Dawson 2014). During fog immersion, changes in the amount of blue and red light as well as spectral band ratios have also been measured (Reinhardt and others 2010).

Fog and the Maintenance of Ecosystems

How does fog impact—contribute to or detract from—the maintenance of ecosystems? On the one hand, fog resource subsidies can extend or sustain ecosystem function where processes would otherwise slow or cease due to water deficits or low/lack of elemental inputs (Jacobson and others 2015). On the other hand, ecosystem processes may be slowed or even impaired where fog inputs promote water saturation or deliver excess pollutants or toxic elements (Weathers and others 1986; Lawson and others 2003; Weiss-Penzias and others 2012). What is clear is that fog modulates the manner and magnitude of the coupling between the atmosphere, vegetation, and soils. In the case of animals, some of the best-known examples are from the Namib Desert, where beetles and microbial communities have adapted in charismatic ways to capture fog water for consumption (Seely 1979; Parker and Lawrence 2001; Nørgaard and Dacke

2010; Warren-Rhodes and others 2013): some of the most notable are Darkling beetle hand-standing and burm-building techniques to enhance fog water capture in this hyper-arid desert (for example, Nørgaard and Dacke 2010).

Crown Wetting

Looking up from the canopy, fog events that do not produce throughfall sustain hydrological connections between tree crowns and the atmosphere. Early fog researchers suggested that fogginess and associated crown wetting could reduce evapotranspiration, and, in turn, carbon (Grubb and Whitmore 1966) or nutrient uptake (Odum and Pigeon 1970) by trees. However, contrary to these hypotheses, recent work in forested ecosystems indicates that crown wetting events can enhance leaf water potential above that expected from soil water availability alone, functionally decoupling tree canopies from soil water supplies (Burgess and Dawson 2004; Simonin and others 2009; Gotsch and others 2014, Dawson and Goldsmith 2018; Berry and others 2018). Further, crown wetting suppresses transpiration and improves leaf hydration (Alvarado-Barrientos and others 2014), extending the time available for foliar fog water (and nutrient) uptake (Limm and others 2009; Goldsmith and others 2013). Thus, fog subsidies may not just allow, but actually enhance, above- and below-ground productivity and carbon sequestration during water-limited periods (Williams and others 2008; Ritter and others 2009; Simonin and others 2009; Carbone and others 2013; Eller and others 2013; Emery 2016).

Looking down through the forest canopy, fog droplets that drip from trees or run down stems increase surface soil moisture (Li and others 2018; Poca and others 2018), providing water for plant uptake and transpiration (Dawson 1998; Ewing and others 2009). Depending on overall precipitation regime and soil water content, added soil moisture may suppress (Chang and others 2008) or stimulate (Carbone and others 2011, 2013) soil respiration. These water inputs are often not evenly distributed over horizontal space, as is the case in landscapes where structural (for example, forest-grass boundaries) and functional (for example, slopes) edges lead to elevated fog inputs (Weathers and others 1992, 1995, 2000). In coastal California, Ewing and others (2009) documented an exponential decline in fog drip along a redwood forest edge-to-interior gradient that was mirrored by similar declines in soil moisture, leaf area, litterfall, fine root production, and soil organic matter accumulation. In hyper-arid deserts such as the Namib, fog inputs to soil are critical to the landscape-scale sustenance of hypolithic cyanobacterial communities (Warren-Rhodes and others 2013) and to decomposition dynamics (Jacobson and others 2015; Evans and others 2018). Jacobson and others (2015) found that within minutes of wetting, fog activated fungal growth on the litter of the Namib dune grass *Stipagrostis sabulicola*, with implications for desert food webs and biogeochemical cycling. Thus, from the tallest forest trees to the smallest desert rocks, in the absence of rain, fog may well act to sustain ''normal'' tree (microbial) functions at different points in the landscape.

By intercepting and routing water to soils during dry periods, canopy dominants—or rock surfaces—may well facilitate understory or nearby plant growth (Warren-Rhodes and others 2013; Baguskas and others 2016). Using hydrogen isotopes to trace water inputs and use in a California redwood forest, Dawson (1998) estimated that 6–100% of the water used by herbs and shrubs growing below *Sequoia sempervirens* was obtained through fog drip inputs to the forest floor. Regeneration in rain forest islands has also been linked to spatial patterns of fog input (Rigg and others 2002; Del-Val and others 2006; Stanton and others 2014). In coastal Chile, seedling and sapling abundance were significantly greater at windward fog-receiving than leeward edges, whereas tree mortality exhibited the opposite pattern, suggesting an advancing regeneration front in the direction of fog input (Del-Val and others 2006). The potential for saplings to benefit more from dry-season, fog-mediated improvements in water status than adult trees may explain such patterns (Baguskas and others 2016). Whether through changes in nutrient or carbon cycling it is indeed plausible that fog influences species' distributions, but beyond the role of changing water dynamics, it is unclear how. These studies highlight the need for closer examination of plant-plant interactions and functions occurring below trees, plants, and rocks in fog-enshrouded ecosystems, and raise new questions about fog's role in biogeochemical cycling.

Elemental Interactions

It is well established that fog can deliver essential limiting nutrients, such as N and P (for example, Weathers and other 2000, Nyaga and others 2015; Vandecar and others 2015), as well as pollutants (for example, Masson and others 2015) to soils and vegetation. The effects of fog pollutant inputs on plant anatomy and physiology were demonstrated beginning in the mid- to late twentieth century. Misting experiments showed that acid fog had the potential to directly alter leaf epicuticular wax structure and chemistry (Percy and others 1992) and to indirectly influence leaf nutrient status via foliar leaching of cations and other plant compounds (for example, Scherbatskoy and Klein 1983; Figure 1). Foliar nutrient leaching (for example, membrane-associated Ca) has since been linked to decreased stomatal conductance (Borer and others 2005) and leaf number (Shigihara and others 2008) and increased leaf abscission (Shigihara and others 2008) in seedling experiments, suggesting the potential for associated positive or negative effects on CO_2 assimilation and/or decomposition.

In contrast to the early focus on fog pollutants, only relatively recently have tracer studies demonstrated that nutrients (for example, glycine, NO_3^-, NH_4^+) deposited to fog-wetted canopies can be absorbed directly through plant foliage (Lai and others 2007; Nyaga and others 2015)—enhancing leaf-level photosynthesis (Templer and others 2015)—and transported to the roots (Lai and others 2007). Foliar nutrient uptake has also been inferred through correlative measures. For example, in a study of atmospheric bromeliads growing on coastal desert sands, positive correlations between fog N input and plant N content and fog P input and plant growth rate were detected (González and others 2011). Although the relative importance of direct foliar vs. indirect root fog-borne nutrient uptake remains elusive (Templer and others 2015), evidence from several fog-affected ecosystems now indicates that the supply of limiting nutrients in fog waters can sustain plant growth in resource-poor environments. Fog can also be an important vector of carbon—organic and elemental (Collett and others 2008)——to ecosystems, although the effects of these added carbon inputs to ecosystem function remain unknown.

Light Scattering and Absorption

The influence of fog on the light environment has implications for critical ecosystem processes, including primary productivity, water cycling, and nitrogen deposition (Figure 1). Fog reduces the amount of total and photosynthetically active radiation received by plants (Letts and Mulligan 2005; Brant and others Unpublished Data), but the overall effects on carbon gain appear to be species- or forest-dependent (Johnson and Smith 2008). For many woody species, these lower light intensities are often at or below the light compensation point for photosynthesis resulting in net C loss. However, a growing literature suggests that greater proportions of diffuse light under foggy skies can actually enhance understory as well as canopy-scale photosynthesis (Johnson and Smith 2006; Still and others 2009). The greater penetration and spatial homogenization of diffuse light in forest canopies, for example, is likely to increase the exposure of shade leaves to radiation that would otherwise be unavailable. Further fog-induced changes in the quality of incident light have been reported (Reinhardt and others 2010) although effects on photosynthesis remain undetermined. Through decreases in solar radiation inputs, vapor pressure deficit, and ambient air temperatures, fog may also serve to reduce drought stress among plants and microbial populations (Fischer and others 2009; Carbone and others 2013). Through such microenvironmental changes, fog events have been found to reduce tree transpiration rates by up to 30-fold (Ritter and others 2009) and in turn water-use efficiency (Johnson and Smith 2008). Finally, upon exposure to sunlight, organic N compounds dissolved in fog droplets may be converted to inorganic N species (NO_3^-, NH_4^+, NO_x), increasing bioavailable N for deposition to ecosystems (Zhang and Anastasio 2003). The latter study highlights some of the hidden interactions among water, nutrient availability, and light that are likely to affect ecosystem processes in fog-influenced ecosystems.

Frontiers in fog Research

Fog as a vector and connector: Fog represents a critical nexus among atmosphere, biosphere, and hydrosphere, linking atmospheric, terrestrial, and marine ecosystems. Coastal fog is formed over the ocean as a result of temperature differences between air and water and then advected inland. As such, there are many ''mist'' opportunities to examine cross-system or boundary (Cadenasso and others 2003) influences on ecosystem function. How does ocean biogeochemistry, and productivity, in particular, influence the nature of near-coastal, terrestrial fog subsidies, for example? Fog water has been shown to carry not only sea salt, but also nutrients (Weathers and others 2000), pollutants (Weiss-Penzias and others 2012), and microbes (Evans and others 2018) originating from biotic processing in marine systems, and delivered to adjacent terrestrial ecosystems. Thus, in some cases, the ocean may be ''feeding'' the forest (sensu Weathers and others 2000). In other cases, the ocean is sharing pollutants with adjacent terrestrial ecosystems via fog as a vector (Reyes-Rodríguez and others 2009). In another recent example, the ocean is the source of microbes and pathogens whereby fog not only moves biological materials from ocean to air to land (Dueker and others 2011, 2012) in a direction that we are unused to considering but does so while possibly providing suitable habitat for microbes to prosper (Evans and others 2018)—in essence, "seeding" terrestrial ecosystems. The fog system is a dynamic connector across earth system boundaries; many mist connections have yet to be explored, however.

The controls and consequences of atmospheric microbial dynamics (aerobiology) represent one outstanding, fundamental knowledge gap in understanding these cross-system dynamics. Environmentally beneficial and pathogenic microbes can travel short to long distances adhered to particles in tiny fog droplets before eventual deposition to terrestrial ecosystems; an emerging literature suggests that microorganisms differ in how they are transported and deposited (Reche and others 2018). Bacteria are often the dominant microorganism in fog water (Hu and others 2018) and there is evidence that fog waters protect and sustain bacterial communities from harsh conditions following aerosolization by providing water and nutrients and via increased settling rates (Dueker and others 2012; Amato and others 2017).

Even as we begin to understand and quantify the relative importance of fog subsidies and fluxes to ecological systems, and the details of how fog affects ecosystem processes, global change is altering the nature of fog itself and the ecosystems that have evolved to capture this ephemeral resource. Daily and seasonal timing of fog events, as well as fog immersion time (that is, duration and frequency), governs the volume of fog water inputs to ecosystems; they also affect the chemistry and biology of fog. Yet there are only a handful of examples where spatial and temporal data for fog frequency and immersion are available; it is a crucial data gap that may be filled, in part, using remote sensing technology (for example, Cermak 2012). Changes in frequency and distribution of fog for some regions of the world have been inferred using general circulation models, meteorological data, climate proxies, and observations of cloud ceiling height. In fact, there are now several regions where fog frequency is on the decline (LaDochy 2005; Vautard and others 2009; Johnstone and Dawson 2010; Baldocchi and Waller 2014; Williams and others 2015; Gautam and Singh 2018), with potentially important effects on agroecosystems and forests. A comparison of clear-sky and foggy conditions showed that fog contributes to decreased canopy-scale water loss and canopy-level photosynthesis, but an overall increase in water-use efficiency, on strawberry farms (Baguskas and others 2018). In another study conducted in a major fruit and nut growing region, foggy days had lower mean solar radiation load, lower maximum, and lower mean temperatures than clear days contributing to the winter chill required by trees for high productivity (Baldocchi and Waller 2014). Therefore, declining fog could affect crop yields by reducing winter chill and/or plant-water-use efficiency. In regions where fog events buffer native ecosystems against periodic drought, presumably fog reductions will result in increased evapotranspiration rates and vulnerability to drought stress (Johnstone and Dawson 2010). Of crucial importance, therefore, is quantification of immersion time, distribution, and frequency of fog for fog-dominated systems, as well as their changes over time.

Whether the influence is direct or indirect, fog has the potential to control ecosystem function in fog-enshrouded ecosystems. Fog can be a resource, pollutant, and master driver variable in the fixation of carbon, decomposition, hydrological fluxes and dynamics, and overall biogeochemistry of terrestrial systems. Fog is a vector and connector for the biotic and abiotic movement and dynamics across major earth systems. Although fog-dominated systems may cover a small proportion of the Earth's surface (crude estimates range from < 10–30% of the Earth's surface), they are located in coastal and montane regions that support high biodiversity, as well an increasing human population, and/or are surrounded by highly polluted aquatic and atmospheric systems: They are hot spots of Earth ecosystem dynamics, but much research remains to be done to reveal the ecosystem consequences of changing fog frequency and distribution. Further, because changes—differences, in fact—in air temperature in large part control fog formation, climate change scenarios which include warming will have an important role in altering fog occurrence on a global scale. Finally, understanding the feedback dynamics among and between marine, terrestrial, and fog (atmospheric) systems are crucial for being able to predict and unravel cross-system, fog dynamics (Figure 1). Remote sensing tools combined with in situ ecosystem process measurements, and models, made across fog-enshrouded ecosystems are near-term research needs and frontiers.

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