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Roots and fruits: Highlighting the BIPOC Botanists legacy

Viewpoint

Water from the Air: The Role of Foliar Uptake in Science, Education, and Environmental Policy

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ABSTRACT

The traditional representation of the water cycle often overlooks the active role of vegetation in absorbing atmospheric moisture, rendering it incomplete. This oversight is particularly evident in the classic soil–plant–atmosphere continuum (SPAC), which describes a unidirectional water flow from soil to atmosphere. However, increasing evidence highlights reverse fluxes, such as the downward movement of water from the atmosphere to plants and potentially into the soil. One key mechanism enabling this is foliar water uptake (FWU), through which leaves directly absorb moisture from sources like fog, facilitating rapid hydration and internal redistribution of water. Despite growing documentation in eco-physiological research, FWU remains largely absent from broader scientific discourse, public policy, education, and ecosystem management frameworks. Neglecting FWU and fog as hydrological inputs limits our understanding of water dynamics in ecosystems, especially under climate change scenarios that alter fog and dew formation patterns. This viewpoint emphasizes the urgency of integrating FWU into ecological models, science education, and environmental decision-making. By rethinking the water cycle through this lens, we highlight a transformative pathway to enhance conservation strategies, understanding plant functional traits related to climate change, and the science–policy–society interface.

Keywords: Decision-making; Ecohydrology; Fog; Incomplete Water Cycle.

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Introduction

The traditional representation of the water cycle is incomplete when it overlooks the role of vegetation in absorbing alternative atmospheric water sources. The well-established soil–plant–atmosphere continuum (SPAC), which describes a unidirectional flow of water from the soil through plants to the atmosphere, fails to encompass the full range of hydrological processes observed in nature (Tyree & Zimmermann, 2002). The water cycle is far more complex, dynamic, and can exhibit reverse fluxes, including the downward movement of water from the atmosphere to the plant, and eventually to the soil (Burgess & Dawson, 2004; Eller *et al.*, 2013; Chin *et al.*, 2023).

One of the physiological traits enabling this reverse water flux is foliar water uptake (FWU), by which leaves directly absorb atmospheric moisture, such as fog, resulting in rapid hydration of foliar tissues and subsequent water transport to internal tissues, including stems and roots (Berry *et al.*, 2019). Although this process has been extensively documented in the ecophysiological literature over the past decade (Limm *et al.*, 2009; Schreel & Steppe, 2020; Li *et al.*, 2023a), it remains largely underrecognized by researchers from other disciplines, educators, decision-makers, and broader sectors of civil society.

Neglecting FWU has direct implications for how ecosystems are understood and managed. Fog represents an often-overlooked pathway for water input in hydrological models (Matos *et al.*, 2022), despite its critical role in various biomes, especially those experiencing water stress or heavily influenced by atmospheric condensation. Recognizing and validating the hydrological importance of both fog and FWU is essential for advancing ecological understanding of natural systems, particularly in the context of climate change (Bittencourt *et al.*, 2019; Henschel *et al.*, 2019).

Climate change models project a global increase in air temperatures and vapor pressure deficits (IPCC, 2021), which in turn alter the conditions for fog, dew, and rainfall formation due to a decrease in relative humidity. Discussing this topic offers an opportunity to foster the transversality of scientific knowledge by promoting its integration into educational, conservation, and policy agendas. This article adopts a reflective and forward-looking perspective, highlighting not only scientific advances but also the silences and gaps that persist between knowledge production and its practical application. The aims of this viewpoint are to emphasize the overlooked role of foliar water uptake and fog in the hydrological cycle, advocating for a more complete understanding of water dynamics in ecosystems. It highlights the need to incorporate these processes into scientific, educational, and policy frameworks.

Foliar water uptake: what we know so far

Foliar water uptake (FWU) is a physiological trait through which some plants are capable of absorbing water directly from the atmosphere via their leaf tissues. This process is driven by water potential gradients between the atmosphere and the internal tissues of the plant. For FWU to occur, the atmospheric water potential must be higher (less negative) than that of the leaves, allowing for the passive movement of water from the atmosphere into plant tissues (Rundel, 1982; Eller *et al.*, 2015; Vesala *et al.*, 2017; Cernusak *et al.*, 2018).

During rainfall events, although atmospheric humidity increases, the primary hydration pathway in plants is through root water uptake. Rainwater infiltrates the soil, where it is readily absorbed by roots and transported to the leaves via the xylem. This upward flow of water occurs primarily when plants are transpiring, which is more intense under conditions of low atmospheric water potential. As water moves from the soil to the atmosphere through the plant, leaf water potential tends to increase, making leaf tissues less likely to absorb additional water from external sources (Passioura, 1982). Consequently, these conditions effectively inhibit or reduce FWU, in contrast to the special microclimatic situations, such as fog or dew presence, under which foliar uptake becomes more prominent (Breshears *et al.*, 2008).

Fog, on the other hand, represents a form of atmospheric precipitation characterized by high relative humidity, often without significant soil wetting (Bittencourt *et al.*, 2019). Under these conditions, leaf tissues generally maintain a lower (more negative) water potential compared to the surrounding atmosphere, creating the gradient necessary for the direct uptake of water through the leaves.

Once this gradient is established, water can penetrate leaf tissues through various anatomical pathways, including trichomes, hydathodes, stomata, emergences, and directly through the epidermis and phyllosphere (Rosado & Almeida, 2020; Guzmán-Delgado *et al.*, 2021; Roth-Nebelsick *et al.*, 2023). However, the efficiency of FWU is modulated by multiple structural barriers. The composition and structure of the cuticle play a crucial role: cuticles with a higher proportion of hydrophobic compounds, such as n-alkanes, present greater resistance to water entry, whereas those enriched with compounds containing hydroxyl groups tend to be more hydrophilic, facilitating water absorption (Fernández *et al.*, 2017; Boanares *et al.*, 2021). The composition of the cell walls also influences FWU capacity. Walls with higher pectin content exhibit greater porosity and enable faster water absorption, whereas cellulose-rich walls, although more rigid, can retain larger volumes of water but at slower absorption rates (Boanares *et al.*, 2019).

The absorption of water is further influenced by the presence and density of the indumentum on the leaf surface.

Trichomes and emergences can increase the surface area in contact with atmospheric water, serve as nucleation sites for fog droplets, and aid in their retention and subsequent absorption, especially when coated by hydrophilic cuticles (Schreel *et al.*, 2020; Pan *et al.*, 2021). However, in some species, high trichome densities may create hydrophobic surfaces, depending on the droplet contact angle with the leaf surface, thereby reducing absorption efficiency (Papierowska *et al.*, 2018). Structurally, differences in the presence and density of epicuticular wax crystals can also influence leaf-water interactions, commonly referred to as leaf wettability (Fernández & Khayet, 2015).

Beyond the mechanisms of water entry, the ability to store water within leaf tissues also influences FWU effectiveness. Some species exhibit slower absorption rates but store greater volumes of water compared to those that absorb rapidly (Boanares *et al.*, 2018). This higher storage capacity is associated with either specialized water-storage cells or a generally higher number of cells per leaf area, as water is primarily stored in the vacuoles of plant cells (Boanares *et al.*, 2018; Li *et al.*, 2023b).

The diversity of anatomical and ecological mechanisms involved in FWU underscores its importance as an underestimated yet widespread physiological strategy across global vegetation. In fact, over the past decades, increasing empirical evidence has confirmed that FWU is a physiological trait present across a broad range of taxonomic groups and ecological contexts (Berry *et al.*, 2019; Schreel & Steppe, 2020). These include major biomes such as tropical montane cloud forests, temperate seasonal forests, temperate rainforests, tropical rainforests, and woodland/shrubland ecosystems. Examples of specific ecosystems where FWU has been observed include *campos rupestres*, páramos, mangroves, and coastal redwood forests (Limm *et al.*, 2009; Boanares *et al.*, 2018; Santos Garcia *et al.*, 2022; Li *et al.*, 2023a). Thus, foliar water uptake possibly influences the distribution of plant species across different habitats by enabling them to survive conditions of low water availability in the soil, as observed for arid regions, steep slopes, or areas with high salinity (Schreel & Steppe, 2020).

The growing body of evidence from FWU across diverse biomes and plant taxa suggests that this process should not be viewed as an exception, but rather as a recurring component of adaptive strategies that enable plants to deal with variations in water availability in natural environments (Schreel & Steppe, 2020). Nevertheless, systematic mapping of FWU remains limited to a few taxonomic groups and regions, highlighting the need for broader investigations that integrate physiological, ecological, and phylogenetic analyses (Berry *et al.*, 2019).

Although FWU can provide important benefits for maintaining leaf turgor during drought and fog events, it is also associated with potential costs. Because FWU is a passive process that depends on water potential gradients (Eller *et al.*, 2015; Chin *et al.*, 2023; Rosado & Matos, 2025), leaves and twigs that are permeable to water uptake may also be more prone to water loss when atmospheric water potentials are more negative than those of the leaves. In such cases, species with high FWU capacity may experience greater transpirational water loss, becoming more dependent on frequent fog events to avoid desiccation. This duality highlights that FWU should not be interpreted solely as a beneficial trait, but rather as part of a broader spectrum of plant water-use strategies, in which high FWU capacity can trade off with greater vulnerability under conditions of high vapor pressure deficits or reduced fog incidence.

The water cycle beyond rainfall: an expanded perspective

The traditional water cycle describes the continuous movement of water within the Earth-atmosphere system, beginning with evaporation from surfaces such as oceans, rivers, and vegetation. The resulting water vapor rises, cools, and condenses into clouds, eventually precipitating as rain, snow, sleet, or hail. This precipitation then infiltrates the soil, recharges groundwater, or flows as surface runoff back into water bodies, completing the cycle (Oki & Kanae, 2006). However, this conventional model primarily emphasizes large-scale atmospheric processes, often neglecting alternative precipitation such as fog.

Fog is a meteorological phenomenon of considerable hydrological relevance, particularly in tropical and subtropical forests located at higher altitudes. Its formation can result from nocturnal cooling (leading to ground fog), the interaction between warm and cold air masses, or the development of low-lying clouds (Burgess & Dawson, 2004). Factors such as topography, air mass stability, wind direction, and relative humidity levels directly influence the frequency and intensity of these fog events (Money, 2000).

Several studies have shown that fog can account for 30 % to 60 % of the total precipitation in certain ecosystems (Dawson, 1998), contributing not only to water availability but also to plant nutrition (Fernández *et al.*, 2021). Fog further modulates microclimatic conditions by attenuating the atmospheric vapor pressure deficit (VPD), thereby suppressing evaporation and transpiration rates in vegetation (Juvik & Nullet 1995). A portion of the fog water may be intercepted by plant surfaces and redirected to the soil through stemflow (Hutley *et al.*, 1997) or directly absorbed by the leaves, representing an active mechanism of water uptake (Chin *et al.*, 2023).

Despite the ecological and hydrological importance of fog, its role as a direct water source for plant tissues remains underappreciated. Studies in tropical montane forests have reported that fog can contribute up to 60 % of the annual water input (Bruijnzeel & Proctor, 1995; Dawson, 1998). Under such conditions, FWU contributes directly to tissue hydration, the maintenance of water homeostasis, and the continuity of photosynthetic activity, particularly during periods of water limitation. However, traditional literature mostly describes the interception of fog by plant parts and the role of stemflow to ensure plant hydration, overlooking the possibility of direct foliar absorption. By failing to account for FWU, hydrological models may overestimate the amount of water returned to the atmosphere via evaporation and underestimate the water retention capacity of plants. Recognizing and incorporating the roles of FWU and fog into both scientific discourse and conservation practices is essential for a more accurate understanding of plant ecophysiology, ecosystem water balance, and the development of effective environmental management strategies.

The classical formulation of the hydrological niche segregation theory (Silvertown *et al.*, 2015) is largely focused on the partitioning of water within the soil, overlooking atmospheric inputs such as dew, fog, and light rainfall. More recently, it has been recognized that these sources, collectively referred to as "occult precipitation" (Rutter, 1975), can also be accessed by terrestrial-rooted plants through FWU. The inclusion of these atmospheric water sources expands the traditional two-layered model (surface and deep soil) by adding a third one, the atmospheric layer. This broader framework provides a more comprehensive understanding of water partitioning and species coexistence in ecosystems (Matos *et al.*, 2022).

Expanding this model to account for the use of atmospheric water resources by vascular plants with terrestrial roots enhances our ability to understand how different species share available water and how this influences their distribution, abundance, and coexistence in natural habitats. This approach is especially relevant in the face of climate change and land-use alterations, which are expected to modify water dynamics both in the soil and in the atmosphere, with direct consequences for hydrological niches and plant community composition (Matos *et al.*, 2022).

Relevance for conservation and ecological restoration

Recent studies indicate that the direct absorption of water and nutrients from the atmosphere can significantly enhance photosynthesis, growth, and overall plant survival (Eller *et al.*, 2013; Berry *et al.*, 2019; Weathers *et al.*, 2020). In addition, atmospheric inputs have important implications for ecosystem-scale water and carbon balances, influencing key functional processes across a range of natural environments (Binks *et al.*, 2019; Cavallaro *et al.*, 2020).

Foliar water uptake contributes substantially to plant water conservation by reducing transpiration losses and improving plant water status, particularly during the dry season, when fog often represents the primary source of precipitation. Fog has been proven essential for maintaining leaf hydration throughout both dry and wet seasons, reinforcing its functional role in ecosystems such as *campos rupestres* (Boanares *et al.*, 2020). Plants that absorb greater volumes of water, even at slower rates, exhibit improved photosynthetic performance, increased thermotolerance, reduced photoinhibition, and lower susceptibility to oxidative stress. The capacity to access atmospheric resources may also alter ecological interactions, such as competition and facilitation, among co-occurring species (Matos *et al.*, 2021).

Species capable of absorbing water directly through their leaves have greater opportunities to promote tissue hydration, especially in environments where hidden precipitation is frequent (Boanares *et al.*, 2019). However, projected reductions in fog frequency at specific regions and habitats may lead to the local extinction of species that depend on fog as a water source, with cascading effects on landscape structure and ecosystem services.

Understanding the ecological benefits provided by FWU and fog is essential for effective conservation and ecological restoration strategies. The successful conservation of a species depends on a detailed understanding of its ecological requirements, particularly those related to water availability. For species adapted to fog-prone environments, it is critical to consider this alternative water source in translocation efforts, ex situ cultivation, and reintroduction programs. Ignoring this factor may jeopardize the successful establishment of individuals in new or restored environments. Furthermore, this knowledge can inform species selection in restoration projects. Choosing species capable of efficiently absorbing water through their leaves, especially during drought periods, may enhance vegetation recovery and provide facilitative effects for more drought-sensitive species, thereby increasing the overall effectiveness and resilience of restoration initiatives.

The growing unpredictability of precipitation patterns, coupled with the intensification of extreme climatic events (IPCC, 2021), calls for new approaches to species selection in environmental management programs. In this context, recognizing FWU and the use of nonconventional atmospheric water sources, such as fog, emerges as a valuable criterion for identifying species that are more resilient to climate change. Integrating this knowledge into species selection processes represents a critical advancement for developing strategies that enhance the ecological and functional success of conservation and restoration efforts under shifting environmental conditions.

Many wetting events can promote foliar water uptake, including dew, mist, light rain, and fog (Breshears *et al.*, 2008; Limm *et al.*, 2009; Berry *et al.*, 2019). All these processes represent important pathways of non-rainfall water input into plant canopies. While we emphasize fog in our discussion due to the greater number of studies and stronger empirical basis available for this event (Gotsch *et al.*, 2014; Oliveira *et al.*, 2014), we acknowledge that FWU is not restricted to fog and can occur under different wetting conditions. Thus, fog should be interpreted as one among several wetting events that may contribute to FWU, even though it has received more attention in the literature (Dawson & Goldsmith, 2018). Considering climate change scenarios that project reductions in fog frequency and increases in vapor pressure deficit in tropical montane cloud forests (Alvarado-Barrientos *et al.,* 2015), species with high FWU capacity may be particularly vulnerable, not only because they rely strongly on fog to maintain leaf water balance, but also because other wetting events such as dew and light rain may also become less frequent or less effective under warmer and drier conditions.

Implications for education, science communication, and policy makers

Foliar water uptake represents an ecologically significant phenomenon that remains largely underexplored in educational settings. School curricula tend to present the water cycle in a simplified manner, focusing primarily on conventional processes such as evaporation, condensation, precipitation, and runoff, often neglecting the vital role vegetation plays in this cycle. This limited approach overlooks lesser-known yet equally important mechanisms, such as the ability of certain plants to absorb water directly from the atmosphere through their leaves. The absence of such content in science education not only restricts students' understanding of the complexity of natural systems but also misses an opportunity to connect scientific concepts to real-world ecological phenomena, such as plant traits to arid conditions or the role of fog-dependent ecosystems in biodiversity maintenance.

Integrating FWU into science education could transform how students perceive the interactions between plants and their environments. Rather than presenting the water cycle as a linear and uniform process, educators could highlight the diversity of biological strategies developed to access water resources: one striking example being the success of plant species thriving in fog-prone ecosystems, such as *campos rupestres*. This approach enriches scientific literacy while encouraging students to think critically about how life adapts to extreme environmental conditions, a topic of growing importance in the face of climate change.

Furthermore, raising awareness of FWU among science communicators and decision-makers can help bridge the gap between ecological research and environmental policy. By disseminating accurate and accessible information about this process and its relevance for plant resilience, ecosystem functioning, and climate change, FWU can be repositioned as a key concept in public discourse and conservation planning. Educational initiatives and outreach programs that incorporate FWU can contribute to more informed decision-making processes, particularly in regions where fog and occult precipitation are vital water sources. Ultimately, acknowledging and communicating the role of atmospheric water uptake in plant survival can foster broader societal support for conservation strategies that align with emerging ecological insights.

The study of foliar fog water uptake also presents a valuable opportunity for interdisciplinary learning and the recognition of traditional ecological knowledge. In many cultures, particularly in arid regions such as the Atacama Desert or island environments like the Canary Islands, local communities have long acknowledged the importance of fog as an alternative water source, developing techniques to harvest it (Fessehaye *et al.*, 2014). These empirical practices offer rich material for science education, fostering contextualized learning that connects academic knowledge with practical, culturally grounded solutions.

Bringing these traditional insights into the classroom can help educators promote a more holistic view of science, one that respects and integrates multiple ways of knowing. By connecting scientific explanations with community practices, students can better understand how diverse forms of knowledge contribute to addressing environmental challenges. This approach also highlights the relevance of ecological science to real-world issues and fosters a deeper appreciation of cultural diversity in environmental stewardship.

To make the topic more accessible and engaging, hands-on teaching strategies can be employed, for example, simple experiments measuring water absorption by leaves through weighing them before and after immersion in water or comparing the FWU capacity of plant species from different ecosystems. Such activities not only clarify abstract concepts but also spark curiosity and promote investigative thinking.

Integrating FWU with other disciplines can further enhance its educational impact. Geography lessons can explore the global distribution of fog-dependent ecosystems, while chemistry classes can examine the physical and chemical properties of water that enable atmospheric uptake. These cross-curricular connections demonstrate the interconnectedness of scientific fields and highlight the applicability of ecological knowledge in multiple contexts.

Integrating FWU into science education is more than the inclusion of a curious biological phenomenon; it represents a way to present science as a dynamic field in constant dialogue with nature and society. FWU is not solely a scientific topic; it also holds significant practical implications for public policy, water resource management, and climate-related traits. Ecological restoration plans often overlook the ability of certain species to absorb water directly through their leaves, which may compromise plant survival in areas with limited soil water availability. Including this knowledge in environmental education and in the training of technicians and land managers enhances understanding of the hydrological cycle's multiple dimensions, fostering more informed and locally appropriate actions.

Although foliar fertilization has long been explored in agriculture, the hydric dimension has not yet been fully considered. FWU has the potential to complement this practice, since the capacity of plants to absorb water directly through their leaves could significantly reduce overall water consumption, particularly if breeding programs focus on cultivars with such traits. In the agricultural sector, developing cultivars capable of FWU offers a promising strategy to reduce irrigation demands. Such traits would allow plants to hydrate efficiently from atmospheric water, such as in misting systems, without the need for soil saturation, optimizing water use and promoting more sustainable agricultural practices. FWU knowledge offers a valuable opportunity for collaboration with civil society organizations and community-based conservation movements. Non-governmental organizations, agricultural cooperatives, and traditional communities can serve as key partners in applying this understanding. The integration of scientific research with local knowledge can inform agroecological practices, agroforestry systems, and participatory reforestation efforts, highlighting species that are well-adapted to regional water regimes.

Among traditional and Indigenous communities, co-producing knowledge about adaptive strategies such as FWU can strengthen autonomous land management and support both water and food security. Recognizing the value of these strategies contributes not only to biodiversity conservation but also to the empowerment of local populations in the face of environmental change.

Opportunities and responsibilities

This article highlights the significance of FWU and so-called hidden sources of precipitation, particularly fog, as key components of ecosystem water balance, especially in water-limited environments. More than a topic of academic interest, FWU represents strategic knowledge that must be integrated into public policy, basic education, and actions led by civil society organizations (Figure 1).

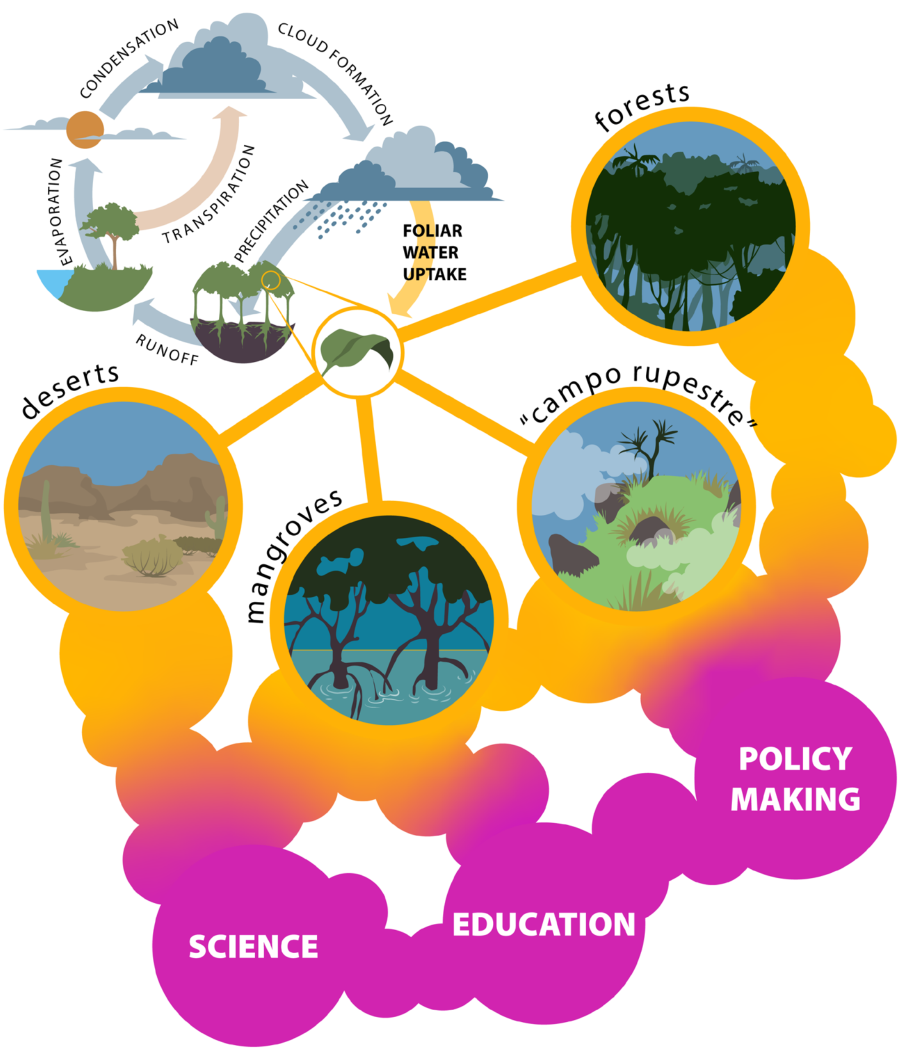

Figure 1. Conceptual representation of foliar water uptake (FWU) as an integral component of the water cycle. The illustration emphasizes how FWU operates in different ecosystems and underscores its relevance to scientific understanding, environmental education, and the formulation of public policies for climate-related traits and biodiversity conservation.t

In this context, I offer both a reflection and a call to action that is imperative that researchers actively engage in disseminating their findings beyond academic circles, ensuring that educators, policymakers, and communities are empowered to appropriate this knowledge and translate it into practical solutions. FWU provides compelling evidence that the conventional understanding of the water cycle, as typically taught, is incomplete. Incorporating this often overlooked but ecologically vital process represents both a conceptual and practical advance in how we understand and manage water resources.

Recognizing FWU as a tool for decision-making means acknowledging nature as part of the solution to contemporary socio-environmental challenges. Whether through public policies that are more attuned to ecological processes, integration into climate-related traits, or collaboration with grassroots conservation movements, FWU offers a promising pathway to enhancing both environmental and social resilience. Its application goes beyond improving water use efficiency: it represents a new way of thinking about the interface between science, policy, and society. A science that inspires, informs, and transforms, reminds us that some of the answers to global challenges may, quite literally, be in the air.

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Authors' Contributions

The author was responsible for the conception and writing of the manuscript.

Conflicts of Interest

The author declares no conflict of interest.

Data Availability

Not applicable.

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