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EXAMINING DYNAMIC ECOHYDROLOGY IN DRYLAND RIPARIAN FORESTS

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26.1 Introduction

The land areas bordering rivers and streams have high levels of dynamic root-zone water relative to the surrounding landscape and commonly support abundant woody and hydrophytic vegetation (1*,* *2*). As a result, these 'riparian zones' often support high biodiversity (3*,* *4*) and provide habitat to numerous aquatic and terrestrial species, as well as ecosystem services. More generally, riparian zones may be defined as terrestrial areas along wet or dry channels and within adjacent floodplains or terraces, comprising vegetation species assemblages, biomass accumulation, and phenology that are generally in tune with the historical patterns and timing of water availability. The notable distinction between these definitions is that the latter emphasizes that vegetation in riparian zones is variable in space and dynamic through time, and this spatiotemporal variability depends on both inherited factors (basin history) and fluctuating forcing conditions (climate-controls on water availability).

Riparian zones and the vegetation they support are a product of the sedimentary and geomorphic history of river basins, which is inherited from the geology and tectonics of a region (5*,* *6*). For example, riparian zones tend to broaden in lowlands, where there is sufficient accommodation space for alluvial sediment from uplands to spread out and deposit with enough topographic variation across the valley (e.g., (7)) to allow for subsequent colonization by terrestrial vegetation away from the high-energy environment near the active channel, producing high topographical variation. Within these heterogeneous floodplains, water table decline is slow enough within fine surface sediments to keep roots hydrated during seedling germination and growth (8*,* *9*). Once surfaces are colonized with land plants, water availability in deeper and coarser floodplain substrates is maintained by lateral hyporheic flow contributions from the active stream, shallow water tables, and moisture conditions close to field capacity within a mix of course and fine sediments that support plants rooted at different depths (1, 10, 11).

Superimposed on this inherited sedimentary and geomorphic template is the resounding influence of climate and its dynamic control on water availability through flood pulses (12), affecting vegetation distribution and density in riparian zones. Humid areas with strong precipitation gradients from mountains into lowlands and high runoff production through tributary networks tend to produce perennial streams. These are supported by substantial baseflow flowing through porous,

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coarse (post-glacial) alluvium that also contains a shallow alluvial aquifer extending laterally across the floodplain. In these well-watered environments, whether tropical or temperate, riparian zones may consist of closed-canopy evergreen forests or a mix of wet deciduous and conifer species in the overstory with smaller trees, shrubs, and grasses in the understory. These ecotypes are well adapted to an abundance of water to maintain consistent interannual growth, but these plants may struggle under drought conditions (13).

In dryland regions, where runoff from uplands is less uniform and consistent due to low precipitation delivered in brief and spatially restricted storms, river flow may be intermittent or ephemeral and the water table is typically well below the channel bed. Within these water-limited drylands, riparian zones may consist of open-canopy, dry deciduous woodlands comprising trees, shrubs, and grasses have numerous drought adaptations (14). These include deep root systems, strong stomatal control over transpiration (and resulting high water use efficiency), and the ability to derive water from numerous sources depending on hydroclimate conditions (15). Despite these adaptations to water scarcity, riparian trees are nevertheless vulnerable during severe and prolonged droughts, which may induce significant branch dieback and mortality in floodplain woodlands (16).

Regardless of the geography, riparian zones support assemblages of vegetation ranging from woodlands to shrubs to grasses, but the distribution of different plant functional types and their variable responses to drought stress are poorly understood, in particular threshold effects of environmental stressors (17–19). Closing these knowledge gaps is critical for us to detect and anticipate how changes to the climate system and anthropogenic pressures may further impact these critical ecosystems especially because they provide essential ecosystem services (e.g., shade, flood retention, agroforestry).

An essential feature of riparian woodlands is that they are dynamic environments in both space and time. This is especially true in drylands, where streamflow in channels is intermittent or ephemeral and where soils are mostly dry, except after brief, intense rainfall events or following annual flood pulses in snowmelt-driven basins. Riparian vegetation in drylands, which is the focus of this chapter, relies on water availability that may consist of both local and non-local controls (15, 20, 21). For example, shallowly rooted plants use soil moisture, which depends substantially on the local one-dimensional water balance between input precipitation and evapotranspiration. In contrast, deeply rooted dryland plants are adapted to use groundwater, which depends on non-local aquifer recharge from heavy rainfall or snowmelt that often occurs far from the rooting zone (e.g., in uplands and at mountain fronts) and with significant time lags (20, 22–24). Each of these water sources is very sensitive to these processes of climatic forcing, but the controls on each water source are asynchronous and heterogeneous in space, leading to unexpected responses within riparian woodlands for different expressions of climatic extremes.

In many parts of the world, riparian ecosystems are subject to increasing strain from multiple and often compounding environmental stressors (17, 19). Higher atmospheric evaporative demand (e.g., due to globally increasing air temperatures) and more variable precipitation regimes are pushing riparian biomes to their limits and beyond their adaptive capacity based on their inherent hydraulic traits (25). Additionally, riparian woodlands are threatened by human society, with increasing exploitation of river corridors for agriculture, industry, and forestry. Over the last few centuries, riparian woodlands around the world have been decimated, and the remaining riparian forests, even when protected by conservation, face challenges due to water diversions that alter flow regimes and groundwater overdraft (26). These pressures on riparian woodlands require creative approaches and new understanding to plan for a future that supports these biomes as resilient landscape features (27).

In this chapter, we focus on riparian woodlands in dryland environments, where the challenges to these vital ecosystems are particularly acute. We present: (a) methodological approaches for analyzing the interplay between water and vegetation in riparian zones along with examples from published research; and (b) some key challenges facing riparian vegetation in a future dominated by both climate change and anthropogenic impacts on the riparian zone.

26.2 Approaches to understanding ecohydrological relationships

26.2.1 Remote sensing for scaling up understanding of ecohydrology

Remote observations of riparian forests provide a detailed view into both seasonal phenology for mapped species and vegetation responses to hydroclimatic forcing over timescales spanning weeks to decades. Riparian vegetation has been historically difficult to map using remote sensing because riparian areas often form thin, nearly linear features across the landscape that are at, or are finer than, the spatial resolution of most spaceborne sensors (28). A large variety of sensors and techniques have been used to delineate riparian areas, such as manual classification of high spatial resolution imagery, the use of buffers around channels (28–30), automated channel mapping using Light Detection and Ranging (LiDAR) combined with remotely sensed vegetation cover and canopy height using machine learning (31, 32), and the satellite time series to identify riparian areas as seasonally stable areas with high fractional green vegetation cover (33). At very local scales, drones have become an important tool (34).

While a majority of this work has been conducted at local scales, cloud-based computing has recently been used to delineate riparian vegetation over areas as large as the American Southwest (35) and globally (36). For example, McMahon et al. (35) used random forest, combined with Normalized Difference Vegetation Index (NDVI) phenology and digital elevation data to automatically map riparian vegetation in California and Arizona using the same model, achieving high accuracy even when only phenological information was used. Rohde et al. (36) took advantage of the higher remotely sensed water content of riparian vegetation, high dry season evapotranspiration, and thermally cool canopies to map groundwater-dependent ecosystems globally in drylands.

Once riparian areas have been delineated, remote sensing can be used to quantify seasonal variation in evapotranspiration (37, 38), sensitivity to depth to groundwater (Figure 26.1), subsurface geology (23, 39), interannual variability in climate (40), and the presence of invasive species (41). For example, Kibler et al. (39) using Multiple Endmember Spectral Mixture Analysis (42) applied to Landsat time series, demonstrated significant forest mortality with an increase in depth to groundwater, which manifested as a wave of mortality propagating downstream that only stopped in an area where underlying geology forced water closer to the surface.

26.2.2 Tree rings and dendro-isotopes for local understanding of ecohydrology

Tree-ring methods are another approach to understanding the ecohydrology of riparian woodland ecosystems. The effects of climate change may differentially affect dryland riparian tree species based on their water-use strategies, drought susceptibility, and the extent of their groundwater dependence (15, 43). These influences are preserved in tree rings, both as an annual growth signal (ring width and radial growth) and in ratios of stable isotopes of carbon and oxygen in the rings' cellulose (dendro-isotopes), which indicate ecophysiological influences on drought stress and source water use (Figure 26.2). In this context, these indicators can be used singly or jointly to

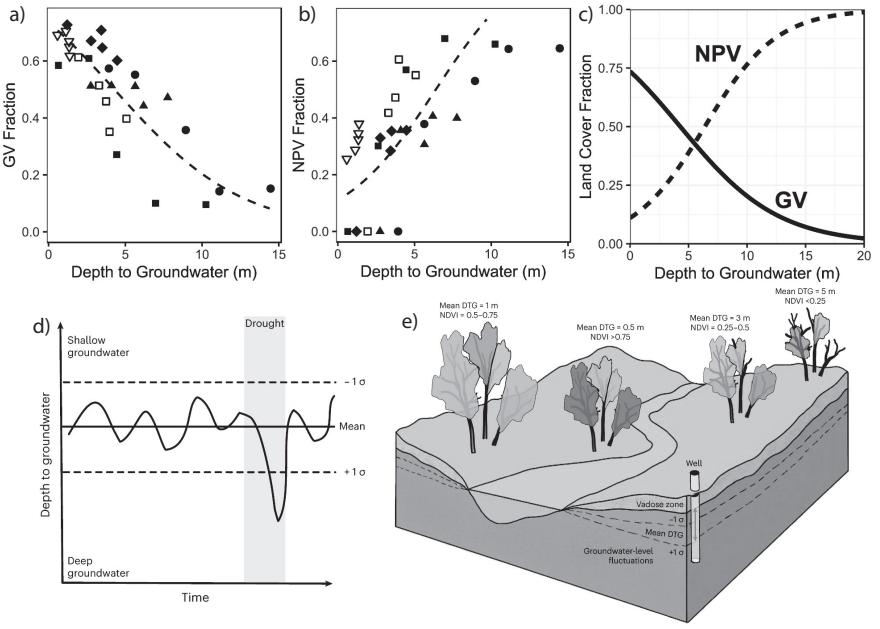

Figure 26.1 Examples of remote sensing methods applied to the analysis of plant water availability showing (a) decline in green vegetation fraction with water table depth at multiple sites; (b) an increase in non-photosynthetic vegetation fraction for the same sites; (c) opposite trends in land cover fraction with depth to groundwater (39); (d) water table depth in response to drought; and (e) links between greenness (NDVI) and groundwater level (40).

investigate historical patterns of drought response and source water use to infer future responses of dryland riparian woodlands to climate change and groundwater decline (44, 45).

Because riparian tree growth is limited by hydroclimatic factors, annual radial growth can be used as a measure of system performance and response to environmental stressors. For example, in riparian and floodplain systems, radial growth of poplars responds to drought stress resulting from changes in water table depth, precipitation, and streamflow because of the limitations that stomatal closure, leaf shedding, and branch sacrifice impose on carbon assimilation (16, 21, 46). Heat stress is another, and in some cases co-occurring, mechanism that limits photosynthesis and leads to reduced growth (47).

In conjunction with radial growth, carbon and oxygen stable isotopes in tree rings can be used to investigate historical patterns of drought stress and source water use of dryland riparian woodlands associated with climate variability and groundwater decline (e.g., (46)). Carbon isotope discrimination ($\Delta^{13}C$) derived from tree rings provides a retrospective measure of canopy-integrated leaf gas-exchange (48, 49), making it a useful tool to evaluate past drought responses of plants (50). Within the same tree-ring series, stable oxygen isotope ratios ($\delta^{18}O$) can be used to infer changes in source water use (51–53) and utilized in coordination with $\Delta^{13}C$ to investigate plant ecohydrologic responses (54–56). Retrospective dendro-isotopic analysis is less labor-intensive than sampling *in situ* water sources and plant xylem, and it has the advantage of registering decades and sometimes centuries of climate variability. Once tree cores are extracted, prepared, and measured, individual rings are sampled annually or subannually (e.g., earlywood and latewood), and alpha-cellulose is

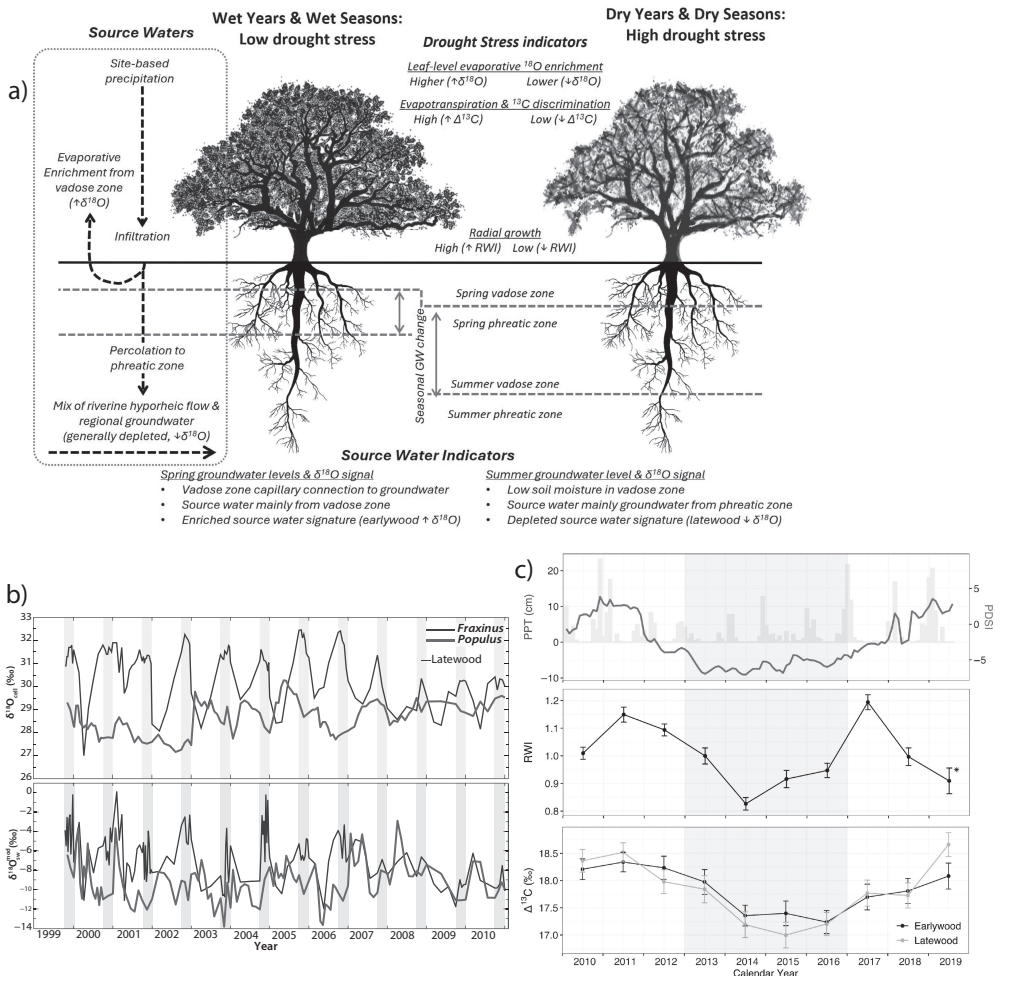

Figure 26.2 Examples using dendro-isotopic methods in riparian ecohydrology. (a) schematic showing key fluxes and stores in the water balance and relative responses of radial growth, isotopic ratios to different levels of drought stress; (b) subannual $\delta^{18}O$ before (upper) and after (lower) correcting by biochemical fractionation model within tree-ring cellulose for shallowly (Fraxinus) and deeply (Populus) rooted trees in a floodplain in SE France (63); (c) climate forcing of precipitation and Palmer Drought Severity Index (PDSI) during the peak of the historic 2013-2019 California drought (top), and response of radial growth (Ring Width Index, middle) and seasonal $\Delta^{13}C$ (bottom) in riparian Populus trees along the Santa Clara River, Southern CA (45).

isolated by chemical means for analysis in a gas source isotope ratio mass spectrometer to obtain isotopic ratios for oxygen and carbon (57).

The environmental processes that determine $\Delta^{13}C$ and $\delta^{18}O$ composition in tree-rings derive from different fractionation mechanisms. $\Delta^{13}C$ reflects the ratio of leaf internal CO_2 concentration to atmospheric CO_2 concentration (Ci/Ca), and the $\Delta^{13}C$ signal in tree rings is therefore determined by the balance between the rate of assimilation (i.e., photosynthesis) and leaf gas-exchange (i.e., stomatal conductance) over the growing season, where an increase in photosynthesis or a decrease

in stomatal conductance results in lower values of $\Delta^{13}C$, and vice versa. For vegetation in dryland systems that are not light-limited, stomatal conductance is the dominant influence on Ci/Ca, and decreases in $\Delta^{13}C$ are often attributed to stomatal closure in response to drought stress (58, 59) and/or root-zone water availability (44, 60). Temperature also influences $\Delta^{13}C$, such that under water-limited conditions, trees close stomata in response to warmer conditions to prevent water loss (61).

For $\delta^{18}O$, the leaf water pool signal that is imprinted in tree-ring cellulose reflects to a great extent the isotopic signal of source water, which does not fractionate during root water uptake; therefore, variation in $\delta^{18}O$ values over time can indicate a relative shift in tree water sources (62). Water in the vadose zone is subject to evaporative loss, making it isotopically enriched relative to groundwater (1, 62). This pattern allows for differentiation among plant water sources at different depths along the soil profile and can be useful for evaluating tree dependence on groundwater, which is typically depleted in $\delta^{18}O$, versus shallow moisture sources (63). This type of analysis is strengthened by converting isotopic ratios of oxygen from cellulose back to the original values of the source waters using an inverse biochemical fractionation model (64, 65), and even perhaps employing an endmember mixing model to identify the combination of waters used (66). In addition, $\delta^{18}O$ in plant tissues reflects changes in vapor pressure deficit because evaporative demand causes enrichment of leaf water that is also recorded in tree-ring cellulose (67). Consequently, enriched (higher) values of $\delta^{18}O$ are often associated with stomatal closure in response to greater evaporative demand (68, 69), yet this signal can be overpowered when changes in source water are considerable (65, 70).

26.2.3 Ecohydrological modeling for generalizing plant-water interactions under different forcings

Observational metrics from remote sensing at coarser resolutions and analysis of isotopic samples from individual trees and rings provide a limited view into how individual and cumulative precipitation events dynamically alter hydrological fluxes and stores, and ultimately control water availability to riparian and other plants. Furthermore, plants respond dynamically to changes in evaporative demand in the atmosphere and available root-zone water based on their water requirements, hydraulic and structural traits, and their adaptive plasticity in response to water limitation (43). The dynamics occur as river basins respond to rainstorms, evolving hydrological fluxes and stores, and thereby controlling water availability to riparian and other plants. Furthermore, plants respond dynamically to changes in evaporative demand in the atmosphere and available root-zone water based on their genetically determined water requirements with significant phenotypic variation.

The first component to represent in dryland ecohydrological models is climate forcing impacts on water fluxes and stores. While there are many existing models for quantifying watershed response (runoff) to rainfall inputs, for routing floods through river channels, and for examining groundwater—surface water interactions (11, 71–75), most existing approaches do not adequately represent the hydrology within dryland basins. In these environments, rainstorms may be intense but brief and flow paths are less predictable because soils dry out quickly due to high evaporative demand. Vegetation on slopes is sparse and soil development is limited, channels are often dry for much of the year (or more) and only flow after intense rainstorms. Within the riparian zone fluctuating water tables are typically well below riverbeds, such that ephemeral channel streamflow contributes water to the alluvial aquifer by focused recharge (76–78), creating feedbacks between infiltrating rainfall and rising groundwater levels (Figure 26.3b). Furthermore, there are few model frameworks that explicitly link infiltrated precipitation and resulting soil moisture

dynamics with lateral groundwater flow contributions from hyporheic exchange with the channel (79, 80), which dissipate with distance into the interior floodplain (Figure 26.3a). Representing all of these processes clearly in a riparian woodland context requires a model that captures the entire water balance, including all key hydrological fluxes and stores, and that is flexible enough to model high-frequency changes (e.g., daily) in rainfall and evaporative demand changes (e.g., daily) in rainfall and evaporative demand that occur stochastically and heterogeneously across the landscape to (e.g., (81–84)). Such a model can capture the influence of individual rainstorms on soil moisture, hillslope runoff, streamflow, groundwater recharge, and even exfiltration (return flow) explicitly across the model domain (Figure 26.3c). Therefore, water availability to plants at any point in the landscape and at different rooting depths can be resolved.

Next, it is important to characterize the seasonal cycles of growth and senescence that occur in deciduous woodlands. Dynamic vegetation changes will create direct feedbacks to/from the water balance through: (a) variations in the leaf area, which affect canopy interception of incoming rainfall; (b) seasonal cycles of root-water uptake within a deciduous growing season, which may

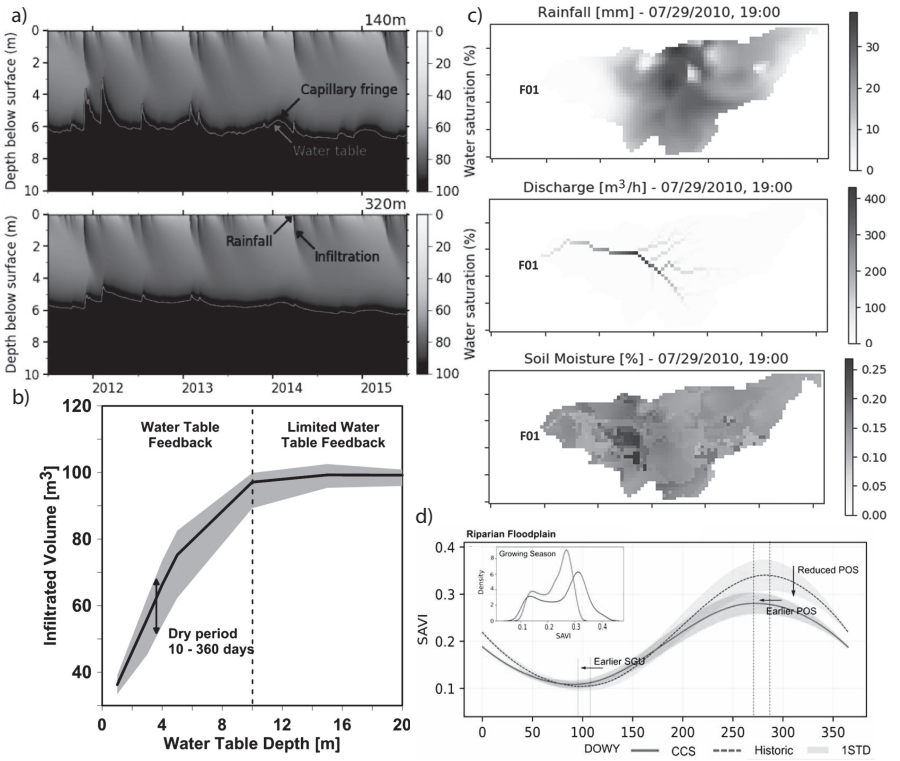

Figure 26.3 Examples of modeling used to assess water availability to riparian vegetation and plant responses over a season. (a) Modeled moisture profiles at 140 m and 320 m from the channel showing infiltrated rainfall and rising/falling water table (11); (b) cumulative infiltration streamflow feedbacks to water table depth (71); (c) output from DRYlands Partitioning hydrological model (DRYP), a one-dimensional hydrologic model, for Walnut Gulch basin, AZ (81) showing rainfall (top), emergent streamflow in ephemeral channels (middle), and soil moisture (bottom); (d) modeled riparian ecosystem greenness (Soil-Adjusted Vegetation Index (SAVI)) and seasonal phenology (Peak of Season) in response to climate forcing by increased temperature and groundwater depth (86).

differ by species and plant functional types (e.g., trees, shrubs, grasses) and which coincide with a stress response in plants when water becomes scarce; and (c) the removal of water from either the alluvial aquifer for groundwater-dependent, deeply rooted species or from the soil store for plants with shallow roots (85–88). Dynamic vegetation model components have been coupled to the water balance component in a spatially explicit way, supporting deeper learning about ecohydrological responses to water availability under different conditions of climate forcing (Figure 26.3d). The outputs of such modeling can be investigated from the perspective of different plant functional types, different parts of the landscape (slopes, floodplains), and for different climatic regimes driving rainfall and evaporative demand. Of course, this approach leaves out the challenge of how the landscape evolves regarding the succession of plant composition and biomes for distinct scenarios of climatic and anthropogenic forcing. This is an important area of future research.

26.3 Challenges for riparian vegetation

Existing published work highlights the potential risks to riparian forests around the globe, and especially in water-limited regions, where protections of these valuable biomes are limited (19, 36). As the climate evolves to a warmer atmosphere overall, evaporative demand will typically rise, leading to higher water loss in the riparian zone, irrespective of the water availability. Some plant species will be well adapted to modify their water use strategies to account for these changes, for example, through stomatal closure, thereby increasing water use efficiency, albeit with limits to maintain growth. Note that the discussion of changes to atmospheric CO_2 and its influence on biomass production is purposely omitted here. However, if climatic changes also alter water availability in different rooting zone depths due to reductions in local rainfall and soil moisture for shallow rooting species and/or through reductions in non-local groundwater recharge for deeply rooting species (20), even more efficient water use strategies may fail under extreme conditions and riparian plants will suffer dieback or even mortality (39, 45, 89–91). This setup may require restoration interventions (92–95) to maintain healthy dryland riparian ecosystems (36).

Here we have outlined several sets of methods that can be used as a suite to investigate past and future responses of riparian vegetation to climate forcing. Remote sensing, dendro-isotopes, and ecohydrological modeling can be used to identify trends and thresholds of vegetation response to climatic changes affecting atmospheric evaporative demand and/or root-zone water availability. They can be used in various settings, but are especially useful where strong seasonal phenology is associated with wetting and drying of the landscape. The methods may also be applied to address changes in riparian ecohydrology driven by anthropogenic pressures including dams/diversions and groundwater pumping, land conversion/urbanization, and agricultural water use.

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