Opinion

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Has water limited our imagination for aridland biogeochemistry?

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The classic ecological paradigm for deserts, that all processes are controlled by water availability, has limited our imagination for exploring other controls on the cycling of carbon and nutrients in aridland ecosystems. This review of recent studies identifies alternative mechanisms that challenge the idea that all soil processes in aridlands are proximately water-limited, and highlights the significance of photodegradation of aboveground litter and the overriding importance of spatial heterogeneity as a modulator of biotic responses to water availability. Aridlands currently occupy >30% of the terrestrial land surface and are expanding. It is therefore critical to incorporate these previously unappreciated mechanisms in our understanding of aridland biogeochemistry to mitigate the effects of desertification and global change.

Setting limits to water's control in aridlands

Immanuel Noy-Meir [1] established for aridland ecology that, "Deserts are water-controlled ecosystems with infrequent, discrete and largely unpredictable water inputs". As a result, the conceptual framework for aridlands has centred on the idea that the magnitude and fluxes of all ecosystem processes are limited by precipitation inputs, serving as the source of the oft-repeated phrase, 'water-limited' ecosystems. Simultaneously, the complexity of responses of belowground processes to a range of environmental constraints, and the importance of alternative controls on biogeochemical cycling in aridlands, has gone relatively unnoticed over time.

Independent of whether annual rainfall, water deficit, or a humidity index is used to define them, aridlands constitute a large fraction of terrestrial ecosystems, with estimates of $\leq$40% of the global land surface [2]. Clearly, water availability plays a central part in affecting many biotic processes in aridland ecosystems, and ultimately determines the limits of vegetation and soil development through its interaction with temperature and soil genesis [1]. Moreover, the ways in which water limits net primary production have been extensively explored in ecological studies. Mean annual precipitation, seasonality of rainfall, and the interaction of precipitation with temperature are key elements that correlate with various measures of aboveground net primary production (ANPP) [3–5].

The relationship between water availability and other ecosystem processes (as well as in particular soil processes) is much less clear. For example, microbial biomass and activity in aridlands is much lower on average relative to mesic or humid ecosystems [6]. However, several studies have demonstrated that litter decomposition [7,8], net nitrogen mineralization [9] and soil enzymatic activity [10] do not correlate with seasonal or annual precipitation. In addition, in hyper-arid environments, carbon turnover can continue in the absence of rainfall for extended periods of time [11], or during rainless seasons [12]. Negative or neutral responses to rainfall inputs suggests that belowground processes have unique controls which are not directly linked to positive precipitation–ANPP relationships [5,13,14].

Glossary

Afforestation: the intentional planting of woody vegetation (usually forest plantations) in areas in which the native vegetation is dominated by herbaceous species (e.g. grasslands). This term is also used for the planting of trees in areas which have experienced an extended period of time without their original forest vegetation (e.g. converted pastures or croplands).

Biogeochemical cycles: the flow of chemical elements and compounds between living organisms and the physical environment resulting in transformations between organic and inorganic forms of these elements.

Decomposition: the transformation of organic compounds to simpler compounds which eventually results in products of inorganic carbon (including CO_2), or inorganic nutrients.

Desertification: degradation of land in arid or semiarid regions caused by climatic changes, human influence, or both. This process includes increased soil erosion, reductions in plant cover and productive capacity.

Extracellular enzymes: enzymes of microbial origin which are exuded and operate in the soil solution, and which degrade large organic compounds into smaller units which can then be absorbed by soil bacteria and fungi.

Islands of fertility: concentrations of soil resources in vegetated patches which differ markedly from the surrounding bare soil areas and which are characteristic of aridland ecosystems.

***k* constant of decomposition**: a simple model of decomposition in which mass loss over time is estimated using a single exponential decay model: $\ln(M_t/M_o) = -kt$, where M_o is the initial mass, M_t is the mass remaining at time t, and k is the slope of this relationship. The k constant represents an integrated measure of decomposition over a given period of time.

Net primary production: the formation of organic compounds from atmospheric carbon dioxide, principally through photosynthesis minus the costs of plant respiration. Operationally defined as the accumulation of biomass in an area over a given unit of time (e.g. g/m^2/year).

Nitrogen mineralisation: the transformation of organic nitrogen to an inorganic form (ammonium or nitrate), modulated principally by soil bacteria and fungi.

Photodegradation: the breakdown of photodegradable molecules in organic matter due to the absorption of sunlight, including ultraviolet and visible radiation.

Soil organic matter: the organic-matter component of soil, including live microbial biomass, decomposed plant and animal residues, and stable recalcitrant carbon compounds (including humus).

Ultraviolet radiation: solar radiation with shorter wavelengths than visible light, in the range 280–400 nm.

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Figure 1. Imagining aridland ecoysystems. The semiarid Patagonian steppe, illustrating some of the key characteristics affecting biogeochemical processes in aridland ecosystems. Discontinuous vegetation cover of shrubs and grasses creates conditions of spatially heterogeneous resources and micro-environmental conditions. Clear skies with high incident solar radiation affect litter in areas of bare soil, which are subject to wind and water erosion, as well as standing dead material that are subject to photodegradative effects on organic carbon and thermal effects on organic nitrogen. Resource-rich patches of soil organic matter under shrubs and subterranean locations of high root biomass are centres of biotic activity and modulate the response to water when it is available. Photograph courtesy of A. Austin.

Several reviews that have advanced our understanding of the unique nature of biogeochemical cycles in aridlands have focused specifically on the pulsed nature of water events, the lag effects of these events on soil water storage, and the complex biotic response to these events [14–16]. It has been difficult, however, for ecosystem ecologists to escape the biased viewpoint that water must be the dominant, immediate limitation on all ecosystem processes. This misconception stems primarily from two sources. First is the exclusion of alternative abiotic controls in our conceptual models of aridland biogeochemistry. Second is the insistence that water is the singular dominant control on all biological activity. Here, I will review recent evidence suggesting that this bias has limited our imagination in terms of understanding other important controls on ecosystem processes in aridlands (Figure 1).

Abiotic controls have their day in the sun

Photodegradation and carbon turnover in aridlands

A puzzle for ecologists has been the unexplained high rates of aboveground litter decomposition in spite of low annual precipitation and microbial activity in aridlands. Recent work examining long-term (10-year) litter decomposition demonstrated that annual precipitation did not correlate with decomposition and nitrogen release in the grassland ecosystems of North America [17], or over multiple years in a single desert site [8]. This pattern supports what has been observed in short-term decomposition studies (Figure 2a), which have failed to demonstrate a relationship between aboveground decomposition and precipitation [7,18–21]. In addition, classic models of litter decomposition based on climate and litter quality [22] do not appear to explain rates of litter decay in arid ecosystems (Figure 2b).

Part of the explanation of this apparent discrepancy between models and data resides in the abiotic process of litter photodegradation. Photodegradation is the photochemical mineralization of organic matter caused by solar radiation (UV and visible wavelengths). Photodegradation leads to the breakdown of cell-wall polymers, releasing gaseous photoproducts of CO_2 and CO, as well as altering the chemistry of the remaining material [23–25]. In the Patagonian steppe, abiotic photodegradation without biotic interaction was demonstrated to be a dominant control on plant litter decomposition [13]. Other experiments showed that reduction in UV-B or total UV radiation decreased decomposition, particularly under dry conditions [23,26–29], and total solar radiation attenuation resulted in reduced mass loss in a range of desert and grassland ecosystems [21,23,30]. The quantitative importance of UV and visible light has now been quantified directly [24,25]. Abiotic photodegradation in aridlands could scale-up to substantial losses of CO_2 at the ecosystem scale, with annual estimates ranging from 1–4 g/m^2 [24] to 16 g/m^2 in semiarid grassland ecosystems [31].

Few studies have examined the importance of plant litter quality on photodegradation. These results have been mixed, with some studies demonstrating idiosyncratic

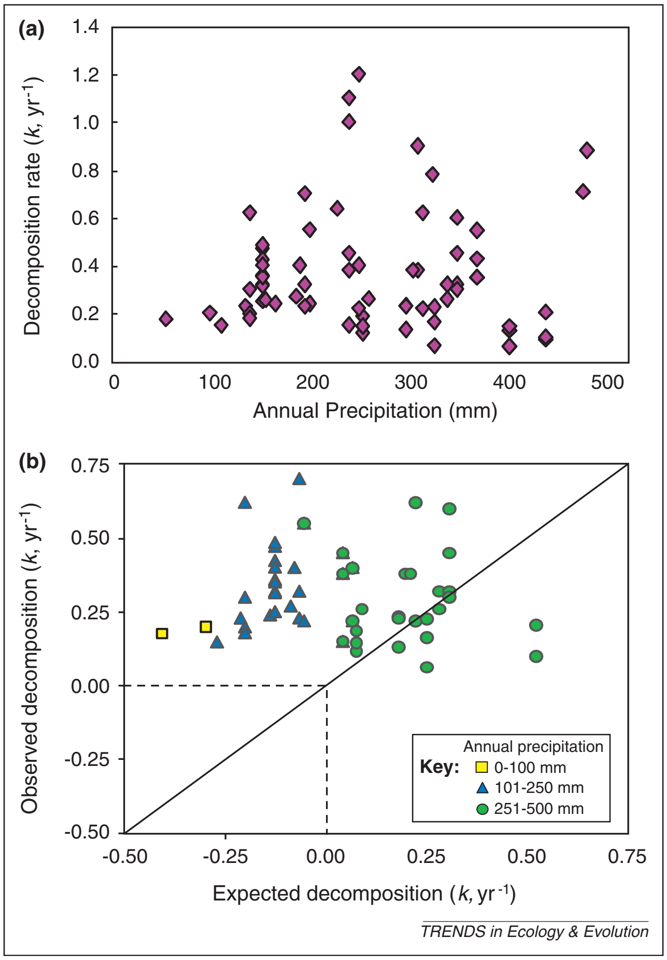

Figure 2. The conundrum of litter decomposition in aridlands. In contrast to studies which demonstrate positive correlations of aboveground net primary production (ANPP) with mean annual precipitation [3–5], aboveground litter decomposition does not demonstrate strong relationships among climate, litter quality and rates of mass loss. **(a)** Aboveground litter decomposition rates (k, yr^{-1}) do not correlate with annual precipitation. The decomposition constant k refers to the slope of the single exponential decay of mass loss over time, and represents an integrated measure of the potential rate of decomposition [13]. In a range of litter types from ecosystems with mean annual precipitation of <500 mm, rates of decomposition do not correlate with water availability, suggesting other factors have important effects on carbon turnover in these ecosystems. **(b)** Climate and litter quality do not predict decomposition in aridlands. The traditional model of the controls on litter decomposition in terrestrial ecosystems includes the key variables of actual evapotranspiration (AET) (which in aridland ecosystems essentially translates to annual precipitation) and lignin content [22]. When this model was applied to calculate expected rates of decomposition with data from aridland ecosystems, these studies consistently demonstrate rates of mass loss that were superior to the predicted values. Different coloured symbols and styles represent ranges of annual precipitation reported for each study. Data for both graphs are from [8,9,13,18,26,30,69,70]. Only studies and data using senescent litter and without solar radiation manipulation are shown.

relationships with lignin or C:N ratios and photodegradative losses [24,32]. Simultaneously, lignin has been identified as an important component of litter quality due to observed reductions in lignin content with solar radiation exposure [12,23,27]. Most recently, a study demonstrated a mechanistic role for lignin in determining photodegradation rates. Lignin, a well-known inhibitor of biotic decomposition in mesic and humid terrestrial ecosystems, acts as a facilitator of light absorption for photochemical reactions, resulting in mass loss [25]. The full nature of the interactions between the direct effects of photodegradation on plant litter and subsequent microbial decomposition has yet to be determined. However, the evidence from aridlands suggests that the effect of photodegradation on litter decomposability could be an underestimated (but significant) factor determining litter decomposition in a wide range of terrestrial ecosystems [25].

Alternative abiotic controls: heat and wind affect aridland biogeochemistry

There is evidence that abiotic controls play a part in nitrogen loss from aridland ecosystems. Abiotic formation of nitrogen gases in hot desert ecosystems has been recently identified as a potentially important flux of nitrogen at soil temperatures in excess of potential biological activity [33]. In addition, the accumulation of nitrate due to leaching below the rooting zone has been demonstrated to be a pool of nitrate that is inaccessible for biological uptake [34]. Accumulation of nitrogen can also occur in hyper-arid zones in the absence of biotic turnover from very low rates of deposition over extended rainless periods [35]. All of these identified fluxes are relatively small, but the cumulative long-term effect could be substantial, particularly if rates of biotic activity are severely inhibited due to extreme conditions of drought or low temperature.

The redistribution of soil due to wind and water erosion can have important consequences on soil processes in aridlands. There is evidence that human activity and climate change are contributing to the increased mobilization of these soils, particularly if biological soil crusts are disturbed [36]. Desert winds remove carbon and nutrients from aridlands but can also transfer microbial populations and extracellular enzymes locally and at larger distances. At a local scale, the direct effects of soil redistribution can impact topography, water redistribution and albedo, which can affect the landscape heterogeneity of soil processes [30,37]. In addition, there is evidence that soil redistribution could counterbalance the effects of photodegradation due to the burial of litter under shrub patches [30].

Neglecting the importance of abiotic processes in ecosystem ecology is understandable given that, when compared with biotic fluxes, abiotic processes are nearly always less significant. In aridlands, however, this underlying principle might not be valid to explain the short-term dynamics of the relevant biogeochemical fluxes. These studies bring to the forefront the relative importance of abiotic controls on ecosystem processes and the disproportionately large contribution of these unique abiotic fluxes to carbon and nutrient turnover in aridlands.

The biota responds to more than just water

Spatial heterogeneity and soil carbon and nitrogen cycling

It has been well established that 'islands of fertility' associated with vegetated patches have higher levels of microbial activity, nutrient mineralization, and carbon and nutrient pools relative to unvegetated patches [e.g. 10,38,39]. This 'patchiness' in resource availability appears to be principally driven by the discontinuous distribution of the vegetation [39,40], and suggests a fundamental role for spatial heterogeneity in modulating the ecosystem response to precipitation inputs (Figures 1 and 3). Principally, responses to precipitation pulses can be highly dependent upon the presence of labile organic matter [37,41], differences in soil texture (and their impact on soil water storage) [42], and environmental variation in microsites [10], all of which can be highly modified by spatial heterogeneity in aboveground plant cover.

The variability in response of belowground processes to pulsed water additions [15] suggests that the response of carbon and nitrogen turnover to moisture changes can be substantially modified by the spatial heterogeneity of vegetation. Indirect evidence for alternative factors modulating nitrogen turnover come from studies where net nitrogen transformations in unvegetated patches in the Patagonian steppe showed no response to variable seasonal or annual precipitation inputs [9,10,43], and net nitrogen mineralization with soil nitrate accumulation continued well into the dry season in vegetated patches in a North American desert [44]. Direct nitrogen limitation, as opposed to water availability, however, does not have much support as an alternative control because nitrogen additions alone have also shown little or no microbial response in semiarid ecosystems [13,45], and a much larger response to nitrogen addition is consistently observed in combination with labile carbon addition [13,46].

These studies suggest that the magnitude of the biotic response to changes in water availability (particularly for nitrogen turnover) can be highly dependent upon the concentration and quality of soil organic matter. Labile organic carbon in the soil under vegetated patches could be considered as a proximate limitation on microbial activity, determining the magnitude of the microbial response to changes in water availability [10,37,46]. As such, this heterogeneous pattern in resources creates a two-phase mosaic in which bare soil patches have almost no biotic activity and where abiotic controls dominate turnover. In contrast, if water is available, fluxes in vegetated patches can be on par with mesic or humid ecosystems, comparable with the dynamics of a tropical forest, with low soil organic matter and relatively high rates of turnover [14]. These alternating microsites with very different cycling rates and controls illustrate a much more complex biogeochemical framework than the idea of water as a singular limitation on all biotic activity.

High resistance: fungi and their enzymes

Another explanation for the lack of correlation between water availability on soil biotic activity is due to the differences in water use among trophic groups and the resistance of microorganisms to extended dry conditions. Many microorganisms in arid ecosystems can remain active far beyond the wilting point of most plants [47], and soil biological crusts have a rapid response and recovery after extended drought [14,36]. In addition, there appears to be particular mechanisms which lend an advantage for maintaining rates of microbial activity in spite of low water availability. Several authors have suggested that the persistence of carbon-degrading enzymes and, in particular, phenol-oxidases, provides the possibility of rapid turnover of soil organic matter given a window of favourable climatic conditions [14,21,48]. Soil enzymatic activity in the dry valleys of Antarctica had no response to changes in moisture and temperature variations, and the microbial community appears to be stable and unresponsive [19,49]. In addition, direct evidence of the stabilization of oxidative enzymes in alkaline desert soils [48], even after autoclaving, and a large pool of potentially hydrolysable cellulase enzymes in deserts [50], support the idea that microbial activity might not be limited by the biosynthesis of extracellular soil enzymes.

The ubiquitous presence of these enzymes in the soil as well as their persistence and resistance to environmental change might provide an advantage for the rapid turnover of soil organic matter in aridland ecosystems in spite of long periods of unfavourable conditions. The persistence of oxidative enzymes might be due to the abundance of fungal groups [14], which have been shown recently to resist long-term drought better than their bacterial counterparts [51]. It would be reasonable to imagine that the adaptation of microbial communities under arid conditions, together with the evidence of photodegradative carbon losses from solar radiation, explain why the connection between water-controlled net primary production inputs and belowground microbial activity is more tenuous than we have previously assumed [13,14].

Taken together, the interaction of abiotic controls, which are largely independent of water availability, and the important mechanisms that modulate the response of soil processes to water input suggests an integrated model for understanding litter decomposition in aridlands (Figure 3).

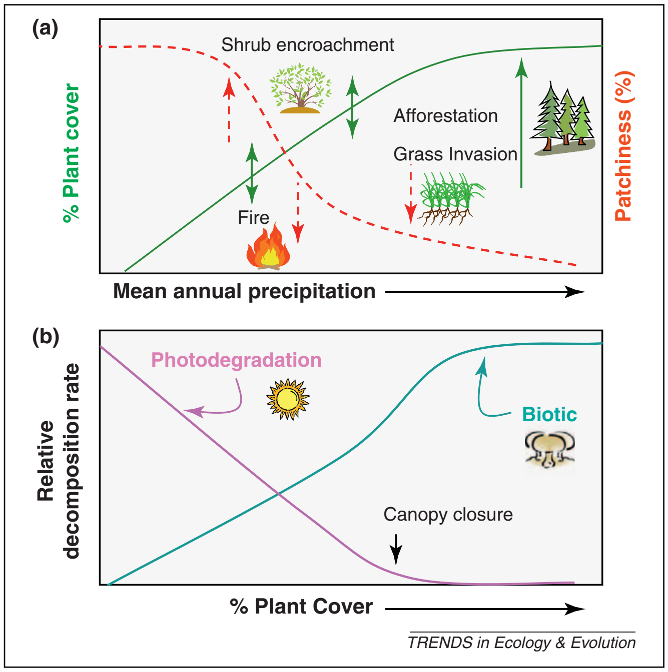

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Figure 3. The mix of abiotic and biotic controls on ecosystem processes in aridlands. A conceptual framework for the key controls on aboveground litter decomposition in aridlands where: **(a)** changes in water input (mean annual precipitation) directly modulate net primary productivity and biomass [4], creating a co-varying matrix of increasing water availability and simultaneously degree of plant cover (green line) and spatial heterogeneity (red dashed line). Changes resulting from human activity such as afforestation and fire frequency (indicated by red and green arrows, respectively) affect plant cover or patchiness at a given level of precipitation. **(b)** The consequences of changes in plant cover for litter decomposition will be determined primarily by the interaction of abiotic and biotic controls. The exposure to solar radiation in standing dead material and litter is determined by plant cover, and decreases linearly with increased plant biomass. As rainfall increases, the direct effects of water availability increase biotic decomposition coupled with the elimination of photodegradation as a factor when canopy closure occurs. As a result of the interactive effects of photodegradation and biotic decomposition, litter decomposition might not vary across with increasing precipitation in the range of aridland ecosystems.

The direct effect of water input on ecosystem processes will determine plant biomass and productivity [5], whereas indirect effects from changes in plant cover and spatial heterogeneity will determine the relative importance of abiotic controls and biotically driven processes.

Global change and extending our imagination

Aridlands continue to be among the terrestrial ecosystems most profoundly transformed for agricultural exploitation and domestic grazing [2]. Of particular current concern is the risk of increased aridity from climate change and its feedback to increased desertification from land degradation due to unsound management practices [40,52]. As a result, our need to understand the mechanistic controls on belowground processes in aridland ecosystems is particularly relevant in this context of human impact.

There are several human-induced changes in aridland ecosystems that will probably alter the importance of abiotic controls on fluxes of carbon and nitrogen, and the net effect of precipitation on soil processes through changes in plant cover and biomass (Figure 3a). Seasonal shifts in precipitation due to climate change, grazing effects, changes in fire frequencies, and the introduction of non-native life forms are associated with changes in the aboveground spatial distribution of vegetation, particularly through woody shrub encroachment, 'afforestation' (the intentional planting of trees in areas with no previous woody vegetation) and grass invasions. In cases where a novel life form is introduced which then becomes a dominant component of the vegetation, there can be impacts on carbon and nitrogen pools and transformations as well as the spatial heterogeneity of plant cover (Figure 3a).

Woody shrub encroachment due to grazing and other human activity and afforestation can considerably affect the relationship between woody and herbaceous vegetative cover, with positive and negative consequences for biogeochemical cycles. Increases in carbon and nitrogen pools have been observed [39,53,54], as well as climate-dependent declines in belowground pools [55]. The impact on ecosystem processes is also variable with increased soil respiration due to increased shrub cover [38], as well as decreased carbon mineralization in shrub-encroached ecosystems [56]. While some argue that shrub encroachment that alters spatial heterogeneity enhances the risk of desertification [40], others have demonstrated the positive effects of shrub encroachment on ecosystem-scale carbon and nitrogen pools [38,39]. In contrast, the intentional planting of woody species in aridlands (particularly afforestation projects) has, in general, been shown to increase carbon pools [57], whereas the consequences for the hydrologic cycle and other nutrient cycles are much less clear [58].

Large-scale grass invasion in aridlands demonstrate additional consequences on soil processes, especially for carbon and nutrient pools and their short-term turnover [30,59,60]. For example, the widespread naturalization of the annual western cheatgrass (*Bromus tectorum*) throughout the western USA has had profound effects on ecosystem processes in invaded ecosystems. Cheatgrass invasion has been shown to increased litter biomass pools and stimulate nitrogen mineralization [61] but, over time, increased fire frequency has contributed to overall nitrogen losses from volatilization and the reduction of biological soil crusts [62].

Increased fire frequency or suppression due to human activity can interact with other ecosystem controls to exacerbate or reduce impacts on belowground ecosystem processes in aridlands. Fires transform aboveground vegetation pools, causing the redistribution of nutrients such as phosphorus [63], although the effects of fire can be secondary to soil organic matter availability for nitrogen mineralization after burning [64]. Feedbacks from grass invasion can result in increased fire frequency and N losses through volatilization [62]. In contrast, fire suppression can result in shrub encroachment [56,65], thereby affecting carbon pools and the spatial heterogeneity of vegetation.

Independent of the precise mechanisms resulting from human activity which cause these vegetation shifts, the magnitude of change observed with woody encroachment or plant invasion and the alteration of the spatial heterogeneity of resources can exert a substantial control on biogeochemical processes and their response to precipitation inputs (Figure 3). Changes in the relative importance of abiotic controls and the response of vegetation to changes in water input can therefore be strongly influenced by these human-caused modifications, with prominent effects on carbon and nitrogen turnover. In addition, ecohydrological feedbacks involving changes in the water balance can exacerbate the direct effects of these vegetation shifts [58]. In summary, these studies demonstrate that the concentration of soil organic matter and the distribution of vegetated patches can be primary drivers for biogeochemical cycles in their own right. Moreover, all forms of human activity that elicit substantial changes in plant cover or that substantially alter the spatial heterogeneity of vegetation are likely to be more important for ecosystem processes than future predicted changes in annual precipitation and seasonality.

Conclusions and future directions

Our predictive power for understanding how global change will affect aridland ecosystems will be dependent upon our understanding of the fundamental controls affecting net primary production as well as carbon and nutrient turnover in soil. It is impossible to deny the importance of mean annual precipitation and water pulses affecting litter inputs and biotic activity. However, it is becoming increasingly clear that, as our understanding of alternative factors other than water-controlling belowground processes grows, it will be necessary to focus on potential global changes other than modifications in annual rainfall and seasonality. In particular, we need to assess the importance of alternative climatic changes such as increases or decreases in cloud cover or changes in plant cover which could alter solar irradiance. Human activity that increases or decreases the photochemical or thermal mineralization of plant-derived organic matter could result in alterations of the carbon cycle which far exceed predicted changes based purely on climatic shifts in rainfall or temperature.

Determining the potential feedbacks of aridland ecosystems as ecosystem carbon sources or sinks is critically important for the global carbon balance [66,67]. In summarizing the evidence for alternative controls on soil processes in aridlands, these studies collectively suggest that we are currently underestimating carbon losses from these ecosystems. Previously undocumented losses from photodegradation (particularly gaseous losses), more rapid turnover of soil organic matter due to the persistence of hydrolysable soil enzymes, and export of sediments from aridlands due to wind or soil erosion suggest that carbon sequestration potential might be substantially less than previously thought based on climatic predictions of water and temperature as the principal controls on aridland biogeochemistry. At present, there are many unknowns regarding the importance of photodegradation as a vector of carbon loss and thermal degradation as a vector of nitrogen gas formation. However, these studies highlight a strong disconnect between surface soil and subterranean processes in aridlands. Moreover, it is likely that these aboveground and belowground controls will respond to climate change or other ecosystem alterations in very different ways [20]. As such, an accurate quantitative assessment of carbon losses from aridlands is important to mitigate desertification and accurately assess potentials for carbon sequestration [13,66]. Aridland ecosystems currently occupy >30% of the terrestrial land surface, and are among the most vulnerable ecosystems to the impacts of global change [68]. Hence, the identification of these alternative controls demonstrates the importance of looking beyond 'water-limited' ecosystems in order to fully imagine the complex nature of biogeochemistry in aridlands.

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