

# A MECHANISTIC UNDERSTANDING OF GLOBAL CHANGE ECOLOGY

Functional Ecology



## Trait selection and community weighting are key to understanding ecosystem responses to changing precipitation regimes

Robert J. Griffin-Nolan<sup>1,2</sup> | Julie A. Bushey<sup>2,3</sup> | Charles J. W. Carroll<sup>1,2</sup> |  
 Anthea Challis<sup>4</sup> | Jeff Chieppa<sup>4</sup> | Magda Garbowski<sup>2,5</sup> | Ava M. Hoffman<sup>1,2</sup> |  
 Alison K. Post<sup>1,2</sup> | Ingrid J. Slette<sup>1,2</sup> | Daniel Spitzer<sup>3</sup> | Dario Zambonini<sup>3,6</sup> |  
 Troy W. Ocheltree<sup>2,3</sup> | David T. Tissue<sup>4</sup> | Alan K. Knapp<sup>1,2</sup>

<sup>1</sup>Department of Biology, Colorado State University, Fort Collins, Colorado; <sup>2</sup>Graduate Degree Program in Ecology, Colorado State University, Fort Collins, Colorado; <sup>3</sup>Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, Colorado; <sup>4</sup>Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW, Australia; <sup>5</sup>Department of Bio-agricultural Sciences and Pest Management, Colorado State University, Fort Collins, Colorado and <sup>6</sup>Università degli studi di Trieste, TS, Trieste, Italy

### Correspondence

Robert J. Griffin-Nolan, Department of Biology, Colorado State University, Fort Collins, CO 80523.  
 Email: rgriffi2@colostate.edu

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### Abstract

1. Plant traits can be used to predict ecosystem responses to environmental change using a response–effect trait framework. To do this, appropriate traits must be identified that explain a species' influence on ecosystem function (“effect traits”) and the response of those species to environmental change (“response traits”). Response traits are often identified and measured along gradients in plant resources, such as water availability; however, precipitation explains very little variation in most plant traits globally. Given the strong relationship between plant traits and ecosystem functions, such as net primary productivity (NPP), and between NPP and precipitation, the lack of correlation between precipitation and plant traits is surprising.
2. We address this issue through a systematic review of >500 published studies that describe plant trait responses to altered water availability. The overarching goal of this review was to identify potential causes for the weak relationship between commonly measured plant traits and water availability so that we may identify more appropriate “response traits.”
3. We attribute weak trait–precipitation relationships to an improper selection of traits (e.g., nonhydraulic traits) and a lack of trait-based approaches that adjust for trait variation within communities (only 4% of studies measure community-weighted traits). We then highlight the mechanistic value of hydraulic traits as more appropriate “response traits” with regard to precipitation, which should be included in future community-scale trait surveys.
4. Trait-based ecology has the potential to improve predictions of ecosystem responses to predicted changes in precipitation; however, this predictive power depends heavily on the identification of reliable response and effect traits. To this end, trait surveys could be improved by a selection of traits that reflect physiological functions directly related to water availability with traits weighted by species relative abundance.

**KEYWORDS**

community-weighted traits, hydraulics, plant traits, precipitation, response–effect framework

**1 | INTRODUCTION**

Global climate change models predict a future with more frequent climate extremes (e.g. drought) and increased inter- and intra-annual variability in precipitation, which will fundamentally alter the spatial and temporal patterns of water availability in terrestrial ecosystems world-wide (Ciais et al., 2013; Dai, 2011, 2013; IPCC, 2013; Trenberth, 2011). These predicted changes in precipitation will alter terrestrial ecosystem properties such as NPP, carbon (C) cycling and biodiversity, along with other important ecosystem services. The sensitivity of these ecosystem functions to changes in precipitation can vary among ecosystems, although a mechanistic understanding of this variability remains unresolved (Knapp et al., 2015; Luo et al., 2011; Smith, Knapp, & Collins, 2009).

One approach to advance our understanding of ecosystem responses to environmental change is to use a response–effect trait framework (Suding et al., 2008). This framework categorizes species in a community based on “effect traits” representing their relative influence (strong or weak) on specific ecosystem functions, such as NPP. For example, plant functional traits such as specific leaf area (SLA), leaf nitrogen content and leaf area index have been used to explain plot level variability in NPP from grasslands to forests (Forrestel et al., 2017; Garnier et al., 2004; Reich, 2012). “Response traits” are used to describe the change in relative abundance or size of a species in response to environmental change. In the context of water availability, traits related to hydraulic function (e.g. plant hydraulic conductance) are most likely to respond to precipitation (Reich, 2014), yet the extent to which these traits are used in the response–effect framework has yet to be surveyed (Rosado, Dias, & de Mattos, 2013). Appropriate response and effect traits, once identified, can be used to understand shifts in community composition due to environmental filtering (Suding et al., 2008).

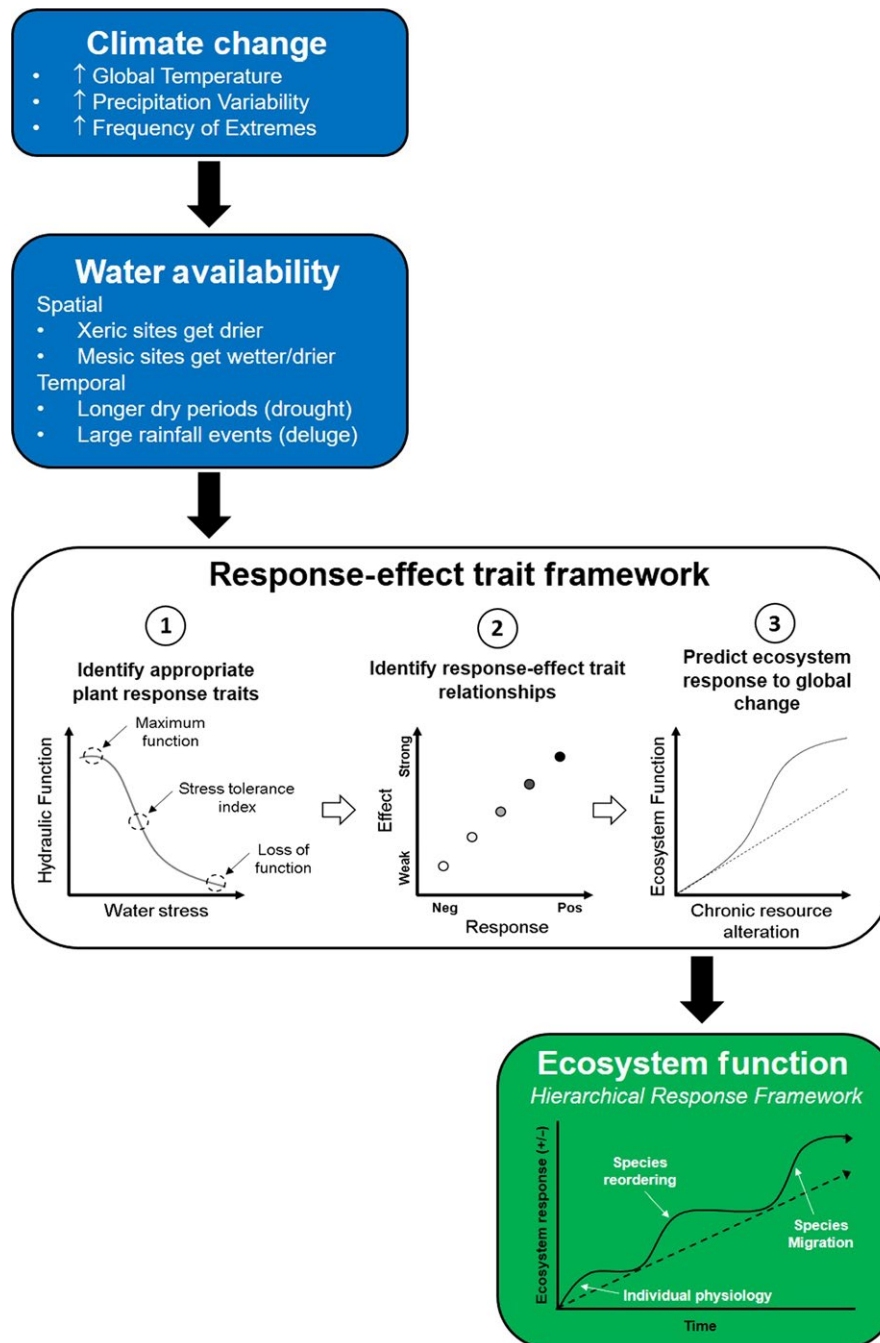
Experimental tests of the response–effect trait framework have generally been conducted over short time-scales (i.e. 1–2 years; Klumpp & Soussana, 2009); however, climate change is expected to cause long-term chronic alterations in plant-available water (Smith et al., 2009). Thus, the response–effect trait framework may be most useful for predicting ecosystem responses to altered precipitation if merged with the hierarchical response framework (Smith et al., 2009), which describes temporal dynamics of ecosystem responses to chronic changes in resource availability (Figure 1). The response of an ecosystem to chronic resource alteration can be predicted over time depending on the relative importance of (a) dominant species physiology, (b) species reordering within communities and (c) species migration (Smith et al., 2009). A wealth of literature describes the physiological responses of dominant species to extreme climate events (reviewed by Felton & Smith, 2017);

however, a community-wide survey of plant response and effect traits is required to predict community shifts in response to long-term chronic alterations in water availability. The predictive power of “effect traits” is dependent on relevant “response traits” of the dominant species as well as the response/effect traits of subordinate and transient species that may change in abundance with climate change (Grime, 1998; Suding et al., 2008). Thus, incorporating the response–effect trait framework into the hierarchical response framework requires the identification of appropriate response and effect traits (Figure 1).

Plant ecologists have long observed and measured traits along climatic gradients to determine environmental filters of community assembly (Diaz, Cabido, & Casanoves, 1998). These trait–climate relationships can be used to identify plant “response traits,” a key research objective in community ecology (Suding et al., 2008); however, precipitation explains very little global variation in commonly measured plant traits (Forrestel et al., 2017; Moles et al., 2014; Wright et al., 2004). This is surprising given the utility of traits for understanding ecosystem function (Diaz & Cabido, 1997; Garnier et al., 2004; Reich, 2012; Reich, Walters, & Ellsworth, 1997; van der Sande et al., 2017) and the strong relationship between precipitation and NPP, which is widely considered a key metric of ecosystem function (Fahey & Knapp, 2007; Huxman et al., 2004; Knapp, Ciais, & Smith, 2017; Knapp & Smith, 2001; Sala, Parton, Joyce, & Lauenroth, 1988). To address this issue and better understand how traits might be used to forecast ecosystem responses to alterations in precipitation regimes, we conducted a systematic review of plant traits literature in the context of altered water availability. We aim to categorize how plant traits are measured across biomes to (a) identify potential reasons for weak trait–climate relationships and (b) reveal relevant knowledge gaps that can be addressed with future research. More specifically, we aim to highlight the value of hydraulic traits for providing a mechanistic understanding of plant responses to water availability, especially when assessed at the community level. Lastly, we discuss the ecological significance of identifying response and effect traits for predicting differential ecosystem responses to precipitation.

**2 | SYSTEMATIC REVIEW**

We reviewed the literature on plant trait research within the context of water availability to categorize the most commonly measured traits and their method of measurement. In total, 1,341 manuscripts (published in 215 peer-reviewed journals from the years 1991 to mid-2017) were identified using key words broadly related to plant traits and water availability (see Supporting Information Appendix S1).



**FIGURE 1** Climate change will impact ecosystem functioning in many ways, with changes in water availability one of the primary mechanisms; however, ecosystems may differ dramatically in the magnitude and time-scale of their responses to changes in water availability. A response–effect trait framework can be used to predict ecosystem responses to altered water availability (the following is modified from Suding et al., 2008). First, reliable mechanistic traits must be identified. In the context of water availability, hydraulic traits linked to maximum hydraulic function (e.g. leaf hydraulic conductance), loss of function (e.g. stomatal closure) and stress tolerance (e.g. vulnerability to xylem cavitation and turgor loss) are appropriate trait candidates given their physiological link to plant-available water (#1). Second, traits must be measured for multiple species within the community and regressed against traits linked to their effect on ecosystem function (#2; shades of grey represent different species in the community, each with a unique environmental response (positive/negative) and effect (strong/weak) on ecosystem function). An understanding of which species will respond to resource alterations along with the effect that those species have on ecosystem function can help improve predictions of ecosystem responses to chronic resource alteration (#3; shown are both linear and nonlinear ecosystem responses to changes in resource availability driven by different combinations of response and effect traits). Once these goals are met, the predictions from the response–effect trait framework can be incorporated into long-term predictions made by the hierarchical response framework. While physiological responses of species suffice for short-term predictions, response and effect traits can be incorporated into later stages of the hierarchical response framework to include community change via species reordering/migration (Smith et al., 2009)

Each manuscript was screened and included in our review if it met the following criteria: (a) One or more plant trait(s) were measured on vascular plants from nonagricultural terrestrial ecosystems; (b) plant traits were measured across contrasting levels of water availability; and (c) inclusion of a statistical test relating trait values to water availability. A list of plant traits (defined as: "Any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization"—Violle et al., 2007) was compiled from the TRY database ([www.try-db.org](http://www.try-db.org)) and the standardized plant traits handbook (Pérez-Harguindeguy et al., 2013) to help define criteria #1. Modelled or simulated traits were not included in this review. Plants in pots or common garden experiments were included only if plant-available water was manipulated. Criteria #2 was met by precipitation gradients and/or experimental manipulations of soil moisture. Criteria #3 was included in our screening protocol to exclude studies that measured plant traits at varying levels of water availability but did not explicitly analyse plant responses to water (e.g. traits were measured at different soil moisture levels, but statistical significance of trait–water relationships was not assessed).

The plant functional type (PFT) surveyed in each manuscript was recorded as either (a) graminoid, (b) forb (nongraminoid herbaceous), (c) shrub, (d) broadleaf tree, (e) needle-leaf tree or (f) other (e.g. ferns). If multiple plant PFTs were studied in one manuscript and the traits measured were specific to each PFT, then the manuscript was counted as two separate studies, one for each PFT. For each manuscript, the source of variation in water availability was recorded as either a (a) spatial precipitation gradient, (b) temporal

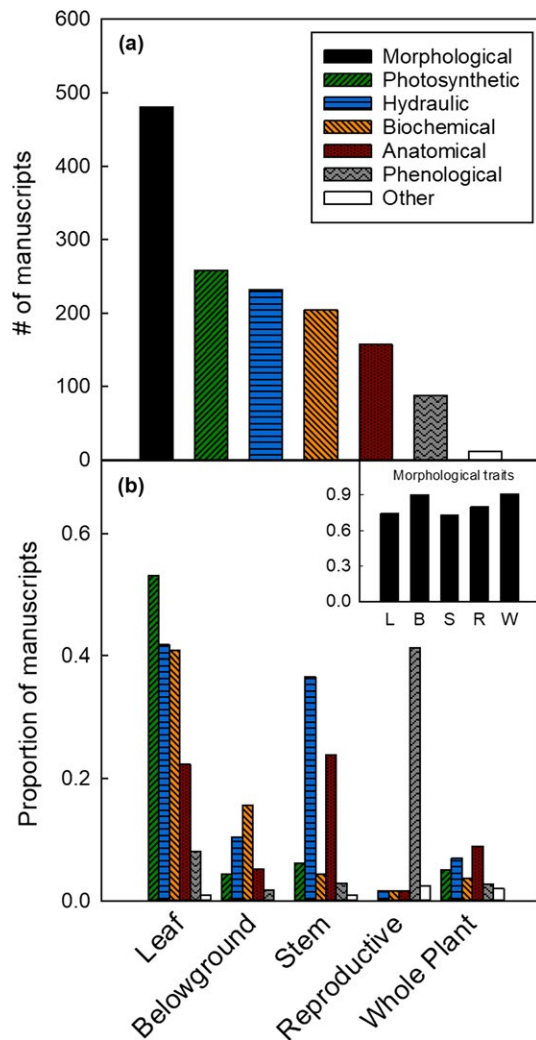
(seasonal) precipitation gradient, (c) temporal (interannual) precipitation gradient, (d) local microclimate/edaphic differences (i.e. shallow vs. deep soils), (e) water addition/removal (field setting) or (f) water additional/removal (greenhouse setting). Traits were categorized according to the organ measured (leaf, stem, root/below-ground organ, reproductive organ or whole-plant trait) and by trait category (morphological, anatomical, biochemical, photosynthetic, hydraulic, phenological and/or other; Table 1). Lastly, the ecological scale at which traits were measured was recorded as: (a) single population of a single species, (b) multiple populations of a single species, (c) single populations of multiple species, (d) multiple populations of multiple species or (e) community-weighted trait (CWT; trait values presented as the mean of a plot/community with each species' trait value weighted by relative abundance, such as per cent cover/basal area).

### 3 | PLANT TRAITS AND WATER AVAILABILITY: PROGRESS TO DATE

A total of 568 manuscripts (42% of those initially identified) were included based on our screening protocol. Within these papers, a clear division was observed whereby publications have focused on plant traits of either woody (W) or herbaceous (H) growth forms with relatively few studies comparing the two forms (W = 334 manuscripts; H = 183 manuscripts; both = 51 manuscripts; Supporting Information Figure S1). Thus, at present, woody species (primarily tall-statured trees) dominate this field of plant traits research. The striking divide within plant trait ecology between W- and H-focused

**TABLE 1** Definitions of categories used to classify traits, and examples for each category, used in a literature review of manuscripts with a focus on plant trait responses to altered water availability. Definitions and examples were modified from those presented by Pérez-Harguindeguy et al. (2013) and the TRY database

Trait category	Definition	Examples
Morphological	Traits dealing with (a) plant size, shape, mass and form, or (b) organ ratios or (c) growth rate; generally measured at the organ scale and mostly associated with external parts of a plant.	Specific leaf area, seed mass, plant height, leaf thickness, specific root length, root:shoot ratios
Anatomical	Traits dealing with the presence, absence, density or size of key plant characteristics at the tissue level (vascular, dermal or ground tissue)	Trichome density, stomatal length, palisade mesophyll thickness
Biochemical	Traits involving concentrations, ratios and use efficiencies of plant nutrients, secondary compounds, or pH (not including biochemical compounds involved in photosynthesis)	Leaf N content, C:N ratio, lignin concentration, enzyme activity, leaf pH
Photosynthetic	Physiological/biochemical traits involved light capture, gas exchange and carbon assimilation (including biochemical compounds such as chlorophyll and rubisco)	Net photosynthesis, stomatal conductance, chlorophyll fluorescence, chlorophyll a/b
Hydraulic	Physiological traits involved in plant water status, water transport and water storage all in the liquid phase (including osmolytes concentrations)	Hydraulic conductivity, leaf turgor loss point, osmotic potential, minimum water potential
Phenological	Traits associated with timing, seasonality or life span	Flowering time, leaf life span
Other	Traits related to nonhydrological disturbances or biogeochemical cycles. Only used if trait does not fall within an above category	Frost resistance, flammability, decomposition rate or palatability



**FIGURE 2** A comparison of the frequency with which traits are measured within each plant organ and trait category in response to altered water availability. (a) The total number of manuscripts that measure each trait category across both herbaceous and woody species. (b) Data for trait category by organ comparisons are shown as the proportion of manuscripts that measure traits of each organ (e.g. proportion of “leaf manuscripts” that measure morphological traits). As manuscripts often present several traits (i.e. both leaf anatomical and morphological traits), the proportions presented here do not sum to 100. Morphological traits dominate the literature across all plant organs (~85% of manuscripts) and are thus shown separately as an inset (letters correspond to organ type). Leaf traits are well surveyed across all trait categories. Hydraulic traits are well studied in both leaves and stems (woody stems specifically), with very few manuscripts assessing either below-ground or whole-plant traits beyond morphology

manuscripts was unexpected given that many traits, such as those of the leaf economic spectrum, can easily be measured in both growth forms (Weiher et al., 1999; Wright et al., 2004). Increased data sharing and the prevalence of large trait databases (e.g. TRY database; Kattge et al., 2011) should facilitate trait comparisons across functional groups. Additionally, we observed very few differences between W- and H-focused manuscripts in the methods used to alter

water availability (Supporting Information Figure S2A) or the ecological scale of trait measurements (Supporting Information Figure S2B), which should make data synthesis across growth forms more feasible.

The dichotomy between W- and H-focused manuscripts revealed clear growth form differences in types of traits measured (See Supporting Information Appendix S2 and Figure S2). Hydraulic traits were more often measured on W species than H species (W: 47%; H: 26%; percentages based on number of manuscripts relative to the total number per growth form), and photosynthetic traits were more commonly measured on H species (W: 13%; H: 36%). This trend could be due to increased interest in the hydraulic mechanisms of tree mortality within the last decade (Adams et al., 2017; Allen et al., 2010; McDowell et al., 2008). It may also reflect the historical importance of measuring water uptake, storage and transport in long-lived trees compared to herbaceous plants with small water storage capacity and, consequently, more challenging techniques for assessing hydraulic properties. Given that the water transport system and carbon economy in plants are intrinsically linked, dual measurements of these physiological traits would likely reveal more informative “response traits.” One promising linkage between these two trait categories is the quantification of isohydricity, based on stomatal and hydraulic sensitivity to drought, a technique that has been used successfully in both woody (Skelton, West, & Dawson, 2015) and herbaceous plants (Ocheltree, Nippert, & Prasad, 2016); however, isohydricity has yet to be incorporated into community scale response–effect trait surveys.

Combining W- and H-manuscripts revealed several trends across this subset of plant traits research. For example, leaf hydraulics (and stem hydraulics in the case of woody species) have been highly studied in response to water availability, while the hydraulic traits of other organs have received minimal attention (Figure 2). An understanding of leaf hydraulics is important given that leaves contribute the largest portion of hydraulic resistance in a plant (Sack & Holbrook, 2006); however, root hydraulics also provide critical understanding of whole plant recovery from extreme events such as drought (Lo Gullo, Nardini, Salleo, & Tyree, 1998) and merit increased attention. In general, our survey identified a striking lack of research on root traits beyond simple morphological measurements (Figure 2). Given the sensitivity of below-ground processes to precipitation (Fay, Carlisle, Knapp, Blair, & Collins, 2003) and the importance of root traits as drivers of ecosystem function (Bardgett, Mommer, & De Vries, 2014), future response–effect trait surveys should consider measuring root traits. Indeed, a consideration of traits across all plant organs is necessary and currently lacking (Figure 2). Recent evidence suggests that an economic trait spectrum describing plant strategies for acquiring light, nutrients and water exists for both stems and roots, not just leaves (Prieto et al., 2015; Reich, 2014). Thus, surveys of traits along gradients in water availability should include traits across all organs and trait categories (Table 1) to better identify appropriate response and effect traits.

Here, we have categorized trait measurements within the context of water availability and identified several key research



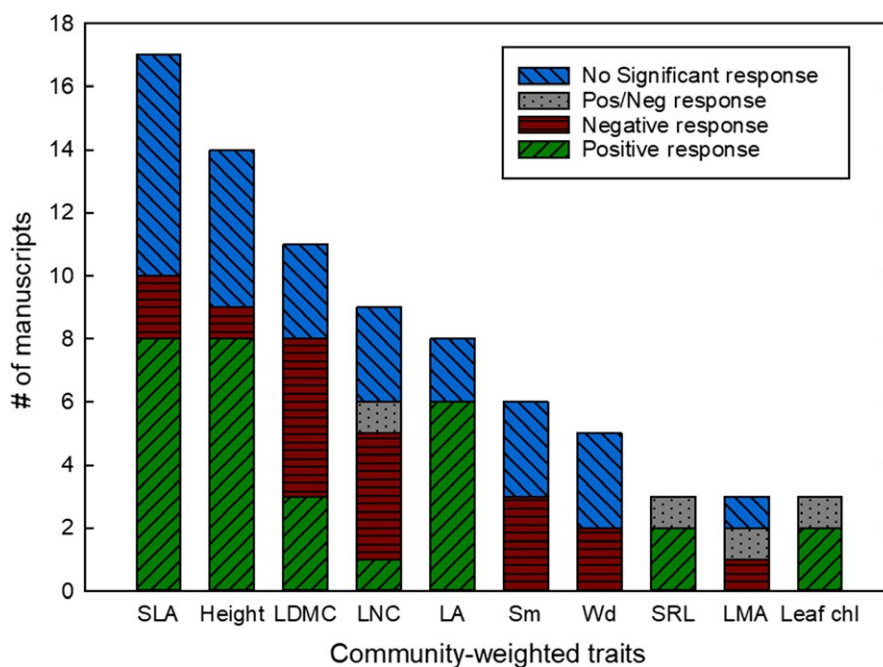
gaps needing attention (see Supporting Information Appendix S2, Figure 2, Supporting Information Figures S1 and S2). A subset of these 568 manuscripts, however, was further analysed to determine why traits do not align well with precipitation gradients and develop suggestions for how trait sampling methods can be altered to identify more appropriate “response traits.”

#### 4 | COMMUNITY-WEIGHTED RESPONSE TRAITS

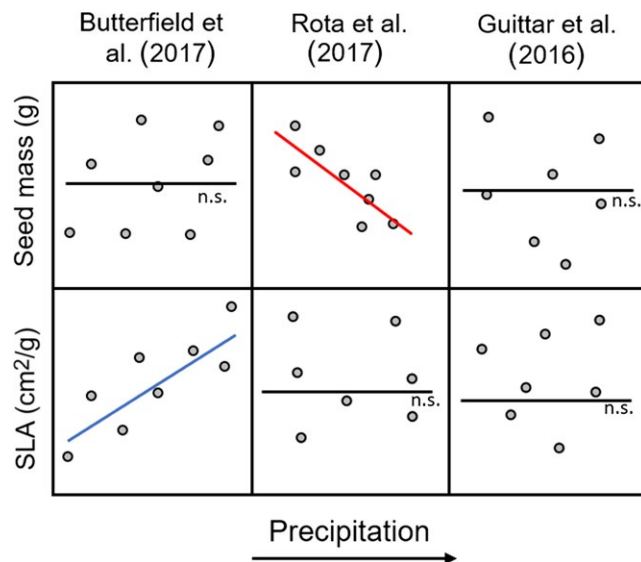
Plant traits have been used to assess functional variation along climatic gradients (Diaz et al., 1998; Peppe et al., 2011; ter Steege et al., 2006; Wright et al., 2004) which assists model predictions of community assembly and species distributions with climate change (Suding et al., 2008; Thuiller, Lavorel, Midgley, Lavergne, & Rebelo, 2004). But as noted above, most commonly measured plant traits do not align well with precipitation gradients. For instance, mean annual precipitation (MAP) explained <1% of the global variance in SLA (leaf area to dry mass ratio—correlated with maximum photosynthetic rate) across biomes (Wright et al., 2004) and was not significantly related to SLA within grasslands (Forrestel et al., 2017). Furthermore, the combination of several climatic variables (mean annual temperature, MAP, vapour pressure deficit and solar irradiance) explained <20% of the variance in five functional traits related to resource acquisition strategies (Reich, Wright, & Lusk, 2007). These weak relationships have been attributed to MAP as a poor

proxy for plant-available water. Indeed, other indices of aridity, and even temperature, may explain a larger portion of trait variation (Moles et al., 2014). However, the large precipitation gradient (MAP: 133–5,300 mm/year) spanned in the Wright et al. (2004) analysis likely captured significant spatial variability in plant-available water. Additional complexity arises from well-documented shifts in community composition due to chronic alterations in water availability (Collins et al., 2012; Smith et al., 2009). Thus, “response traits” that can explain community shifts likely exist and are masked along precipitation gradients due to high within-site trait variability (Freschet, Cornelissen, van Logtestijn, & Aerts, 2010; Onoda et al., 2011; Siefert et al., 2015).

Plants often display patterns of apparent niche differentiation which can be identified from observations of species abundance along hydrologically defined niche space (Silvertown, Dodd, Gowing, & Mountford, 1999) and more recently demonstrated within the context of water availability using isotopic proxies for rooting depth (Nippert & Knapp, 2007). Niche differentiation can be manifest within a single site as high trait diversity, which must be accounted for in broad spatial surveys of plant traits. This can be accomplished by community-weighting traits, whereby community average trait values are presented for a single site with species traits weighted by their % cover or contribution to overall biomass. Assessing plant traits at the scale of the community inherently requires more time and effort. It is thus not surprising that only 23 of the 568 studies (4% of surveyed manuscripts) measured CWTs (Supporting Information Figure S1). While time-consuming, these



**FIGURE 3** The specific plant traits that are most commonly measured as community-weighted traits (CWT) arranged in order of decreasing frequency (traits shown here were assessed in at least three of the manuscripts we surveyed). Also depicted is the proportion (stacked bars) of the manuscripts that show statistically significant ( $p < 0.05$ ) trait-by-water relationships as well as the directionality of those relationships. Note that the overwhelming majority of CWTs are morphological with very few physiological traits (hydraulic or photosynthetic). SLA, specific leaf area; height, maximum plant height; LDMC, leaf dry matter content; LNC, leaf nitrogen content; LA, leaf area; Sm, seed mass; Wd, wood density; SRL, specific root length; LMA, leaf mass per area; Leaf chl, leaf chlorophyll content



**FIGURE 4** Specific leaf area (SLA) and seed mass (Sm) were identified as two of the most commonly measured community-weighted traits (CWTs). The expected individual and community-level responses of these traits to resource availability are well described. In resource-limited environments, SLA is expected to decrease as individuals produce smaller leaves and/or more conservative species increase in abundance. Sm tends to decrease with resource availability due to increased success, and thus abundance, of smaller seeds with neutral effects on large seeds, which tend to be successful across resource gradients. The above examples describe results from three separate studies that assessed community-weighted SLA and Sm across spatial precipitation gradients within grasslands. Butterfield et al. (2017) show a significant SLA response (+) to increased water availability, but no significant Sm response. Rota et al. (2017) show a significant Sm response (–) to increased water availability, but no significant SLA response. Guittar et al. (2016) show no significant response for either trait. The inconsistent relationships seen across these studies conducted in the same vegetation type with similar methodologies suggest that these traits are not the appropriate “response trait” candidates for assessing community responses to water availability. While CWTs are necessary to produce significant trait–climate relationships, it is also important to choose the correct trait candidates given the specific environmental and physiological context. Note: figures do not display actual data, but rather depict general relationships presented in these manuscripts

community-scale trait measurements often improve trait–climate relationships, with 91% of CWT manuscripts presenting statistically significant relationships between CWT means and water availability (see Supporting Information Table S1).

Community-scale trait measurements can account for a large portion of within-site trait variability, yet not all CWT–climate relationships are useful for predicting responses to changing water availability (Figure 3, Supporting Information Table S1). For example, the most commonly measured CWT, SLA, was not significantly related to water availability in ~40% of studies. Moreover, those relationships that are significant often explain very little trait variability. A recent survey across >15,000 grassland locations in France revealed that community weighting commonly measured functional traits

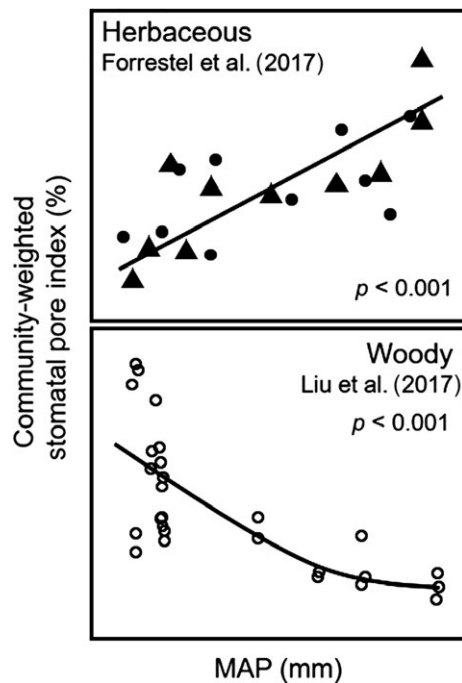
(e.g. SLA, leaf dry matter content (LDMC), and leaf N and P concentrations) yielded a statistically significant relationship between traits and precipitation, yet precipitation still explained <1% of trait variability (Borgy et al., 2017). Additionally, the most common CWTs (SLA, height and LDMC) do not show consistent directional relationships with water availability (Figure 3), which may suggest the utility of traits is site- or biome-specific.

To test this, we compared three similar studies that all measured seed mass (Sm) and SLA (two commonly measured CWTs related to reproductive and resource acquisition strategies, respectively) across precipitation gradients within grassland ecosystems. While these traits are expected to respond predictably to water availability (Butterfield, Bradford, Munson, & Gremer, 2017; Guittar, Goldberg, Klanderud, Telford, & Vandvik, 2016; Rota, Manzano, Carmona, Malo, & Peco, 2017; Wright et al., 2004), we observed variable CWT–precipitation relationships (positive, negative and lack of relationship) across these studies even though the type of biome and water availability gradient was consistent (Figure 4). Specific leaf area is dependent on a variety of environmental variables and is constrained by leaf size (Milla, Reich, Niinemets, & Castro-Díez, 2008); thus, it is unsurprising that this trait does not consistently respond to altered water availability; nonetheless, SLA is the most commonly measured CWT (Figure 3). Community-weighting is necessary to account for trait variability to identify likely “response traits”; however, it must be combined with an appropriate selection of traits (Rosado et al., 2013). Hydraulic traits are likely candidate “response traits” given they are mechanistically linked to precipitation (Reich, 2014).

## 5 | HYDRAULIC RESPONSE TRAITS

After reviewing the literature, we argue that traits of the leaf economic spectrum—the trade-off between allocating resources to high photosynthetic rate and rapid growth vs. nutrient storage, herbivory defence and longevity (Reich, 2014; Wright et al., 2004)—are useful for assessing plant responses to nutrients (Niinemets & Sack, 2006) and light (Richardson, Peltzer, Allen, & McGlone, 2005), yet are unreliable within the context of water availability (Reich et al., 2007; Wright et al., 2004), even when community-weighted (Figure 3). A transition away from leaf economic traits and towards traits mechanistically linked to water transport is necessary to identify appropriate “response traits” related to precipitation.

Recent work in diverse tropical rainforests suggests that anatomical traits related to hydraulic function, such as stomatal characteristics and vein density, are decoupled from common LES traits such that two trait spectrums exist: the economic spectrum (associated with light capture and carbon economics) and the hydraulic spectrum (associated with water transport; Li et al., 2015). Indeed, Reich (2014) has noted that LES traits should be measured in combination with traits related to the hydraulic safety vs. efficiency trade-off (Blackman et al., 2014; Meinzer, McCulloh, Lachenbruch, Woodruff, & Johnson, 2010; Nardini, Pedà, & Rocca, 2012; Ocheltree et al., 2016; Zimmermann, 1983) to provide a more accurate description of



**FIGURE 5** Relationships between mean annual precipitation (MAP) and community-weighted stomatal pore index (SPI; % of leaf area composed of stomata) in herbaceous-dominated (South African [●] and North American [▲] grasslands; Forrester et al., 2017) and woody-dominated communities [○] (temperate to tropic forests in China; Liu et al., 2017). Stomatal pore index is an anatomical index of maximum stomatal conductance and plant water-use efficiency. Community-weighted SPI is a likely candidate for determining broad-scale trait–precipitation relationships, although its interpretation may change depending on ecosystem type (woody- vs. herbaceous-dominated). Plotted data taken from Forrester et al., 2017 and Liu et al., 2017 (note: axes for MAP and SPI are not to the same scale for each study)

water acquisition strategies. Water availability in natural ecosystems is transient, depending on rainfall patterns and extreme events (i.e. drought), which are inherently rare and unpredictable (Smith, 2011). Thus, the inclusion of these traits related to water transport (leaf, stem or root maximum hydraulic conductance— $K_{max}$ ) and drought tolerance (leaf turgor loss point ( $\psi_{TLP}$ ) and vulnerability to xylem cavitation) allows for better understanding of plant responses to both high and low levels of water availability (Reich, 2014). Additionally, these traits align well with precipitation gradients (Blackman, Brodribb, & Jordan, 2012) and are related to relative plant performance during drought (Kursar et al., 2009). Thus, we posit that the incorporation of hydraulic traits into community-scale surveys of plant response–effect traits should improve temporal predictions of ecosystem responses to chronic alterations in water availability (Figure 1).

Hydraulic traits were well surveyed in the manuscripts we reviewed (Figure 2;  $n = 232$  or 41% of surveyed manuscripts); however, few hydraulic traits or even anatomical traits related to hydraulic function (e.g. xylem vessel area or stomatal density) were surveyed at the community scale (<10% of CWT manuscripts; Supporting

Information Table S1). Additionally, a large portion of hydraulic trait papers present trait values for a single species ( $n = 114$  manuscripts) or make comparisons between species with no inclusion of relative abundance ( $n = 107$  manuscripts). The lack of community-level hydraulic trait measurements likely reflects the lengthy laboratory procedures required to measure traits such as leaf hydraulic conductance and  $\psi_{TLP}$  (Brodribb & Holbrook, 2003; Sack, Melcher, Zwieniecki, & Holbrook, 2002) vs. the rapid field assessments of plant morphology (the most commonly measured trait category; Figure 2).

Recent developments in high-throughput methods for assessing drought tolerance should encourage surveys of community-weighted hydraulic traits (Bartlett et al., 2012). Bartlett et al. (2012) describe a method for assessing  $\psi_{TLP}$  with a vapour pressure osmometer which increases measurement speed 50-fold and has since been used in broad-scale surveys of drought tolerance of tropical tree species (Maréchaux et al., 2015).  $\psi_{TLP}$  has long been recognized as a valuable indicator of plant water stress and is correlated with plant-available water, as well as vulnerability to xylem cavitation (Blackman, Brodribb, & Jordan, 2010). Rapid assessment of  $\psi_{TLP}$  will facilitate surveys of community-weighted hydraulic traits across broad spatial scales; however, this technique still requires validation in herbaceous-dominated communities.

Anatomical traits related to hydraulic transport and water-use efficiency, such as stomatal pore index (SPI; % of leaf area composed of stomata; Sack, Cowan, Jaikumar, & Holbrook, 2003), can be easily measured at the community level as samples can be collected and preserved for later trait determination. Indeed, recent work suggests that community-weighted SPI is well correlated with MAP across both herbaceous and woody-dominated ecosystems and is linked to spatial variation in NPP (Forrester et al., 2017; Liu et al., 2017; Figure 5). These findings suggest that SPI, and other anatomical traits linked to hydraulic function, are promising trait candidates for predicting NPP responses to chronic alterations in water availability (Suding et al., 2008; Smith et al., 2009; Figure 1).

## 6 | CONCLUSIONS

Climate change will intensify Earth's hydrological cycle leading to chronic alterations of plant-available water (IPCC, 2013), which will differentially affect terrestrial ecosystems. Commonly measured plant traits (e.g. SLA, plant height, leaf N) have been successfully used to predict plant growth and NPP dynamics (Díaz & Cabido, 1997; Díaz et al., 2016; ; Forrester et al., 2017; Garnier et al., 2004; Reich, 2012; van der Sande et al., 2017), yet often do not align with gradients in water availability (Wright et al., 2004). We attribute these weak trait–precipitation relationships to an improper selection of traits. We argue that more useful “response traits” can be identified along precipitation gradients if traits related to hydraulic function are measured at the community level. Once identified, “response traits” can be



regressed against well-known “effect traits” to aid in predictions of ecosystem responses to global climate change (Suding et al., 2008; Figure 1). However, key to linking these traits to community and ecosystem responses is scaling them by their abundance (i.e. community-weighting). At present, trait-based approaches that adjust for trait variation within communities are uncommon (only 4% of studies measure CWTs). Adopting this approach is critical, however, for incorporating shifts in community composition, or species reordering, that occur with chronic alterations in water availability—as predicted by the hierarchical response framework (Smith et al., 2009).

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## AUTHORS' CONTRIBUTIONS

R.J.G.N., T.W.O., D.T.T. and A.K.K. conceived the ideas, designed the methodology and led the writing for this manuscript. R.J.G.N., J.A.B., C.J.W.C., A.C., J.C., M.G., A.M.H., A.K.P., I.J.S., D.S. and D.Z. collected and analysed data, and all authors provided comments on the final manuscript.

## DATA ACCESSIBILITY

Data for this manuscript was taken from published sources referenced in the text.

## ORCID

Robert J. Griffin-Nolan  <http://orcid.org/0000-0002-9411-3588>

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