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Review article

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Plant responses to changing rainfall frequency and intensity

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Abstract

Regardless of annual rainfall amount changes, daily rainfall events are becoming more intense but less frequent with anthropogenic warming. Larger rainfall events and longer dry spells have complex and sometimes opposing effects on plant photosynthesis and growth, challenging abilities to understand broader consequences on the carbon cycle. In this Review, we evaluate global plant responses to rainfall regimes characterized by fewer, larger rainfall events across evidence from field experiments, satellites and models. Plant function responses vary between −28% and 29% (5th to 95th percentile) under fewer, larger rainfall events, with the direction of response contingent on climate; productivity increases are more common in dry ecosystems (46% positive; 20% negative), whereas responses are typically negative in wet ecosystems (28% positive; 51% negative). Contrasting responses in dry and wet ecosystems are attributed to nonlinear plant responses to soil moisture driven by several ecohydrological mechanisms. For example, dry ecosystem plants are more sensitive to large rainfall pulses compared with wet ecosystem plants, partly driving dry ecosystem positive responses to fewer, larger rainfall events. Knowledge gaps remain over optimal rainfall frequencies for photosynthesis, the relative dominance of rainfall pulse and dry spell mechanisms and the disproportionate role of extreme rainfall pulses on plant function.

Sections

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Introduction

Plants are an essential component of the climate system. Photosynthesis is responsible for the largest flux of carbon on global land surfaces[1] and drives the terrestrial sequestration of ~25% of anthropogenic CO_2 emissions each year[2]. Plants also transpire moisture and thus contribute greatly to evapotranspiration[3], which controls processes such as cloud formation[4], surface temperatures[5] and regional weather patterns[6]. Plant processes themselves also depend on environmental drivers such as rainfall, temperature, humidity, solar radiation and atmospheric carbon dioxide concentrations[7,8,9]. Therefore, plants modulate how water, carbon and energy cycles of Earth respond to climate variability[1,10,11].

When considering what controls annually averaged plant function, decadal-to-centurial trends in the mean annual climate, such as soil moisture trends, can change the annually averaged photosynthesis and growth of plants[7,12]. Potentially even more important, interannual climate variability and extremes[13,14] can also drive variations in annual averaged plant function[15,16]. These longer-timescale phenomena have been studied extensively[7,12]. However, variations in total annual rainfall often explain <50% of variability in annually averaged net primary production, even in water-limited ecosystems[16–18]. Because rainfall regimes tend to be highly uneven, with most rainfall concentrated in large events occurring on single wet days[19,20], it is likely that shorter, sub-seasonal timescales of rainfall variability also control annually averaged plant responses[21], thus influencing their mean trends and interannual variability.

Regardless of trends in annual rainfall amounts, rainfall is becoming more extreme globally, with wet days becoming less frequent but experiencing higher rainfall intensity on these days[22–24] (hereafter, 'fewer, larger rainfall events' describe this change; we refer to 'intensity' in daily units here[20], acknowledging that it is common in hourly units). Increased rainfall depths on wet days typically result in more and deeper infiltration of water into the rootzone, at least during rainfall events[25,26] (Fig. 1). By contrast, increased rainfall on wet days might also result in more water lost to runoff[27], and the longer dry spells (also referred to as drydowns or interstorm periods)[28–30] associated with fewer wet days can cause extended periods of low soil moisture, high vapour pressure deficit (VPD; also known as atmospheric aridity) and high incoming solar radiation[31,32] (Fig. 1). With the opposing effects of higher intensity daily rainfall and longer dry spells, both the direction and magnitude of plant response to these sub-seasonal rainfall changes can vary across ecosystems[33]. Indeed, field experiments in tropical, temperate and dryland ecosystems have shown substantial but varying mean ecosystem carbon uptake responses (−30% to 30%) to temporal repackaging of wet days into fewer, larger rainfall events while holding seasonal or annual total rainfall constant[34–37]. These uncertainties must be reconciled as plant responses to sub-seasonal rainfall shifts might be creating feedbacks on the carbon cycle by altering global greening trends[38] and interannual carbon cycle variability[10,11].

In this Review, we summarize evidence for how fewer, larger rainfall events are influencing plants at annual timescales across low-latitude and mid-latitude regions, where plants respond more strongly to water availability[7]. Plant responses to fewer, larger rainfall events, which are sub-seasonal rainfall features (also referred to as rainfall intermittency)[39], are evaluated independently of longer-timescale rainfall variability trends[29,40] (Box 1). Owing to their nonlinear responses to water availability, plants have been hypothesized to respond differently to rainfall variability in climatically dry and wet ecosystems[33,41,42] and we evaluate these differences here. Distinguishing dry ecosystems from wet ecosystems serves to highlight the large role of dry ecosystems in the climate system[10,43], owing to their relatively high sensitivity to climatic variability[44], and their extensive coverage, encompassing at least 40% of the land surface of the Earth. First, we examine observed and modelled trends of global sub-seasonal rainfall variability. Next, we evaluate plant responses to changes in rainfall frequency and intensity across ecosystems. We then discuss the ecohydrological mechanisms associated with larger rainfall pulses[45] (single wet days or several consecutive wet days) and longer dry spells to reconcile differing plant responses to fewer, larger rainfall events. Finally, we identify key knowledge gaps that must be addressed to better estimate plant responses to fewer, larger rainfall events.

Sub-seasonal rainfall changes

Rainfall trends in response to global temperature increases have previously been hypothesized to follow a 'wet-get-wetter, dry-get-drier' pattern, in which wet regions experience more rainfall and dry days experience less rainfall[46]. In principle, the Clausius–Clapeyron relationship predicts more rainfall over already-wet surfaces because warmer air increases atmospheric water vapour content[46]. Less rainfall in dry regions should also occur given less available surface moisture. However, this paradigm was later found to be an oversimplification and does not hold on average over land[47–49]. Instead, observed trends and model projections suggest that increasing global temperatures are causing shifts in sub-seasonal rainfall variability[22,23] where wet days are less common but experience more intense rainfall on average across the globe[24,42,50] (Fig. 2). Observations of daily-scale rainfall changes between 1980 and 2020 (refs. 51–53) show that 36% of the global land surface has fewer, larger rainfall events; smaller fractions of the land surface show the other possible trend combinations (more, larger rainfall events; more, smaller rainfall events; fewer, smaller rainfall events) (Fig. 2a,b). As rainfall patterns are highly uneven in time – typically, more than half of the total yearly rainfall of a location occurs in the 12 wettest days of the year[19] – the trend towards fewer, larger rainfall events will concentrate total rainfall into even fewer days[19]. CMIP6 projections from 28 models suggest that these observed trends will continue[23], with more spatially coherent trends toward fewer, larger rainfall events across 70% of the globe between 2020 and 2100 (Fig. 2c). Indeed, significant trends ($P < 0.05$) towards decreasing wet day frequency and increasing rainfall volumes on wet days are most common across global ecosystems as reflected in both observations and models (Fig. 2b,d).

Rainfall is increasing on wet days of all magnitudes, with the most extreme rainfall events increasing in intensity the most[23,54]. According to observations and models, the amount of rainfall on wet days is increasing by 1.6% and 1.3% per decade, respectively, with more global land area showing a statistically significant increase in wet day rainfall intensity than a statistically significant decrease ($P < 0.05$) (Fig. 2b,d). In locations with significant trends ($P < 0.05$) that have a mean wet day rainfall intensity of 6.4 mm per day, the mean wet day rainfall intensity is expected to have increased by 1.0 mm per day (+16%) by 2100 under the representative concentration pathway 8.5 (RCP8.5) scenario in CMIP6 models. Such increases in wet day rainfall intensity are attributed to both thermodynamic changes and changes to atmospheric circulation. Thermodynamic changes tend to increase daily rainfall intensity: for example, daily-scale rainfall depths increase with greater lower-tropospheric humidity[55] as well as with more latent heat release during convection[54,56]. Weakening atmospheric circulation, such as weakening of the Hadley and Walker cells, mediates the global increase in daily rainfall intensity by causing both regional increases and decreases in wet day rainfall depths[23,57–59]. Increases in daily rainfall

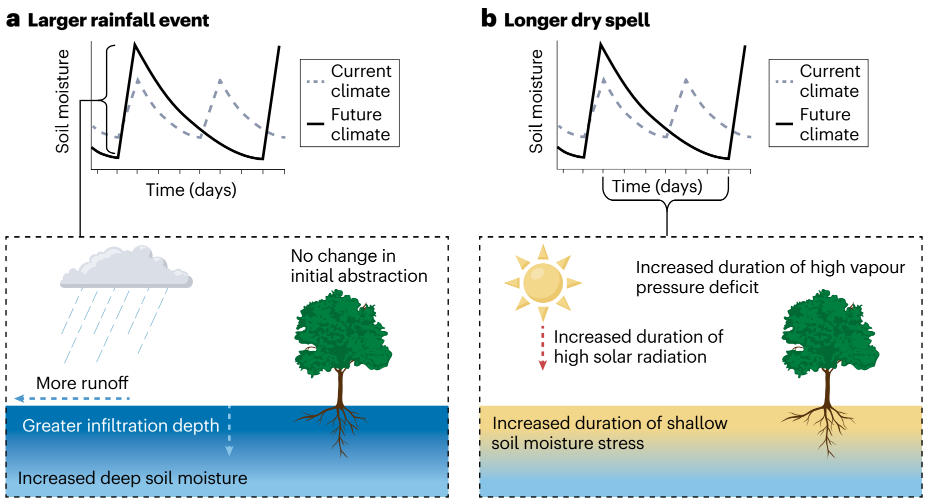


Fig. 1 | Fewer, larger rainfall events change hydrological conditions for plants. Changes in land surface hydrological conditions under higher daily rainfall intensity (left) and longer dry spells between wet days (right). For the larger rainfall event (left), the respective quantities are described in the context of their change under more intense daily rainfall. For the longer dry spell (right), the respective quantities are described in the context of their change under longer durations of dry spells between rainfall events. Changing sub-seasonal rainfall variability will alter plant-available soil moisture and atmospheric water stress.

intensity are occurring regardless of whether the land surface climate is dry or wet[60,61] and are thus likely to impact all ecosystem types.

As rainfall depth increases on wet days, the number of dry days between rainfall events is lengthening[47,62]. According to observations and models, wet day frequency is decreasing by −0.6% and −0.8% median per decade, respectively, with more global land area having significant decreases in wet day frequency than increases ($P < 0.05$) (Fig. 2b,d). In locations with significant trends ($P < 0.05$), which have a mean annual count of 118 wet days, it is expected there will be an average of 13 fewer wet days (−11%) by 2100 under the RCP8.5 scenario in CMIP6 models. Dry spell lengthening is thought to be caused by increasing atmospheric static stability, which creates more resistance for convection initiation, although the exact causes of this change are unclear[22]. Regardless, an increase in rainfall on wet days under greater atmospheric humidity, concurrent with total annual rainfall having less consistent signs of trends, ultimately requires longer dry spells[23,24].

The sub-seasonal rainfall changes described do occur among spatially heterogeneous annual rainfall amount trends[22,47] (Fig. 2). Observations from 1980 to 2020 show that annual rainfall amounts are changing by a median magnitude of 0.8% per decade, but with inconsistent direction of change across ecosystems (Fig. 2b). Compared with observational data, CMIP6 projections show a smaller median magnitude for the change in annual rainfall amounts (0.6% per decade), but a more widespread occurrence of significant trends (Fig. 2d). Although there is a tendency towards increasing annual rainfall amount, this trend is not as globally consistent as the trend towards fewer, larger rainfall events (Fig. 2b).

Plant response to rainfall variability

Plant responses to changes in rainfall frequency and intensity are assessed using many different approaches, including field manipulation experiments[26,35,37,63–76], observation-driven approaches with regional or global data sets[32,77–86], minimalist analytical process models[39,87–89] and numerical terrestrial biosphere process models[25,90–93]. These approaches aim to determine how plants and ecosystems will respond to a future climate with fewer, larger rainfall events in the context of constant annual rainfall amounts. Each approach has advantages and disadvantages and the complementary use of different approaches is required to best understand global plant responses to fewer, larger rainfall events (Fig. 3).

Types of evidence

Field manipulation experiments typically involve monitoring vegetated plots in rainout shelters where the timing and intensity of rainfall events are inversely altered, thereby keeping total rainfall amounts (annual or growing season) constant[94,95]. This approach arguably represents the smallest in situ spatial scale of inference, which allows for control over rainfall, soil and vegetation conditions (Fig. 3a). However, these experiments are expensive and thus have limited applicability for understanding global ecosystem behaviour.

Observation-driven approaches span large spatial scales (Fig. 3b) and apply statistical methods to satellite-based vegetation indices or tower-based carbon flux measurements to estimate how plants respond to variations in daily rainfall frequency and intensity. Such approaches benefit from vegetation observations that integrate over ecosystems and span regional-to-global scales. However, observation-driven approaches rely on uncertain statistical approaches to partition vegetation responses to rainfall variability. Additionally, if the observational record is short, this approach often relies on space-for-time substitutions, which use an uncertain assumption that variations in vegetation behaviour across different regional or global locations can predict vegetation changes over time[77].

Process models range from minimalist models that develop analytical representations of vegetation response to climate with the fewest parameterizations possible[96,97] (Fig. 3c) to numerical, gridded dynamic vegetation models with interactive land surface hydrology schemes[91] (Fig. 3d). Minimalist models represent variability in daily-scale rainfall inputs using a stochastic process (parameterized by the mean wet day frequency and intensity) and propagate its effects across the soil–plant system through mass and energy balance equations that account for evapotranspiration, drainage and runoff[96–98] (Fig. 3c). Additional plant responses, such as photosynthesis, assimilation or growth, are then coupled to the soil moisture balance equations using soil moisture stress functions[99–101]. Although these models represent a simplification of natural processes, they provide a testbed to attribute drivers of the vegetation response to rainfall frequency and intensity. Numerical terrestrial biosphere process models include similar soil moisture

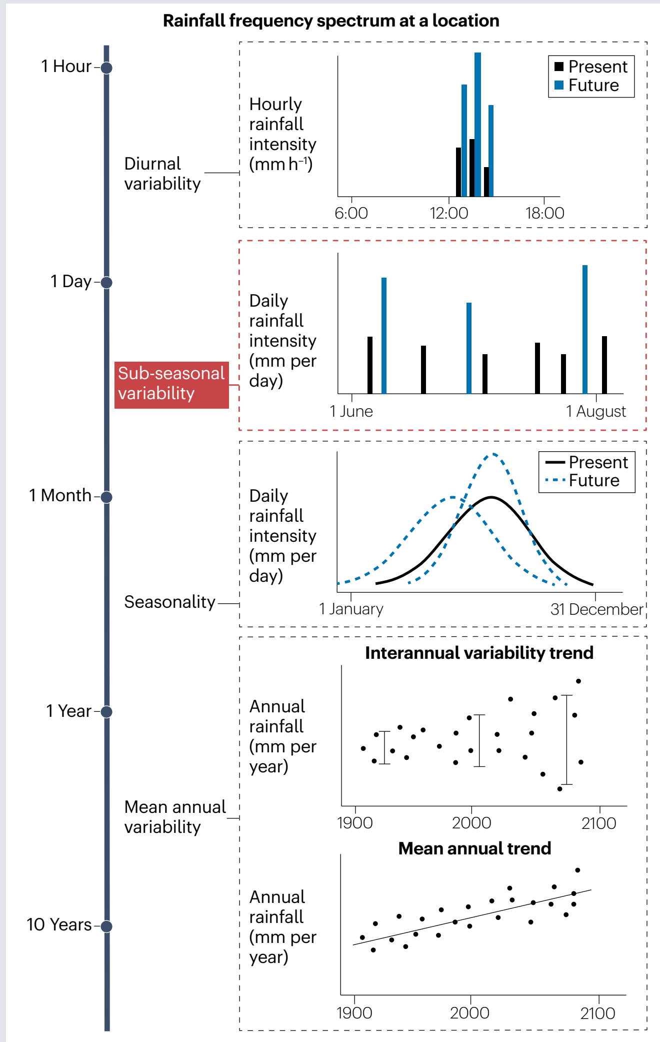
Box 1

The role of sub-seasonal rainfall variability across timescales

Although the focus in this Review is on less frequent but more intense rainfall events, these sub-seasonal rainfall features occur among and even influence rainfall variability and trends at other timescales[246–249], making the study of these phenomena more impactful beyond these shorter timescales. Considering even shorter timescales, rainfall is intensifying at hourly timescales (diurnal variability)[20] (see the figure). As such, these more intense hourly storms are partly driving wet days to experience more intense daily rainfall. Longer durations are occurring between these wet days, resulting in more consecutive dry days over a week to months. Changes in these daily-scale rainfall variations take place over days to weeks within a rainy season and thus form rainfall sub-seasonal variability (see the figure).

Rainfall can also change at longer timescales than those considered in this Review. These changes include rainfall seasonality (see the figure), which occurs over longer multimonth periods. Rainfall seasonality is intensifying globally with wetter wet seasons and drier dry seasons[250] and more variability in the seasonal cycle year to year[40,54]. Annual and longer rainfall changes are also occurring including long-term trends in the mean annual rainfall amount and trends in the interannual variability of annual rainfall amount[47] (see the figure).

Nevertheless, these seasonal and annual rainfall amounts rely on sub-seasonal rainfall patterns; globally, 48% of the observed interannual rainfall variability is explained by sub-seasonal rainfall variability, in which wet day rainfall intensity and dry spell length (sub-seasonal characteristics) explain 31% and 17% of interannual rainfall variability, respectively[251]. Furthermore, increasing the intensity of the wet day with the greatest rain depth[23,54], a sub-seasonal characteristic, tends to increase both wet season and annual rainfall totals[40,239,251]. Indeed, in many regions, wet years with higher annual rainfall amounts are often caused by a few large rainfall events within the year[239]. Therefore, sub-seasonal rainfall variability trends are likely partially driving rainfall trends at seasonal and interannual timescales.



stress functions[91]; however, they have a higher specificity for climate and plant function in each model pixel and interaction across pixels, which provides scaled-up estimates of vegetation behaviour and their variations across space (Fig. 3d). Biosphere models additionally include soil moisture vertical distributions, atmospheric boundary layer characteristics, effects of VPD and light, seasonal phenology and tree–grass competition[91]. Nevertheless, their vegetation responses to the environment tend to be simplified, and attribution of outputs is more challenging than for minimalist models.

Overview of plant responses

Integrating data from the diverse approaches mentioned earlier provides an opportunity to assess the robustness of plant responses to fewer, larger rainfall events. Published studies were surveyed that used the aforementioned approaches to quantify the magnitude and sign of plant function responses to fewer, larger rainfall events (Supplementary Information). 'Plant function' is broadly defined here as comprising photosynthesis, greenness and growth — and in some cases plant water status and community composition. This synthesis indicates that plants have variable responses to fewer, larger rainfall events across vegetation types, global regions and approaches (Fig. 4a). Namely, plant function increases, decreases or remains approximately constant under fewer, larger rainfall events in 35% (±6%, referring to the bootstrapped standard deviation), 42% (±6%) and 23% (±5%) of cases, respectively. Across approaches, fewer, larger rainfall events cause −28% to 29% (5th to 95th percentile) shifts in plant function (Fig. 4b), related mostly to responses of their above-ground plant biomass[74] and above-ground net primary productivity[26].

Despite annual and seasonal rainfall amounts generally having greater effects on plant function than daily rainfall frequency and intensity[72,77,82], plant responses to fewer, larger rainfall events across global ecosystems are substantial (Fig. 4b). Above-ground plant responses (encompassing biomass, vegetation cover, primary productivity) to sub-seasonal rainfall variability are often found to be less than 20% of the magnitude of plant responses to variations in total annual rainfall[32,72,79,102]. However, fewer, larger rainfall events change annually averaged plant function by an absolute median magnitude of 10% and 35% at the 95th percentile (Fig. 4b). For context, these response magnitudes are generated from daily rainfall treatments on average ranging from daily rainfall depths of 7 mm to 27 mm and dry spell lengths of 8 to 21 days, at least in the case of field manipulation experiments, and thus extreme rainfall scenarios were avoided in computing these magnitudes. Indeed, findings of up to 35% changes in plant function with fewer, larger rainfall events suggest that sub-seasonal rainfall changes alone can greatly influence global ecosystems[34,103].

The magnitude of above-ground plant response to fewer, larger rainfall events varies across climate gradients (Fig. 4b). Magnitudes of response are mixed in dry ecosystems (annual rainfall < 500 mm) and show a 0% median response (based on the subset with reported response magnitudes), although responses are most commonly positive in these ecosystems (Fig. 4c). By contrast, plant responses show a 17% median decrease in transitional ecosystems (annual rainfall 500–750 mm) and a 12% median decrease in wet ecosystems (annual rainfall > 750 mm) (Fig. 4b). Note that dry ecosystems are defined here as those receiving <500 mm of annual rainfall consistent with dryland ecological definitions[104], although we acknowledge that other dryland definitions exist based on metrics that include energy availability[43].

The largest absolute magnitude responses to fewer, larger rainfall events based on the synthesis here occur in regions with a transitional climate. In these transitional regions, the absolute median magnitude plant response is 25% (±5%), which is larger than both drier (4 ± 5%)

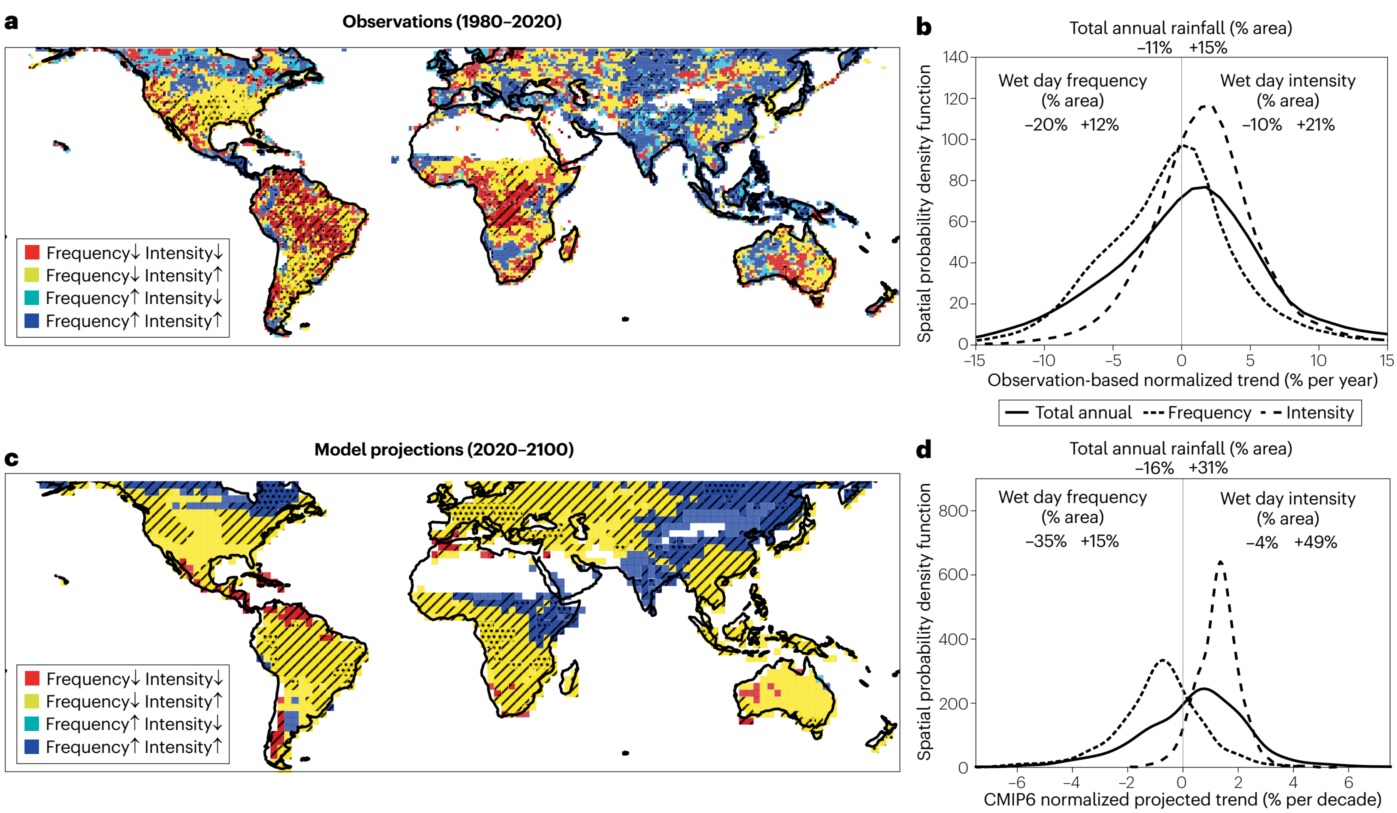


Fig. 2 | Global trends in daily rainfall event frequency and intensity on vegetated land surfaces. a, The rainfall event frequency and intensity direction of the trend, based on the median trends across three observation-based products (1980–2020)[51–53] (Supplementary Information). Pixels are binned based on whether more than half of the data sets show that median wet day frequency trend is increasing (more) or decreasing (fewer), as well as whether the median wet day rainfall intensity is increasing (larger) or decreasing (smaller). Significance is determined if at least one (slash hatching) or both (stippling) of the individual wet day frequency and wet day rainfall intensity trends are significant across more than half of the data sets (using Mann–Kendall trend tests; $P < 0.05$). **b**, Global spatial distributions of ensemble mean normalized trends (in percent-change units) across three observation-based data sets for each individual metric: wet day frequency, total annual rainfall and wet day rainfall intensity. Only regions within −60° to 60° latitude are included. Using Mann–Kendall trend tests, statistically significant ($P < 0.05$) trends are reported as percent land area of increases and decreases for annual rainfall amounts, wet day frequency and wet day rainfall intensity. Percent areas are means across the data sets. **c**, Same as panel **a** but using CMIP6 projections from a 28-member model ensemble with daily data under the RCP8.5 scenario[244,245] (Supplementary Table 1). **d**, Same as panel **b** but using CMIP6 projections. Note that the axes limits in panels **b** and **d** are different. Observations and model projections suggest that rainfall events are becoming less frequent but more intense.

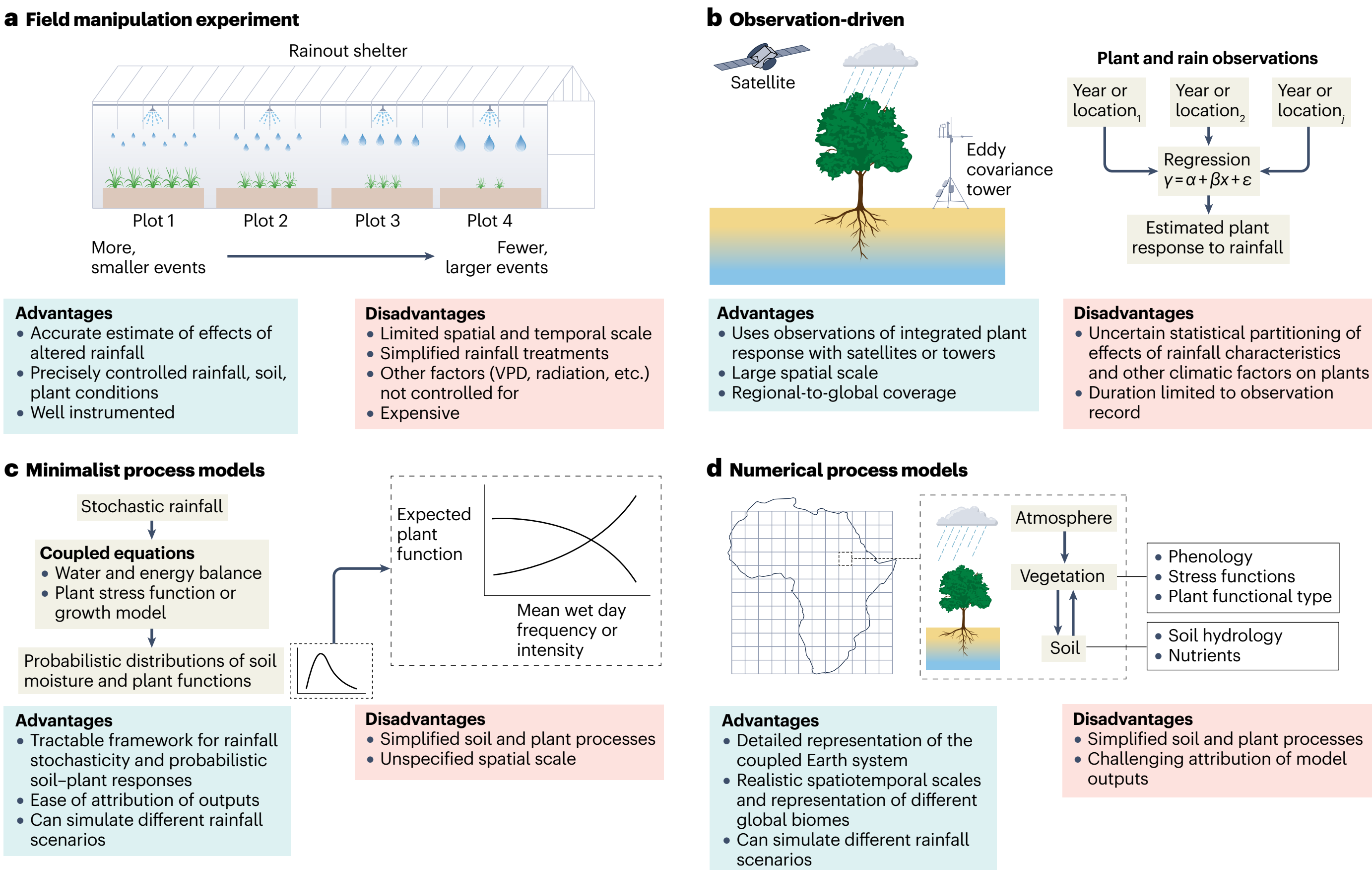


Fig. 3 | Approaches to understand plant response to fewer, larger rainfall events. **a**, Basic descriptions, advantages and disadvantages of field manipulation experiments. Field manipulation experiments typically include vegetated plots with rainfall altered artificially by irrigating the plots in prescribed sequences (such as with higher water additions over a given day, but with longer intervals between irrigation) while preventing ambient rainfall from entering the plot. **b**, As in panel **a**, but for observation-driven approaches. Observation-driven approaches typically involve using statistical models to predict observed vegetation metrics (using satellite or field tower measurements) from observed climate conditions. Specifically, data pairs of plant (y) and climate (x) conditions in different years or different locations are run through a regression to estimate how plant function responds to variations in daily rainfall frequency and intensity. **c**, As in panel **a**, but for minimalist process models. Minimalist process models first simulate a rainfall scenario and then use the rainfall to drive a simplified series of mass and energy balance equations that describe the response of plants to climate. **d**, As in panel **a**, but for numerical process models. Numerical process models are similar to minimalist models but describe vegetation over regional or global grids where interactions among soil, vegetation and atmosphere are parameterized differently in each grid depending on the climate and vegetation types of that location. Given disadvantages of all approaches, combinations of these approach types are necessary to understand global plant response to fewer, larger rainfall events and underlying drivers. VPD, vapour pressure deficit.

and wetter regions (11 ± 4%). There is supporting regional evidence from numerical biosphere models that the highest plant sensitivities to fewer, larger rainfall events occur in transitional, sub-humid environments[90,91]. By contrast, although not captured in our overall synthesis, the highest plant response magnitudes are sometimes found in the driest environments[102], with a decreasing plant response to sub-seasonal rainfall variability as mean annual rainfall increases based on regional observations[32,83], a minimalist analytical model[87] and a field experiment altering annual rainfall amounts at a single site[105].

Above-ground plant responses appear to vary across vegetation types. Among wet ecosystems that have similar mean annual rainfall conditions, grasslands have an approximately twofold-greater absolute magnitude response to fewer, larger rainfall events (median change of 16 ± 5%) than wet forests (median change of 9 ± 3%). However, small sample sizes limit comparison with shrubs and other vegetation types.

Although below-ground plant responses are evaluated less often than above-ground plant responses[35,37], root systems appear to shift deeper with fewer, larger rainfall events. Field experiments have shown that fewer, larger rainfall events increase overall below-ground growth and root–shoot ratios of grasses and forbs by 20% and 33%, respectively[106]. Similarly, there is some evidence of opposing root responses in different soil layers, with grass root biomass increases in deep soil layers under extreme rainfall pulses[107], but fine root growth decreases in shallow layers with fewer, larger rainfall events[67,71,108]. As with above-ground plant responses, below-ground plant biomass does not always change in response to fewer, larger rainfall events[109,110].

Contrasting plant responses in dry and wet ecosystems

Consistent with an earlier hypothesis[42], plant responses to fewer, larger rainfall events tend to change from dry to wet ecosystems. Plants in dry ecosystems generally show more positive but also more variable responses to fewer, larger rainfall events, whereas wet ecosystem plants show mainly negative responses[33,111] (Fig. 4).

Previous syntheses of field experiments suggest that plants in dry ecosystems tend to show increased plant function under fewer, larger rainfall events[33,41,111]. However, the typical dry ecosystem response appears more mixed when also including satellite observations in our synthesis (Fig. 4). According to the field experiments, plants in dry ecosystems increase or do not change their above-ground biomass (AGB)[71], gross primary production (GPP)[70] and net primary production (the net carbon balance of GPP and plant respiration)[26,112] (Fig. 4a) and in some cases even where no mean GPP response occurs, GPP still shows shifts in the timing of its seasonal cycle[70]. Similarly, modelled dry ecosystem AGB[25,39,88] and GPP[91] mainly increase under fewer, larger rainfall events. However, satellite-based observations show mixed responses to fewer, larger rainfall events in dry ecosystems, with satellite-based vegetation greenness staying constant[84] or even declining[81,83]. Although the median magnitude response of dryland plants to fewer, larger rain events is 0%, the range of responses is wide with 90% confidence bounds extending from −11% to 27% (Fig. 4b). Plants in dry ecosystems increase, decrease or maintain function under fewer, larger rainfall events in 46% (±9%), 20% (±8%) and 33% (±7%) of cases, respectively (Fig. 4c).

In contrast with plants in dry ecosystems, plant function in wet ecosystems primarily decreases with fewer, larger rainfall events (Fig. 4). GPP[92], AGB[90], carbon assimilation[87] and normalized difference vegetation index[81] all decrease under fewer, larger rainfall events in the majority of cases across regional observations and models. Negligible plant responses to fewer, larger rainfall events do occur in some wet ecosystems, but are infrequent[83,113]. Field manipulation experiments in wet ecosystems have shown decreased carbon fluxes with these rainfall regime shifts[72,114], although these have been limited to sub-humid biomes (500–1,000 mm of yearly rainfall) with short-statured vegetation. Overall, plants in wet ecosystems have a median response magnitude of −12% with wide-ranging responses with 90% bounds of −33% to 27% (Fig. 4b). These plants show decreased function under fewer, larger rainfall events in 51% (±9%) of cases, while increasing and maintaining function in 28% (±8%) and 20% (±7%) of cases, respectively (Fig. 4c). Therefore, contrasting directions of dry and wet ecosystem responses to fewer, larger rainfall events indicate that differences between these ecosystems cause their behaviour to diverge and that global vegetation responses to changing rainfall sub-seasonal variability are likely variable.

Differences in vegetation types do not appear to explain plant response differences across dry and wet ecosystems. Both trees and grasses in wet ecosystems show typically negative responses to fewer, larger rainfall events, at a 57% (±19%) and 57% (±13%) rate, respectively (Fig. 4d). Additionally, grass responses differ substantially across dry and wet ecosystems; dry ecosystem grasslands have less common negative responses (17 ± 9%) than wet grasslands (57 ± 13%) (Fig. 4d), suggesting that local mean rainfall rates have a greater influence on the frequency of negative responses than vegetation type does. Dry ecosystem grasslands also have a smaller response to fewer, larger rainfall events (median change of 2 ± 4%) than wet ecosystem grasslands (median change of 16 ± 5%). Thus, vegetation types are not likely to be the main drivers of differences between dry and wet ecosystems.

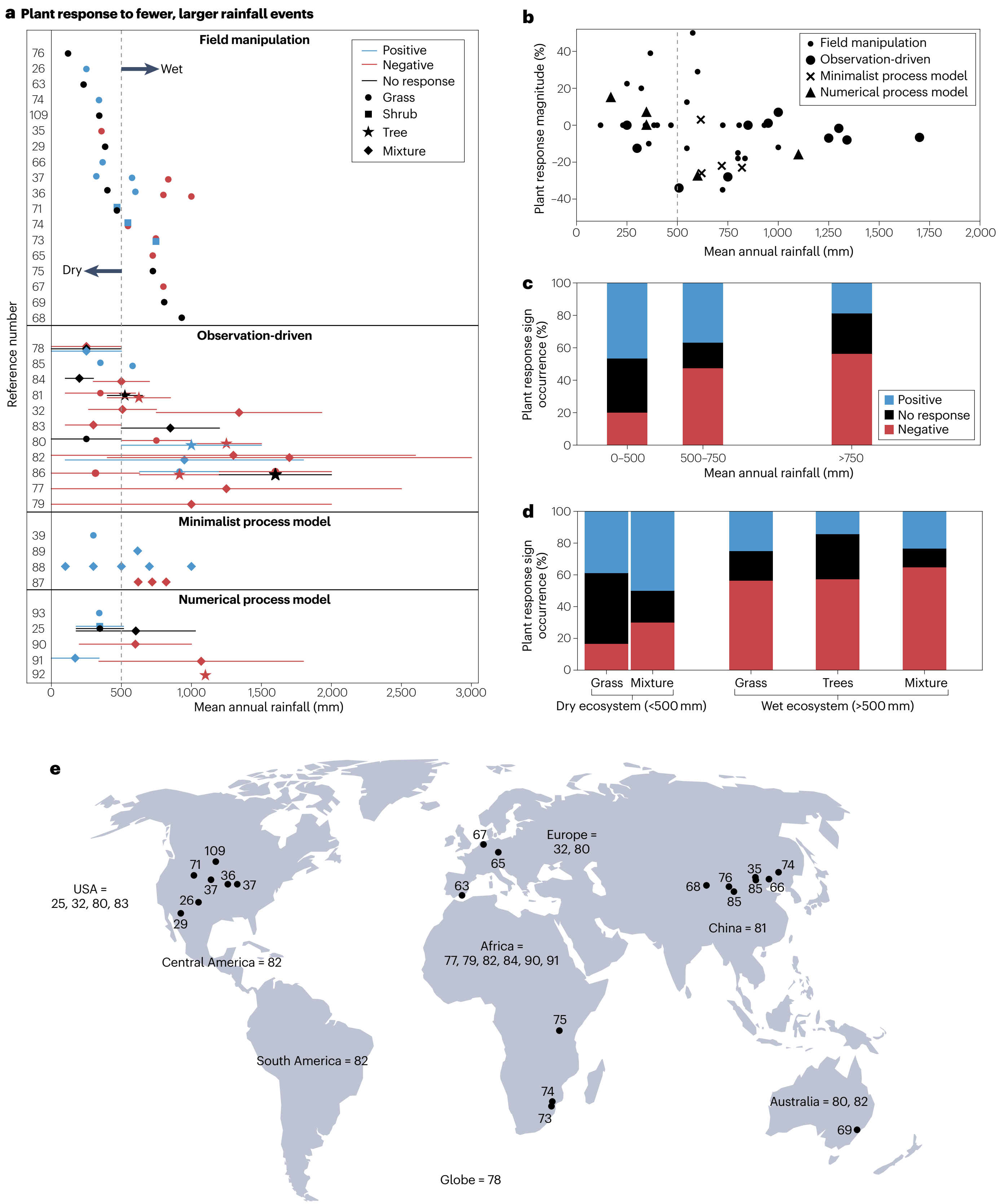
The transition to more positive plant responses to fewer, larger rainfall events in dry ecosystems is not captured by observation-driven approaches. According to observation-driven approaches, 50% of the dry and wet ecosystems studied showed negative plant responses to fewer, larger rainfall events (Fig. 4). The lack of changes in plant function between dry and wet ecosystems in observation-based data is likely a consequence of observation-driven approaches using space-for-time substitutions that assume spatial variations in mean vegetation responses and wet day frequency can predict plant function variations in time[77,80]. Within this approach, a wide range of climates are often considered, including tropical forests[77], in determining a single, overarching plant response across all considered regions. The influence of wet ecosystems incorporated into the space-for-time substitutions might therefore dominate the overall response when evaluating dry ecosystems. Nevertheless, the wide range of wet ecosystems considered[77] support the idea that negative plant responses to fewer, larger rainfall events are occurring in wet ecosystems (Fig. 4a,e).

Assessing long-term plant responses

Sustained changes to fewer, larger rain events over decadal or longer periods might include additional, large plant responses beyond those considered in our synthesis. Most analyses considered in our summarized insights (Fig. 4) mainly only reflect rapid plant physiological responses[115]. This is because most field manipulation experiments are typically short in length, between 1 and 6 years long[116,117], and many modelling approaches implicitly assume that the composition of the plant community and its sensitivity to climate is constant. Sustained climatic changes over multiple decades will likely result in slower plant responses, including mortality, plant acclimation, evolutionary adaptation and species turnover[115,118–120]. The complexity of slower plant responses is highlighted more generally by the hierarchical response framework, which poses that slower responses to chronic resource alterations (such as fewer, larger rainfall events) can occur after a delay and might have the largest cumulative impacts on ecosystem functioning over time[119]. Such climate disequilibria, in which the ecosystem response does not keep pace with rainfall changes, are now recognized as among the greatest sources of uncertainty in projecting the response of plant function to climate change[115].

Although the majority of field experiment lengths have been too short to observe the extent of plant responses to long-term processes, shorter term (sub-decadal scale) plant responses across different species at experimental sites can provide insights into slower plant community changes. First, there is evidence that fewer, larger rainfall events can shift community composition. For example, large rainfall pulses can wet deeper soil layers where shrub rootzones extend and substantially increase their above-ground and below-ground growth, which promotes the replacement of herbaceous plants with woody plants[71,73,121]. Second, there are species-specific differences in responses to fewer, larger rainfall events that can influence community composition. For example, grasses and forbs in the same site can have distinct responses[70,122,123]. Different grass species within the same site can also have disproportionate responses in the same direction[26] or even in opposite directions[35,108]. Therefore, fewer, larger rainfall events can shift community composition (such as woody encroachment) and consequently, owing to differences in species response, change the response of the whole ecosystem[124–126].

Although considering rainfall changes at longer timescales than sub-seasonal scales here, some decade-long field experiments have detected slow plant responses. For example, shifts in grass community composition, including their species diversity and dominant plant functional types, have been tracked over several decades under rainfall and temperature changes[127,128]. A 13-year drought experiment found



a Plant response to fewer, larger rainfall events
Field manipulation
Observation-driven
Minimalist process model
Numerical process model
Positive
Negative
No response
Grass
Shrub
Tree
Mixture
Wet
Dry
Reference number
Mean annual rainfall (mm)
b
Field manipulation
Observation-driven
Minimalist process model
Numerical process model
Plant response magnitude (%)
Mean annual rainfall (mm)
c
Plant response sign occurrence (%)
0–500
500–750
>750
Mean annual rainfall (mm)
Positive
No response
Negative
d
Plant response sign occurrence (%)
Grass
Mixture
Grass
Trees
Mixture
Dry ecosystem (<500 mm)
Wet ecosystem (>500 mm)
e
USA = 25, 32, 80, 83
Central America = 82
South America = 82
Europe = 32, 80
Africa = 77, 79, 82, 84, 90, 91
China = 81
Australia = 80, 82
Globe = 78

Fig. 4 | Synthesis of plant responses to fewer, larger rainfall events. **a**, Plant response to fewer, larger rainfall events by approach type, which evaluates the direction of photosynthesis and/or growth. Each row denotes the results from one study, corresponding to the citation number in the references. These studies were selected using a Google Scholar search of keywords and resulted in 38 studies that evaluated 72 unique sites (Supplementary Information). Horizontal lines denote the range of mean annual rainfall values over which the study was conducted and over which the response was determined. Symbols denote the mean annual rainfall of the study domain and which vegetation types dominate the site. The vertical dashed line denotes the defined transition between dry and wet ecosystems at 500 mm of annual averaged rainfall. **b**, Annual-scale plant response magnitudes to an expected shift to fewer, larger rainfall events on a percent-change basis. Only data from 25 of the 38 studies shown in panel **a** that explicitly report magnitudes of photosynthesis or growth responses are included. The corresponding mean annual rainfall value is the mean of that reported in panel **a**. **c**, Percentage of studies in panel **a** showing positive, negative or no plant response to fewer, larger rainfall events within each mean annual rainfall bin. If the site spans a mean annual rainfall gradient that is less than 1,000 mm, then it is included in a bin based on its average of its annual rainfall span (location of the symbol in panel **a**). **d**, Similar to panel **c** but directions of responses are determined for different vegetation types. Only those with at least five data points are plotted. **e**, Experiment locations, with dots denoting those that took place at a specific location; those with a continent or country name refer to those taking place over a large area within that location. Plants in dry and wet ecosystems diverge in their response to fewer, larger rainfall events.

tree sensitivity to drought decreased over the experiment, suggesting acclimation[129]. In one case evaluating the effects of fewer, larger rainfall events, a shift from grass to forb cover occurred after a 10-year lag[130]. Moreover, lagged effects might occur where fewer, larger rainfall events can initially generate more vegetation growth, but the increased growth and thus water demand leaves the ecosystem more vulnerable to extreme water deficits (referred to as structural overshoot)[131,132]. The timescales of slow acclimation and species responses are uncertain and likely widely varying[119], although the pace of plant species compositional changes seems to lag by decadal timescales[119,133].

Finally, although the focus of this Review is plant responses to changes in daily rainfall frequency and intensity, we note that plant responses to fewer, larger rainfall events will interact with other longer-term climatic changes. Increasing atmospheric CO_2 concentrations are expected to reduce stomatal conductance across ecosystems with more plant carbon uptake per unit loss of water through transpiration, or higher water use efficiency[134,135]. The consequent changes in plant sensitivity to water availability owing to these CO_2 fertilization effects might differentially alter plant responses to larger rain pulses and longer dry spells[136]. Furthermore, increasing air temperature and VPD are expected to have the opposite effect to increasing CO_2 on plants in that they are expected to cause a reduction in plant growth and greater water stress during drydown periods[31,137].

Plant–soil mechanisms under variability

Larger rainfall events and longer dry spells have complex and opposing influences on plant function. Therefore, to explain complex plant responses to fewer, larger rainfall events (Fig. 4), it is important to understand how plants respond to more intense daily rainfall and longer dry spells and specifically the impact on water flow through the soil–plant–atmosphere continuum[138]. Subsequently, we discuss mechanisms through which the soil–plant–atmosphere system responds to larger rainfall pulses and longer dry spells, as well as how the mechanisms explain variable plant responses to fewer, larger rainfall events (Fig. 4).

Impact of larger rainfall pulses on the soil–root system

The impact of more intense rainfall pulses on plants depends on the degree to which this rainfall infiltrates into the soil, how this infiltration alters the vertical distribution of soil moisture relative to the rooting profile and whether soil moisture is increased above thresholds for root water uptake (it also depends on the sensitivity of the plant function to soil moisture increase; see the following section).

The infiltration of rainfall pulses in general depends on modulating factors such as soil texture, antecedent soil moisture, topography and vegetation cover (Fig. 5a). Infiltration is greatest and deepest with coarser soils[139,140], initially moderately dry soils[141–143] and less-sloped surfaces[71]. Vegetation can both increase infiltration, owing to roots creating soil macropores[45,144], or decrease infiltration owing to interception of rainfall by the vegetation canopy, which can be rapidly evaporated[145]. Overall, with larger rainfall events, infiltration is expected to increase[25,70,146] owing to both higher rainfall volumes and globally reduced interception because vegetation tends to intercept proportionally more rainfall under smaller rainfall events[145,147]. Smaller rainfall pulses infiltrate less because of increased soil evaporation and interception relative to rainfall. However, more intense rainfall on wet days can cause increased runoff, for example, when the sub-daily rainfall intensity (mm h^{-1}) is greater than the infiltration rate or when high antecedent soil moisture inhibits new infiltration[142,143,148]. In dry ecosystems, runoff might be less pronounced because wet thresholds are only exceeded briefly during larger rainfall events[42,107] and often result in lateral redistribution of rain water to surrounding soil and plants[149–151]. Furthermore, deep drainage can limit how much infiltrated water remains in the rootzone. Larger rainfall events increase deep drainage more in wet ecosystems[25,27] with only marginal changes in dry ecosystems where deep drainage is often negligible, regardless of soil texture[27,139,152].

For plants to respond to an increase in infiltrating water from larger rainfall pulses, soil moisture increases must overlap with the rooting profile[153]. Across wet and dry ecosystems, large rainfall events increase rootzone soil moisture[154] and at greater depths (>50 cm) than small rainfall events, which might infiltrate only into the top few centimetres of soil[70,122,155] (Fig. 5a). Ecosystems with woody plants, which tend to have deeper rooting[156,157], can disproportionately benefit from larger rainfall events that increase deeper rootzone soil moisture[25,88,158]. Rooting distributions themselves sometimes change from larger rainfall events: for example, below-ground biomass can increase by 20–30% in dry and wet grasslands[106,107], although it often does not change[34,71,109,110]. Despite the observations mentioned earlier, there is a lack of evidence that any specific rooting strategies consistently benefit more from larger pulses. This might be because both soil texture and climate modulate the interaction between soil moisture and rooting distribution. For example, finer soils benefit shallower rooting systems because a larger rainfall pulse is less able to penetrate deeper into the rootzone, and the finer soil is able to retain moisture longer[159]. This case might only benefit plants in wet ecosystems, where the retained soil moisture is lost less to soil evaporation than in dry ecosystems, as suggested under the inverse texture hypothesis[104,160]. Under this hypothesis, root systems in dry ecosystems are likely better served by coarser soils as deeper

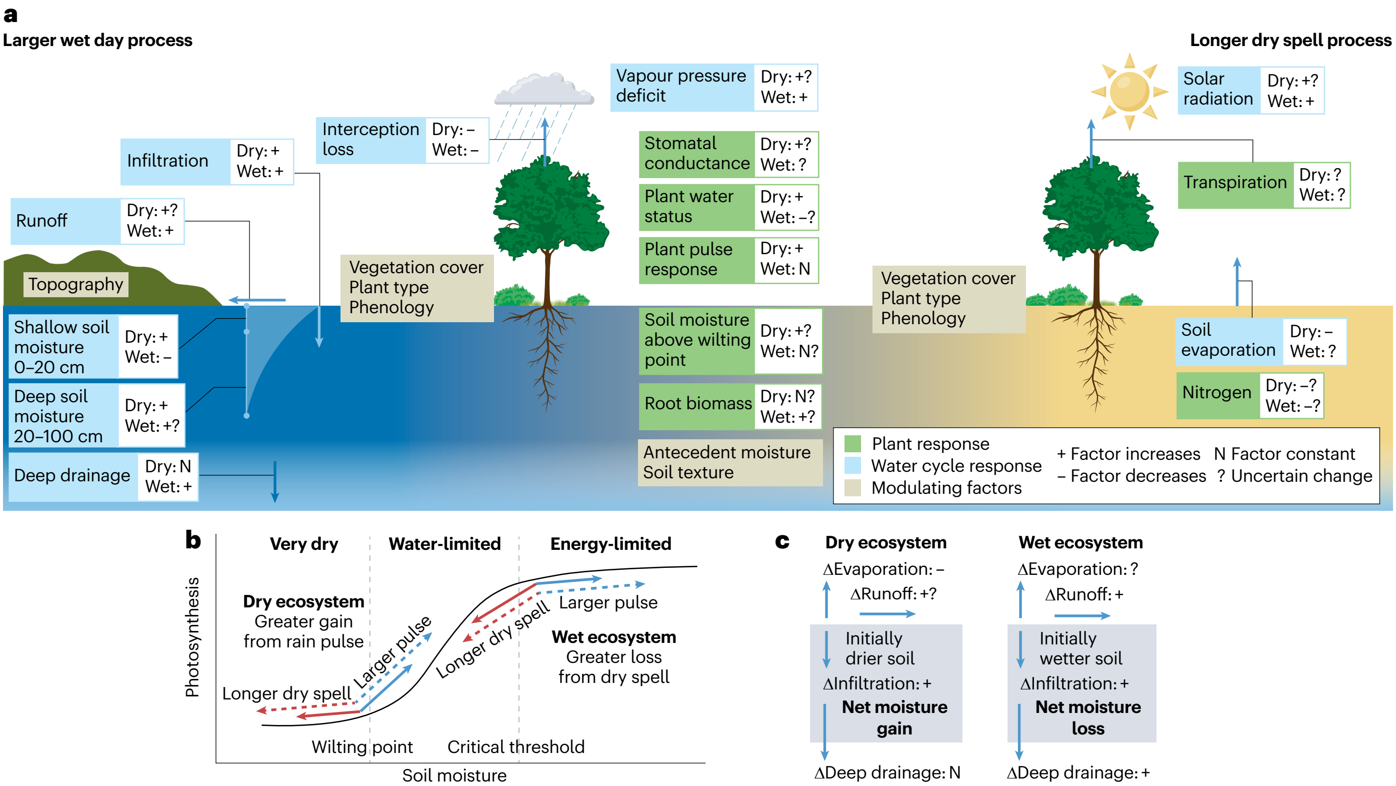


Fig. 5 | Mechanistic drivers of plant function under fewer, larger rainfall events. a, Mean annual soil–plant–atmosphere response to fewer, larger rainfall events. Each box denotes a different state or flux impacted by fewer, larger rainfall events. 'Dry' and 'wet' designations for each factor refer to dry and wet ecosystems. '+', '–' and 'N' symbols represent that the respective factor increases, decreases or does not change with fewer, larger rainfall events, respectively, based on previous findings. The '?' symbol indicates that a low amount of evidence supports the indicated change (supported by only one or two studies). Drivers relating more to the wet day rainfall pulse are concentrated on the left and those related more to the dry spell are concentrated on the right. **b**, Effect of the nonlinear relationship between soil moisture and photosynthesis on plant responses to fewer, larger rainfall events. **c**, Summarized response of annual mean soil moisture and driving mean hydrological flux changes in dry and wet ecosystems under fewer, larger rainfall events. Both the nonlinear photosynthesis–soil moisture relationship and annual mean soil moisture changes can explain differences in plant responses to fewer, larger rainfall events.

infiltration in coarse soils will reduce the amount of water lost owing to high surface soil evaporation rates.

For a plant to respond to a larger rainfall pulse, the rootzone soil moisture needs to increase above a threshold[161,162]. Plants have soil moisture thresholds; for example, the wilting point roughly defines the threshold below which plant hydraulic transport capability is impaired[163] and plants are less able to draw soil water[164] (Fig. 5b). There are also soil moisture thresholds above the wilting point (called 'critical thresholds'), below which plants show water-limited behaviour and above which plants show energy-limited behaviour[100,165,166] (Fig. 5b). Dry ecosystems typically spend more time in water-limited regimes between the critical threshold and the wilting point[42,167], and larger wet day soil moisture increases therefore would lead to a greater increase in photosynthesis and growth given the nonlinear relationship between these plant functions and soil moisture[164,166,168]. In wet ecosystems, plants spend more time in energy-limited regimes above the critical, water-limitation threshold and thus larger rain pulses are typically less ecologically advantageous[167]. There is evidence that even-wetter soil moisture thresholds exist beyond the critical threshold, above which water-logging creates anoxic rootzone conditions[42], and thus much larger rainfall pulses would reduce plant function[169]. Soil texture modulates all of the above thresholds and plants are ultimately sensitive to the soil water potential, which integrates both soil moisture and soil texture[170].

Impact of larger rainfall pulses on above-ground plant function

Plants have varying sensitivities to soil moisture and thus varying sensitivities to larger rainfall pulses. In response to larger moisture pulses, most plants increase water status, stomatal conductance, carbon uptake, transpiration and growth[171–175]. To predict how plants will respond to larger rainfall events, it is key to understand how plants respond to large rainfall events in the present climate, as a proxy for rain pulses that would be more common in a future climate[107,176]. Herbaceous plants – especially in dry ecosystems – appear to be proportionally more responsive to large moisture pulses, with high-magnitude and long-duration plant responses over several days to weeks, even while soil moisture is drying[45,168,173,177–180]. As an example of this dry ecosystem plant pulse response, FLUXNET sites near Tucson, Arizona, have shown that the average GPP in dryland grasses and shrubs increases over several days following large rainfall events (>75th percentile)[181,182] (Fig. 6a,b). Dryland grasses can grow for several-week periods after these large rainfall pulses during the growing season[107,183], suggesting long-lasting effects on plant function caused by large rainfall pulses. This behaviour has been termed the pulse-reserve paradigm, under which rainfall events cause dry ecosystem plants to grow, store carbohydrates into reserves and then downregulate photosynthesis until the next rainfall event[104,139,184]. According to near-daily satellite observations of the vegetation water content, these multiday plant responses are globally widespread across water-limited ecosystems[185,186].

In contrast with plants in dry ecosystems, plants in wet ecosystems show a weaker response to large rainfall pulses than those in dry ecosystems[187]. They behave similarly in response to rainfall pulses of different sizes and are about half as likely to respond to a rainfall event[176,185]. Figure 6a,b shows an example of plant response to rainfall in a wet ecosystem, with data collected in a forested ecosystem in Indiana. In these wet ecosystem cases, plant function increases are usually rapid and occur within a day following the large pulse (Fig. 6c). Ultimately, smaller plant responses to wet days, especially large rain pulses, in wet ecosystems over dry ecosystems suggest that overall plant function would be less likely to increase in wet ecosystems under fewer, larger rainfall events (Fig. 4c).

Several factors modulate plant sensitivities to rainfall pulses. Phenology changes sensitivities to pulses within and across seasons, with the highest sensitivity to rainfall pulses often occurring early in the growing season[107,154,188,189]. Additionally, drier antecedent soil can increase plant sensitivities to soil moisture, as demonstrated by data showing that larger plant hydraulic and photosynthesis responses occur after rainfall pulses on initially drier soils[139,188]. As such, longer dry intervals between rain events dry the soil more and might increase plant sensitivity to the larger rainfall pulse. Finally, increases in limiting nutrients could increase plant sensitivity to rainfall pulses[190]. However, changes in nutrients are inconclusive under fewer, larger rainfall events with foliar nitrogen increasing in one case[37] and soil inorganic nitrogen available for plant use decreasing in another case[191].

Most minimalist and numerical process models use soil moisture stress functions to connect soil moisture to plant function[96,192] (Fig. 6d). Within these modelling frameworks, a large rainfall pulse wets the surface, translates into a same-day carbon uptake response, and then plant function synchronously reduces as soil moisture declines. Soil moisture stress functions might thus better emulate wet ecosystem responses, which tend to respond synchronously with soil moisture (Fig. 6b). However, stress functions across the available model frameworks would not integrate the observed, several-day-to-week plant responses of dry ecosystems, especially under large rain events that are becoming more common. An observed hysteresis in dry ecosystem plant responses occurs in which responses decouple from soil moisture and plant function progressively increases while soil moisture simultaneously declines[179,185,193,194] (Fig. 6d). As a result of not capturing the multiday extent of dry ecosystem plant responses, models might underestimate the magnitude of dry ecosystem plant responses to larger storms under fewer, larger rainfall events.

Impact of longer dry spells on the soil–plant–atmosphere continuum

In post-rainfall dry spells, soil moisture decreases[195], VPD increases[30] and downwelling surface solar radiation increases with cloud dissipation[167] until the next rainfall event. These processes cause drying throughout the soil–plant–atmosphere continuum[30] and such drying will continue during longer dry spells.

Although the effects of dry spell length on plants are not well studied, fundamental insights about plant responses to longer dry spells can

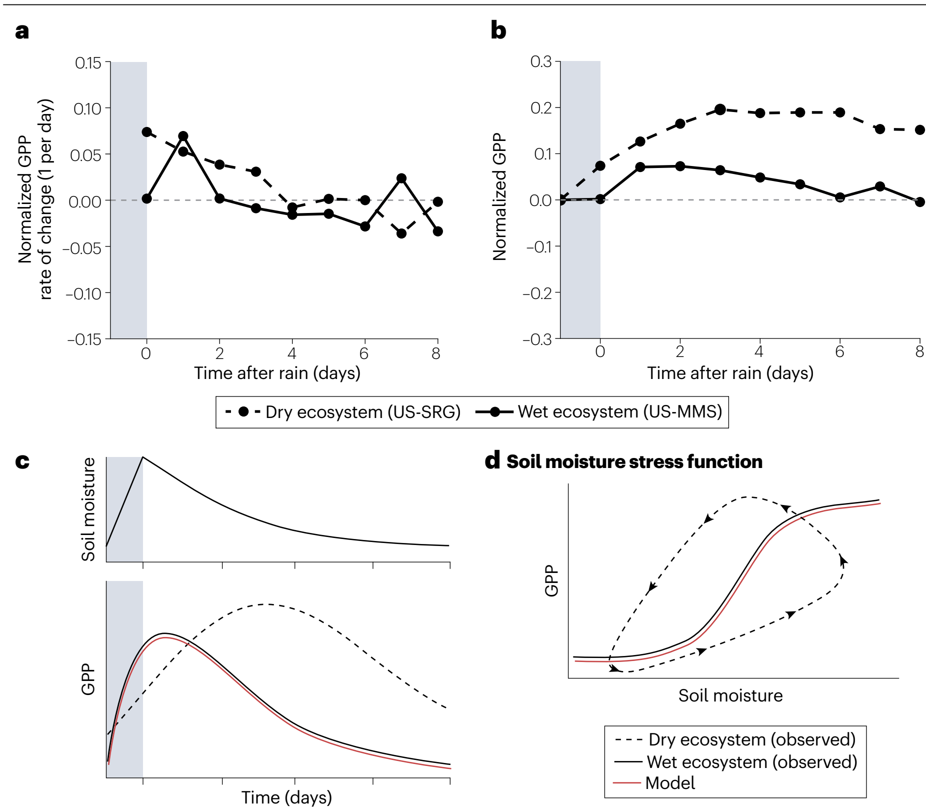


Fig. 6 | Observed and modelled plant response to large rainfall pulses. a, Gross primary production (GPP) in response to a single rainfall event (one wet day or collection of wet days). Only large rainfall pulses are considered (>75th percentile pulse sizes). Field observations are from FLUXNET at a dry, grassland site in Tucson, Arizona (US-SRG; mean annual rainfall is 420 mm)[181] and a wet, forested ecosystem in Indiana (US-MMS; mean annual rainfall is 1,032 mm)[187]. Values are normalized median percentile rates of change; for example, the value at day 1 is the day 1 value minus day 0 value. **b**, Same as panel **a** but GPP cumulative responses are based on the rate of change in panel **a** (Supplementary Information). **c**, Schematic of observed and modelled GPP following a rainfall event for wet (solid) and dry (dashed) ecosystems, as captured in panels **a** and **b**. The hypothesized, modelled (red) response is also shown. **d**, Quantities in panel **c** plotted as a function of soil moisture. Arrows represent the direction of movement along the relationship in time for dry ecosystems, showing a hysteresis. These GPP–soil moisture relationships are considered as soil moisture stress functions. Dry and wet ecosystem plants have different responses to individual wet days, which modelled stress functions might not capture.

be gained from drydown and drought experiments[196], which show loss of soil water potential reduces leaf water potential and increases risk of xylem embolism[197]. Drier leaf conditions, higher VPD and sometimes extended light availability reduce stomatal conductance[198]. Consequently, photosynthesis and growth decrease[30,199,200], and the risk of mortality increases[201]. However, roots can also grow during dry spells[175]. These plant behaviours tend to nonlinearly correlate with soil moisture, and thus thresholds are key to the plant stress response during interstorm drying periods. During the transition from wetter to drier soil conditions, a switch from energy-limited to water-limited evaporation results in a depletion of plant water storage[30]. Continuous reductions in conductance, photosynthesis and growth can then occur with drying[166]. With further drying, drier thresholds (such as the wilting point) are crossed, resulting in xylem embolism, leaf loss and mortality[199,202].

Despite greater wetting and cooling associated with larger rainfall events, the associated longer dry spells generally result in more plant stress during interstorm periods. Fewer, larger rainfall events are associated with at least 10% higher mean annual VPD and downwelling surface shortwave radiation, as determined from field experiments and observation-driven studies[32,80,106] (Fig. 5a). Although such mean annual climate responses do not isolate effects caused by dry spells only, these effects indicate greater transpiration stress during dry spells. The increased mean aridity and light conditions probably occur because the cooling effects of a larger rainfall event are offset by the warming associated with the corresponding longer dry spell, especially amplified, at times, by land–atmosphere feedbacks[30,167]. Furthermore, fewer, larger rainfall events are associated with increased soil moisture variability, meaning that more frequent extreme dryness is experienced during the longer dry spells regardless of the mean soil moisture change[34,42].

Several plant attributes can help to maintain or mitigate loss of function under longer dry spells. The deep rooting profiles of shrubs and trees are advantageous during longer dry spells because shallow soil layer moisture is depleted by dry conditions before deep moisture[45,106,122,203]. Additionally, plants can better mitigate stress during longer dry spells if they have photosynthetic adaptations – for example, plants with C4 photosynthesis and CAM photosynthesis[137,204,205] – or if they actively transport soil water vertically from wet to dry layers using their root systems as a drought adaptive strategy via hydraulic redistribution[206].

The role of soil moisture in plant behaviour between dry and wet ecosystems

The diverse approaches assessed in Fig. 4 have provided a means to gain consensus on shifts in plant behaviour under fewer, larger rainfall events and, by deduction from differences in methodologies[207], have helped to identify the relationship between soil moisture and plant function as a major factor explaining contrasting plant responses in dry and wet ecosystems.

Field manipulation experiments generally alter soil moisture without the concurrent changes in solar radiation and VPD that would naturally occur between wet and dry days[34,35,73,146,208–210]. Under fewer, larger rainfall events, the transition from positive to negative plant responses from dry to wet ecosystems in these experiments supports similar patterns seen in models and observations (Fig. 4), which consider influences of other factors. This similarity between these approaches thus indicates a large role of soil moisture alone in influencing plant responses to sub-seasonal rainfall variability[34,42]. The transition to fewer, larger rainfall events decreasing plant function from dry to wet ecosystems was also reproduced in a greenhouse experiment[211], further supporting a strong role for soil moisture.

Relatively simple minimalist models support the notion that the overall response of vegetation to fewer, larger rainfall events is strongly dependent on the relationship between plant function and soil moisture. According to these models, annual rainfall amounts alone are insufficient to explain observed annual mean plant responses, as rainfall event frequency and intensity are also needed to explain biomass accumulation[89]. A switch to increased biomass in dry ecosystems with fewer, larger rainfall events was also captured from coupling minimalist models to a growth model that contains a soil moisture threshold for growth[39,89]. Using this growth model, fewer, larger rainfall events resulted in occasional exceedance of the soil moisture threshold, which triggered intermittent growth; by contrast, this threshold was never crossed and no growth occurred when rainfall was distributed more evenly across many smaller storms. As such, according to these models, the plant response to sub-seasonal rainfall variability is influenced by the plant function–soil moisture relationship and its soil moisture thresholds. The transition between dry and wet ecosystem behaviour is captured across these approaches that both do and do not consider factors other than soil moisture (for example, light, atmospheric aridity), suggesting that soil moisture is a dominant and consistent driver under fewer, larger rainfall events[91].

Contrasting key soil–plant mechanisms in dry and wet ecosystems

We argue that the differing plant responses to fewer, larger rainfall events in dry and wet ecosystems can be explained, primarily, by the nonlinear relationship between plant function and soil moisture and by differing mean annual soil moisture changes.

Plant hydraulic and photosynthetic functions tend to have a nonlinear sigmoidal relationship with soil moisture[164,166,185] (Fig. 5b). For most plants, low sensitivity to soil moisture occurs either at a very dry state below the wilting point threshold[164,212,213] (Fig. 5b) or under a wet, energy-limited regime where radiation and aerodynamic considerations limit plant function (Fig. 5b). Higher plant sensitivity to soil moisture is experienced in the intermediate, water-limited regime. This relationship between plant function and soil moisture is well known to hold at annual timescales[214,215] and also occurs at daily timescales[165,185].

Dry ecosystems spend more time in the water-limited regime[216,217]. As such, a larger rainfall pulse greatly increases dry ecosystem plant function, either because conditions remain water-limited and more pulsed soil moisture directly results in greater plant function or because conditions are initially very dry and soil moisture is increased above very dry thresholds (wilting point)[188] (Fig. 5b). Additionally, plants in dry environments tend to be more sensitive to soil moisture and larger rain events than in wet environments, both because of their more water-limited conditions on average and because dry ecosystem plants tend to be relatively more sensitive to water in dry conditions than wet ecosystem plants[176,218,219] (Fig. 6). Furthermore, plant function decreases owing to longer dry spells might be limited in dry ecosystems; in dry ecosystem plants, mean plant water potentials increase up to 25% with fewer, larger rainfall events, implying that plant function loss is limited under very dry conditions relative to gains from larger moisture pulses[37,146].

By contrast, wet ecosystems spend more time energy-limited than dry ecosystems[216,217]. Therefore, with longer dry spells, wet ecosystem plants can experience continuous losses of function with drying into the water-limited regime. Furthermore, benefits from larger pulses are limited by energy and moisture increases only lead to marginal plant function increases[166] (Figs. 5 and 6). Indeed, wet ecosystem plant responses to rainfall pulses are weaker than those of plants in dry ecosystems, even in comparatively dry conditions[176,218,219] (Fig. 6). Very wet ecosystems might not respond to rainfall changes at all if dry spells are not long enough to dry soil moisture below moisture thresholds.

Because dry and wet ecosystems exist on different endpoints of the nonlinear relationship between soil moisture and plant function (Fig. 5b), they exhibit different response functions to rainfall variability. Ultimately, we argue that this nonlinearity largely dictates the opposing directions of response to fewer, larger rainfall events, as is broadly observed (Fig. 4) — specifically, a net loss for wet ecosystem plant function and typically a net gain or a net balance in dry ecosystems. This nonlinearity might be largely responsible for any non-zero plant function changes under fewer, larger rainfall events; indeed, a linear relationship between plant function with soil moisture would result in no change in plant function if the larger rainfall event is balanced by an equivalent soil moisture reduction from the longer dry spell. This non-zero response to an input variance owing to the nonlinearity of the response function is referred to as Jensen's inequality[214,220]. Furthermore, the nonlinearity between plant function and soil moisture captures the soil water bucket model paradigm, which argues that fewer, larger rainfall events will provide a net benefit for dry ecosystem plants because larger rainfall events result in more frequent increases of soil moisture above dry moisture thresholds, and a net decrease in plant function in wet ecosystems with more frequent moisture decreases into stress during the longer dry spells[42].

Differences in mean annual soil moisture response to fewer, large rainfall events can also partly explain diverging dry and wet ecosystem plant responses (Fig. 5c). In dry ecosystems, mean annual shallow rootzone soil moisture (0–20 cm) typically increases in response to fewer, larger rainfall events[26,71,221,222], which would increase mean plant function. This increased mean soil moisture in dry environments is supported by fewer, larger rainfall events increasing infiltration[25,26], reducing soil evaporation[25,222], reducing interception loss[145,147] and causing no change in deep drainage[27,152,223], as determined from diverse approaches (Fig. 5a,c). By contrast, wet ecosystems show decreased mean annual shallow rootzone soil moisture under fewer, larger rainfall events[37,91,94,110,224], as supported by increased deep drainage[25,27] and increased runoff with larger rainfall pulses[22,27,42], also determined from diverse approaches (Fig. 5c). Antecedent soil moisture probably controls these differences; on average, dry environments have initially drier surfaces that allow more infiltration than wet environments on average during a larger rainfall event[141–143]. Deeper rootzone soil moisture (<20 cm) also increases in dry ecosystems with fewer, larger rainfall events[70,71,85,122] and with some evidence for increases in wet ecosystems as well[42,73]. In regions within or in proximity to high elevations[225] or high latitudes, moisture storage in snowpack can buffer soil moisture changes in the context of fewer, larger rainfall events by delivering one or several large, prolonged moisture pulses to the soil when snow melts, although it is unclear how this will change soil moisture means in the context of fewer, larger rainfall events.

Summary and future perspectives

Across global observations and CMIP6 model projections of rainfall, rainfall events are becoming less frequent, but more intense in many regions, fundamentally altering how moisture is available to plants. Mean plant responses to fewer, larger rainfall events range between −28% and 29% and the high magnitude of responses suggests that fewer, larger rainfall events might substantially alter plant function trends and, by extension, the carbon cycle[1]. Across diverse approaches, fewer, larger rainfall events mostly decrease wet ecosystem plant responses, while causing positive-to-neutral responses in dry ecosystems. We argue that the nonlinear relationship between plant function and soil moisture largely drives the contrast in plant responses between dry and wet ecosystems, as controlled by mechanisms during rainfall pulses and dry spells. Mean soil moisture changes under fewer, larger rainfall events also modulate the different responses.

Several critical knowledge gaps emerge that require investigation. First, the magnitude of plant response to fewer, larger rainfall events should be determined across the globe. Trends towards fewer, larger rainfall events are more globally consistent than trends in annual rainfall amounts (Fig. 2), suggesting that sub-seasonal rainfall changes might confer spatially prevalent plant function changes. Global determination of plant response will require estimating relative plant response uncertainties across the different observation-based and modelling-based approaches. Second, plant responses to fewer, larger rainfall events must be projected into the future such that their influence on the land carbon sink can be quantified, including on the mean land carbon sink, global carbon uptake interannual variability and greening and browning trends[1,10,38]. To achieve this, trend differences between rainfall observation records and model projections must be reconciled (Fig. 2). This objective also motivates multidecadal field and observation records to assess the role of slower ecosystem changes such as acclimation and species turnover. Third, to better predict diverging plant responses to fewer, larger rainfall events across global climate gradients, further investigation is needed into which mechanisms dominate plant responses, and under what contexts. Many investigations quantify mean plant responses but do not determine underlying driving hydrological and physiological conditions; for example, although soil moisture threshold behaviour was proposed as a major driver of plant function under fewer, larger rainfall events with a soil water bucket model paradigm[42], only the soil moisture mean responses have been investigated. As such, it should be quantified whether fewer, larger rainfall events change the proportion of a year that plants spend below or above soil moisture thresholds (such as, time spent above the wilting point or in water limitation versus energy limitation)[70,216] (Fig. 5b). Additionally, the consequences of plant response to individual rainfall pulses on annual mean observed and modelled plant responses should be investigated (Fig. 6). Finally, further work is also required to understand below-ground plant responses and interactions with soil microbial communities and nutrients[226].

To address the key knowledge gaps discussed earlier, three emerging and related hypotheses require further investigation. In the first hypothesis (hypothesis I), plant responses to wet day frequency are non-monotonic because plant function is maximized at an optimum rainfall frequency. This hypothesized response to sub-seasonal rainfall variability contrasts with the monotonic increase of plant function with annual rainfall amounts[215,227]. Optimal rainfall frequency emerges from several minimalist models[39,98,101,228] and field manipulation experiments[35–37,70,229] and is likely due to non-monotonic effects of wet day frequency and intensity. For example, negative plant responses can occur owing to small wet day rain depths decreasing root infiltration and leading to more soil evaporation, or owing to very large wet day rain depths causing water-logging[101,228].

Addressing hypothesis I requires the determination of how plants respond to shifting wet day frequency and intensity. For example, an empirical relationship between plant function and rainfall frequency can be determined locally, or for specific biomes and climates at larger spatial scales. Such a plant response to rainfall frequency relationship

Glossary

C4 photosynthesis
An evolutionary adaptation of photosynthesis occurring mainly in some grass and crop species under which photosynthesis is more efficient because photorespiration is largely avoided.

CAM photosynthesis
An evolutionary adaptation of photosynthesis occurring mainly in plant species in arid environments that allows them to save water by only exchanging gases with the atmosphere at night.

Community composition
The species types and their relative abundance within a defined ecosystem, here referring specifically to plants.

Clausius–Clapeyron relationship
A thermodynamic equation that describes the nonlinear increase of saturation vapour pressure, or the capacity of air to hold water, with increases in air temperature.

Hadley and Walker cells
Some of the largest organized circulations of air in the atmosphere of the Earth that contribute substantially to weather and climate patterns of the Earth.

Interception
Rainfall that is captured and stored by vegetation, even briefly, such that it is prevented from infiltrating into the soil or running off of the ground surface.

Normalized difference vegetation index
A commonly used satellite-based vegetation index that estimates greenness at the top of the vegetation canopy based on satellite measurements in the infrared portion of the electromagnetic spectrum.

Phenology
The annual cyclic nature of plant functioning, specifically referring to its periodic increase and decrease in functioning during similar months of each year.

Plant water status
A general indicator based on how much water is available for plants to use towards essential plant functions such as photosynthesis and transpiration.

Rainfall intensity
The rainfall rate or rainfall depth over a defined time period. The rainfall rate is often defined hourly across hydrological sciences, although it is designated to be daily in this Review.

Rooting profile
The distribution of the root volume of a plant across the soil depth.

Satellite-based vegetation indices
Vegetation metrics derived from satellite measurements that typically span large spatial extents, including vegetation areal cover, greenness, height, photosynthetic capacity, water content and others.

Soil moisture stress functions
An empirical relationship between decreasing soil moisture and decline in plant functions such as photosynthesis or transpiration.

coupled with observed or projected changes in rainfall frequency can provide a means to predict the current and future terrestrial carbon cycle based on a change in sub-seasonal rainfall variability, at least in the near term.

In the second hypothesis (hypothesis II), the rainfall pulse dominates dry ecosystem plant responses to fewer, larger rainfall events, whereas behaviour during the dry spell dominates wet ecosystem plant responses. Some evidence provides initial support for this hypothesis, including evidence gathered across local climate gradients[85,230]. Given the nonlinearity of plant responses to soil moisture (Figs. 5b and 6), dry ecosystem plants are highly sensitive to rainfall pulses, especially when soil moisture is increased from very dry conditions above a threshold that stimulates photosynthesis[176,185]. Conversely, plants in wet ecosystems show smaller function gains from wet days than those in dry ecosystems[176]. However, plant function in wet ecosystems can decrease during dry spells during progressively increasing VPD[167], declining soil moisture within a water-limited regime, or soil moisture loss below functional thresholds[31,42]. Similarly, soil moisture largely drives dry ecosystem plant function, whereas VPD, a cause of plant water stress during dry spells, disproportionately drives wet ecosystem plant function[210,231–234].

Testing hypothesis II by determining which drivers dominate in different ecosystems will identify key mechanisms that can be used in models to predict plant responses to fewer, larger rainfall events. These experiments will help to identify why the response magnitudes of plants to fewer, larger rainfall events differ, with the largest responses observed in dry-to-transitional ecosystems. As less focus has been devoted to studying plant responses to dry spells, more investigation is required for understanding how VPD and incoming solar radiation (direct and diffuse) influence plant stress during different length dry spells. A focus on surface radiation and other atmospheric measurements would also help to interrogate plant behaviour across aridity gradients (and water and energy limitation) and move beyond a traditional focus on rainfall information.

In the third hypothesis (hypothesis III), the most extreme rainfall events within the year have an outsized influence on plant response to fewer, larger rainfall events[235,236]. Rainfall events can be defined as extreme compared with their historical time series[237]. These extreme rainfall events would have a proportionally larger impact where plants are more sensitive to rainfall pulses (Fig. 6). A challenge in addressing this hypothesis is the poorly understood ecosystem response mechanisms under extremes[237]; for example, in many cases, a climate extreme does not translate to an extreme ecosystem response[238].

Plants in dry ecosystems should respond more to more extreme rainfall events than they do in wet ecosystems[21], given dry ecosystem plants' higher magnitude and longer duration carbon uptake responses than in wet ecosystems[21,84,183,239] (Fig. 6). By contrast, plants in wet ecosystems might have smaller responses to more extreme events because they are more energy-limited[165] and less sensitive to rainfall pulse size[176]. In all cases, it is likely that more common, smaller rainfall events will still impact plants, especially if a substantial proportion of them are large enough to be ecologically relevant[240]. If evidence continues to support this hypothesis, it will be critical for models to properly integrate plant responses to extreme rainfall events to accurately predict ecosystem carbon uptake mean and variability trends. Understanding and modelling the plant pulse response to individual wet days will be essential (Fig. 6).

Globally prevalent trends in sub-seasonal rainfall, as well as plant sensitivity to these changes, motivate the determination of how plants respond to rainfall event frequency and intensity. The −28% to 29% changes in annual mean plant function with fewer, larger rainfall events are likely substantially impacting seasonal weather patterns[186], agricultural yields[241] and the global carbon cycle, including greening trends[38,242] and interannual carbon uptake variability[10,243]. Widespread, long-term monitoring of plant responses to fewer, larger rainfall events and improved understanding of plant pulse and dry spell mechanisms, especially within the context of several key hypotheses, are needed to quantify plant responses to sub-seasonal rainfall variability across the globe, reduce the uncertainty of these plant responses and predict future plant and carbon cycle responses under shifting rainfall.

Data availability

CMIP6 rainfall projections can be obtained from https://cds.climate.copernicus.eu. Observation-based rainfall data sets from MERRA, CPC and GPCC can be obtained from https://gmao.gsfc.nasa.gov/reanalysis/MERRA-2/data_access, https://psl.noaa.gov/data/gridded/data.cpc.globalprecip.html and https://psl.noaa.gov/data/gridded/data.gpcc.html, respectively. FLUXNET observations can be downloaded from https://fluxnet.org.

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The authors declare no competing interests.

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