ENVIRONMENTAL RESEARCH
LETTERS

TOPICAL REVIEW

Regulation of the global carbon and water cycles through vegetation structural and physiological dynamics

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Abstract
Vegetation plays an essential role in regulating carbon and water cycles, e.g. by taking up atmospheric CO_2 through photosynthesis and by transferring soil water to the atmosphere through transpiration. Vegetation function is shaped by its structure and physiology: vegetation structure is determined by the amount of materials for plants and how it is organised in space and time, while vegetation physiology controls the instantaneous response of vegetation function to environmental conditions. Recognizing and disentangling these aspects of vegetation is key to understanding and predicting the response of the terrestrial biosphere to global change. This is now possible, as comprehensive measurements from Earth observations, both from satellites and the ground, provide invaluable data and information. This review introduces and describes vegetation structure and physiology, and summarises, compares, and contextualises recent literature to illustrate the state of the art in monitoring vegetation dynamics, quantifying large-scale vegetation physiology, and investigating vegetation regulation on the changes of global carbon and water fluxes. This includes results from remote sensing, *in-situ* measurements, and model simulations, used either to study the response of vegetation structure and physiology to global change, or to study the feedback of vegetation to global carbon and water cycles. We find that observation-based work is underrepresented compared with model-based studies. We therefore advocate further work to make better use of remote sensing and *in-situ* measurements, as they promote the understanding of vegetation dynamics from a fundamental data-driven perspective. We highlight the usefulness of novel and increasing satellite remote sensing data to comprehensively investigate the structural and physiological dynamics of vegetation on the global scale, and to infer their influence on the land carbon sink and terrestrial evaporation. We argue that field campaigns can and should complement large-scale analyses together with fine spatio-temporal resolution satellite remote sensing to infer relevant ecosystem-scale processes.

1. Background

Terrestrial vegetation is a key regulator of global carbon-water interactions (Monteith and Unsworth 1990). One third of total anthropogenic CO_2 emissions in the atmosphere are taken up by terrestrial vegetation, and the interannual atmospheric CO_2 variability is dominated by terrestrial vegetation response (Friedlingstein *et al* 2022). Vegetation further modulates the land water flux through transpiration, which contributes to about 60% of the annual terrestrial evaporation (Jasechko *et al* 2013). The key components of the water cycle such as soil moisture, evaporation, and runoff are tightly linked with vegetation regulation through multiple biophysical processes (Milly *et al* 2005, Seneviratne *et al* 2010, Masson-Delmotte *et al* 2021).

Vegetation structure and physiology regulate vegetation response to hydro-meteorological and environmental drivers. Vegetation structure can be quantified as the amount and spatiotemporal arrangement of plant materials (e.g. above- or below-ground biomass) (Bonan 2010), and its morphology can be often visually seen, at least above ground (Reichstein *et al* 2014). Above-ground vegetation structure is developed mainly to harvest sunlight, while below-ground vegetation structure is developed to absorb water and nutrients and to provide anchorage. Vegetation structure can be a determinant factor defining the maximum potential for vegetation to regulate the exchange of water and carbon, while the actual functioning is modulated by environmental conditions and plant physiological regulation (Migliavacca *et al* 2021). Common structural characteristics of vegetation can be differentiated as morphology related, such as leaf area and angle, canopy clumping, plant height, above-ground biomass, wood density, rooting depth, or pigment or nutrient related (Bonan 2010, Mantilla-Perez and Fernandez 2017, Yang *et al* 2023). Vegetation physiology adjusts the actual vegetation functional dynamics and performance due to instantaneous environmental stress (Li *et al* 2023a). Common physiological characteristics of vegetation include stomatal, xylem, and root conductance that closely regulate the transport or exchange of oxygen, CO_2, water, or nutrients, and include maximum carboxylation rate and electron transport rate that are closely related to plant photosynthetic traits (Field *et al* 1982, Collatz *et al* 1991, Wilkinson and Davies 2002, Brodribb and Cochard 2009, Luo and Keenan 2020). It is important to note that vegetation structure and physiology are interdependent so they can be approximated but not completely peeled off.

Climate and environmental change influence vegetation structure and physiology in different ways and on different time scales. A drought lasting only a few days or a few weeks may have less impact on tree canopy structure, but more on photosynthetic performance and stomatal response (Wilkinson and Davies 2002, Stocker *et al* 2019). This rapid response of vegetation function modulates light and water use efficiency and alters carbon and water cycles (Reichstein *et al* 2014, Novick *et al* 2016, Piao *et al* 2020). Vegetation structure responds on different time scales, with leaf angles adapting rapidly to changes in light or heat stress, while changes in leaf area or biomass typically occur over longer periods (Kao and Forseth 1992, Yang *et al* 2023). To date, the multifaceted structural and physiological variations of vegetation across broad ecosystems have been monitored with limited observations, and climate and environmental impacts on these variations have not been fully understood (Gentine *et al* 2019, Schimel and Schneider 2019, Piao *et al* 2020). It is also unclear which climate and environmental processes in regulating changes of vegetation structure and physiology are better studied and which are largely understudied.

Physiological and structural responses of vegetation collectively determine functional changes of vegetation, such as, gross primary productivity (GPP) and transpiration, and thereby also mediate changes in other components of the carbon and water cycles (e.g. runoff) (Schimel and Schneider 2019, Smith *et al* 2020, Walker *et al* 2021, Zeng *et al* 2022b). The physiological regulation of vegetation on water and carbon cycles is often direct. Stomatal closure and reduction in maximum carboxylation rate under water stress reduces the instantaneous rates of transpiration and photosynthesis (Novick *et al* 2016). The structural regulation of vegetation on the water and carbon cycles includes both direct and indirect regulation. Increased leaf area index (LAI) can contribute directly to carbon assimilation or precipitation interception, while altering albedo and roughness, which indirectly affect evaporative cooling (Duveiller *et al* 2018, Zeng *et al* 2018). Understanding different vegetation regulating processes on the global water and carbon cycles from historical evidence can help to better predict future trajectories of water and carbon cycles.

Recent studies have focused more on observations of the global vegetation function that go beyond surrogates of overall vegetation dynamics using the amount of green leaves or canopy structural density (Chen *et al* 2022, Li *et al* 2023a). Observations of vegetation function are now widely available, but a large part of these observations are rather short term or with coarse spatio-temporal resolutions (Frankenberg *et al* 2011, Joiner *et al* 2011, Zhang *et al* 2019, Zeng *et al* 2022b). Isolating large-scale physiology signals from overall vegetation functions is therefore key to reconstructing and predicting the past and future functional dynamics. However, disentangling vegetation physiology from structure is rather difficult and needs a clear definition. The globe continues to warm, with climate extremes becoming

more frequent and more severe. How do different vegetation types and ecosystems resist environmental stress? Can vegetation maintain essential functions such as carbon sequestration with increased green leaves yet potentially increased physiological water stress under climate extremes? Multiple dimensions of vegetation are essential in determining the overall ecosystem health and stability, and need to be prioritised for a better understanding of their responses and feedbacks to climate change.

This review proposes a clarification of what is meant by vegetation structure and physiology in Earth System Science and provides means to help disentangle their effects in our measurements. In the next part, section 2, we introduce a systematic review procedure on the topic of vegetation structural and physiological regulation on the water and carbon cycles. In section 3, we list common structural and physiological characteristics of vegetation and their relevant spatio-temporal scales. Environmental controls on these vegetation characteristics are discussed in section 4. Section 5 focuses on carbon and water cycle processes that are influenced by vegetation structure and physiology. Opportunities for observations that can improve our understanding of multiple dimensions of vegetation are synthesized in section 6, together with discussions of potential challenges. In section 7, we outline future research priorities to advance the monitoring and diagnosis of global vegetation transitions in the context of climate change. We emphasize the need to bridge large-scale monitoring and *in-situ* measurements to monitor the multifaceted vegetation dynamics and to better anticipate the vegetation's response to and its impacts on climate change.

2. Methods

Our systematic review consists of 4 main steps: establishing search criteria based on prior knowledge of experts, searching research articles in Web of Science, adjusting search criteria based on abstracts, and summarising selected literature. We apply search criteria by collecting a set of keywords related to 'vegetation structure and physiology regulate carbon and water cycles' in the defined research areas (figure S1; table S1). We ensure that relevant abstracts are found by manual inspection of randomly selected abstracts from the search results. We classify the selected literature into different categories by restricting additional keywords in table S1: vegetation structure, vegetation physiology, carbon cycle, water cycle, global, regional, remote sensing, *in situ*, and models.

Figure 1 shows the increasing number of research articles since 1990 that specify vegetation physiological or structural characteristics of vegetation and focus on the topic of vegetation regulating the carbon
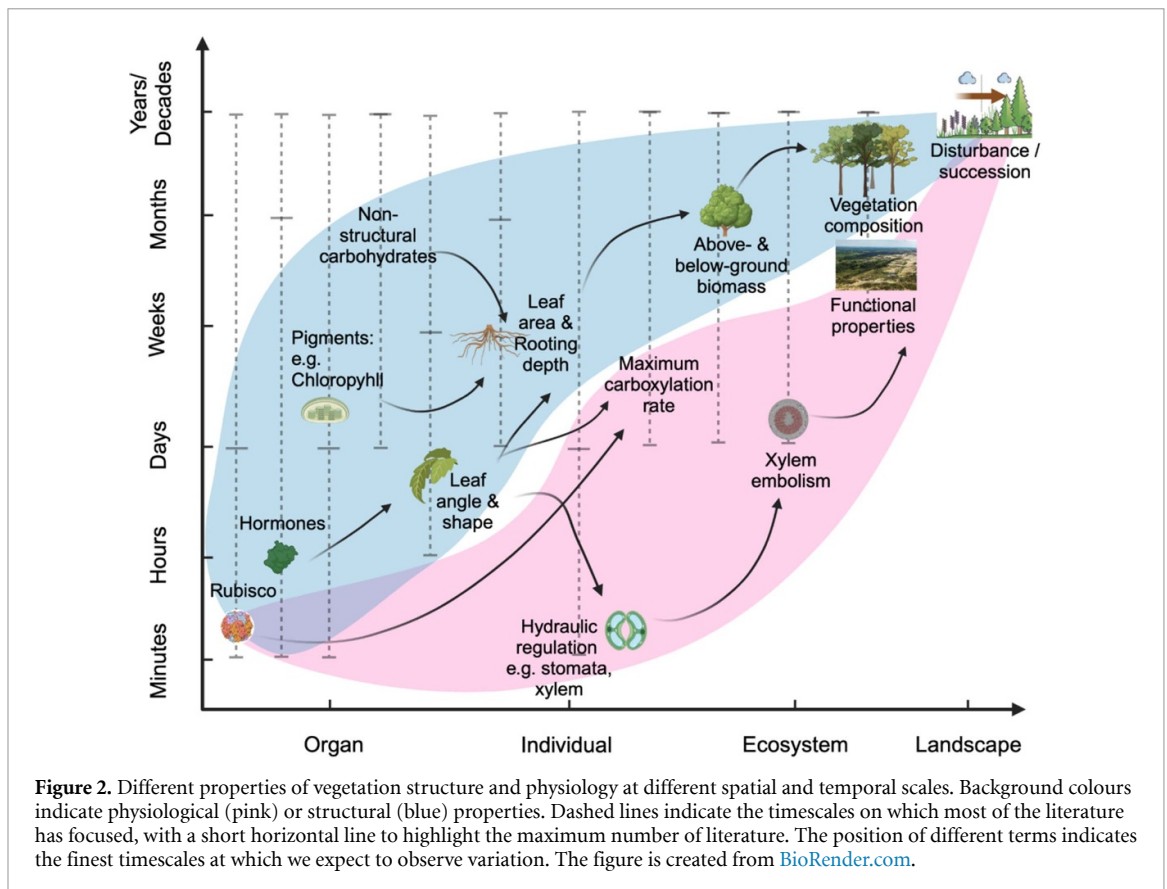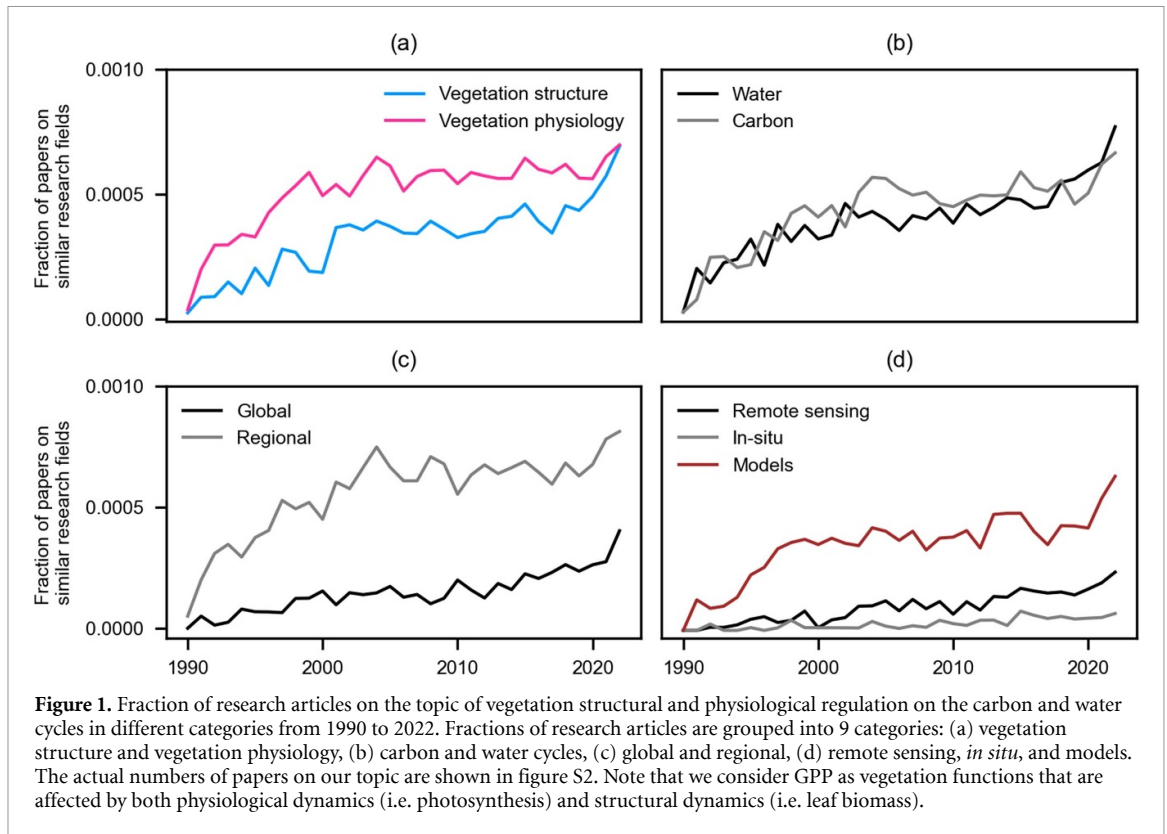
and water cycles. To remove the general increasing trend of the scientific literature that occurs in this scientific field, we show normalised numbers of papers in figure 1, which are calculated as the number of papers we reviewed divided by the total number of papers in the defined research fields per year (see table S1).

Among all defined research fields, the articles relevant to our topic showed a rapid growth since 1990 followed by a weaker growth during the years 2000–2018, with a second acceleration after 2018. Among all the relevant articles, vegetation modelling has a much larger share compared to the sum of *in-situ* measurements and remote sensing. Vegetation physiology was apparently studied more often than vegetation structure. When leaving out keywords of photosynthesis and transpiration in the category of vegetation physiology, vegetation structure occupies a larger share than physiology (not shown). Water and carbon cycles have been studied with similar numbers of articles. Global studies are much fewer than regional studies.

By reviewing the abstracts of all research articles, we identify a set of major research directions: (i) spatio-temporal scales of vegetation structural and physiological dynamics; (ii) hydro-meteorological and environmental drivers of vegetation structure and physiology; (iii) vegetation controls on the global carbon and water cycles; (iv) vegetation responses to climate extremes such as drought, and heatwaves. By focusing on these directions we are also supporting research in other directions which have also been studied in the literature, such as trends of vegetation and management of vegetation and its impacts. We propose to prioritise a better understanding of the drivers of vegetation structural and physiological variables at large scales. This is essential for a better prediction of the terrestrial carbon sink and the global water cycle, as well as impacts of the increase in frequency of climate extremes.

3. Structural and physiological characteristics of vegetation

Vegetation structure consists of morphology, pigment concentration, and the spatial organization of single or multiple vegetation types. Different structural characteristics of individual plants can change at different time scales, and the time scale of structural changes at the ecosystem level can be longer than that at the plant or organ levels (figure 2). At the organ-structure level, pigments such as chlorophylls or xanthophylls (which change from weeks to months) can control the photosynthetic light-harvesting complexes or reflect leaf flushing or senescence (Latowski *et al* 2011, Magney *et al* 2019). The individual plant structure can be divided into

Figure 1. Fraction of research articles on the topic of vegetation structural and physiological regulation on the carbon and water cycles in different categories from 1990 to 2022. Fractions of research articles are grouped into 9 categories: (a) vegetation structure and vegetation physiology, (b) carbon and water cycles, (c) global and regional, (d) remote sensing, *in situ*, and models. The actual numbers of papers on our topic are shown in figure S2. Note that we consider GPP as vegetation functions that are affected by both physiological dynamics (i.e. photosynthesis) and structural dynamics (i.e. leaf biomass).

Figure 2. Different properties of vegetation structure and physiology at different spatial and temporal scales. Background colours indicate physiological (pink) or structural (blue) properties. Dashed lines indicate the timescales on which most of the literature has focused, with a short horizontal line to highlight the maximum number of literature. The position of different terms indicates the finest timescales at which we expect to observe variation. The figure is created from BioRender.com.

three parts: the canopy to capture light, the stem or branches to support the weight and to transfer water from soil to the leaves, and the roots that absorb water and nutrients and function as anchorage. For an

individual plant, leaf angle and leaf shape change from the hourly to daily time scales, regulated by hormones and leaf water potential (Mantilla-Perez and Salas Fernandez 2017). Leaf area and rooting

Figure 3. Numbers of research papers studying different characteristics of vegetation structure (a) and physiology (b). Note that light and water use efficiency are emerging ecosystem functional properties instead of typical physiological characteristics. Red edges highlight observation-based analysis in the literature review.
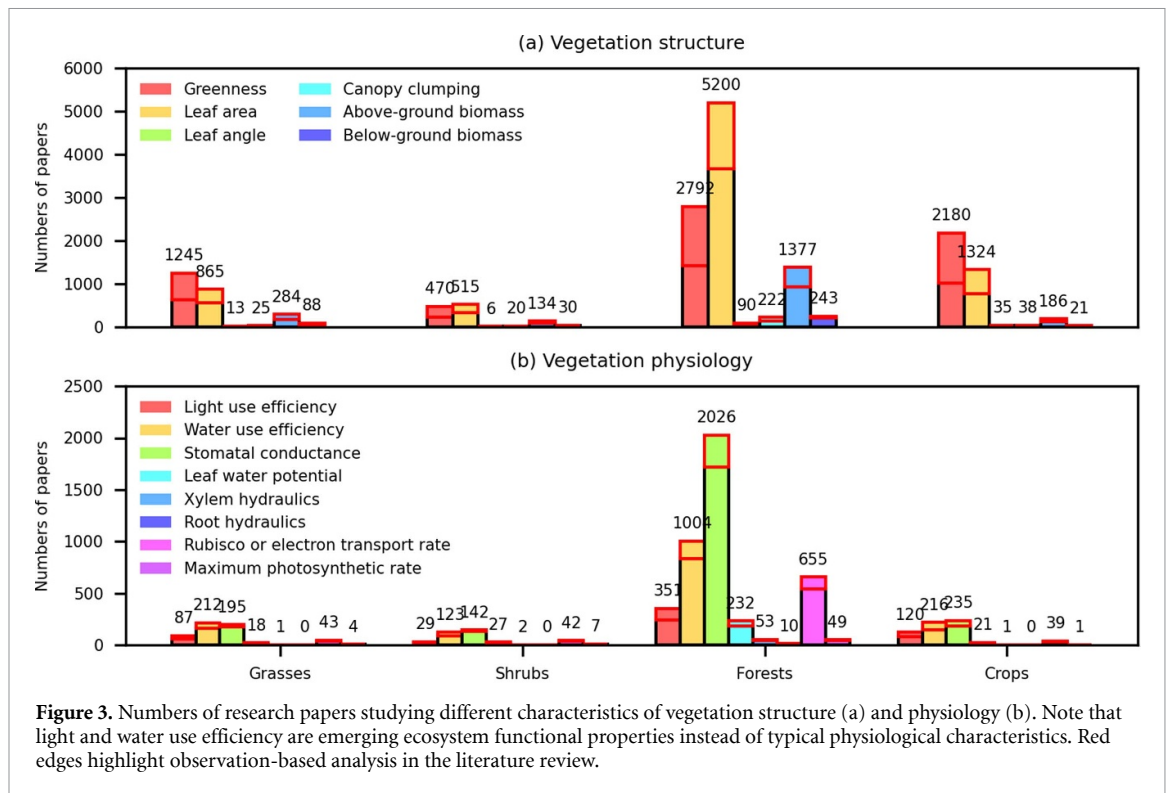
depth change from days to weeks, whereas canopy and stem biomass change gradually from weeks to months (Zhang *et al* 2019, Nair *et al* 2023). The organization of vegetation at scales ranging from ecosystems to larger scale encompasses more than the three essential components of individual plants mentioned above. Vegetation composition (species and age) and fragmentation organize the pattern of single or different vegetation types and hence integrate the mixed architecture of above- and below-ground elements. Changes in the total fluxes of water and carbon in an ecosystem can occur from instantaneous to daily to weekly time scales, but changes in the general vegetation structure, vegetation greenness, and above-ground biomass, may occur at the monthly or longer time scale (e.g. Reichstein *et al* 2014). Vegetation composition can be altered and influenced by species competition, abnormal climate or nutrient changes, and can also be reshaped by external disturbances such as land management (e.g. logging, harvest, agriculture expansion), fire, or the insect outbreaks, ultimately shaping the vegetation succession.

Vegetation physiology determines vegetation functions by responding to instantaneous environmental conditions and also to plant genetic traits. Hormones and Rubisco are organ-level physiological triggers that can change from minutes to hours. Hormones such as abscisic acid (ABA) can be released from roots and transported to the xylem and stomata to regulate diurnal changes in stomatal conductance and gas exchange when roots perceive depletion of soil moisture (Wilkinson and Davies 2002). In addition to hormonal controls, atmospheric conditions

also directly regulate stomatal behaviour, leading to fast stomatal changes. Maximum carboxylation rate (Vcmax) can vary across multiple days and is a measure of leaf photosynthetic capacity that is often controlled by temperature-dependent Rubisco activities, and Vcmax. From weeks to an entire growing season, when atmospheric demand exceeds soil water supply, plant hydraulic tension in the xylem tends to increase the risk of xylem embolism and dysfunction, which can happen during several dry-down days but could cause irreversible damage over years (Brodribb and Cochard 2009). There are also some ecosystem functional properties emerging from the interplay of physiological processes, such as water and light use efficiency. They describe the effectiveness that vegetation utilizes water and photosynthetically active radiation to assimilate carbon dioxide. From years to decades, changes in ecosystem functional properties, local climate, topography, soil texture, or disturbance can interact to cause succession on a landscape.

Figure 3 shows the numbers of peer-reviewed papers investigating different characteristics of vegetation structure or physiology across vegetation types, with the largest number focusing on forests, followed by crops, grasses, and shrubs. Vegetation greenness and LAI are the two most commonly studied objectives, as part of a long research tradition. Those indices are primarily inferred through the remote sensing signals in the visible and near-infrared ranges (Nelson *et al* 1988), which happen to be available since the 1980s from satellite platforms (Seto *et al* 2004, Tucker *et al* 2005). Above-ground biomass has often been studied for forests, as forests cover less than one third

of the global land area but contribute over two thirds of terrestrial net primary productivity (Lefsky *et al* 2002). Common ways to quantify above-ground biomass are forest inventory and remote sensing techniques such as passive and active microwave remote sensing. Canopy clumping describes the shape of the canopy, which determines the size and distribution of gaps in the canopy. Clumping of needles in conifer forests, for example, has larger values than in broadleaf evergreen forests and can impact the remote sensing retrieval of LAI by changing the light transmission (Jonckheere *et al* 2004). Recent European droughts have accelerated upper canopy thinning, so that increased canopy gaps have the potential to also alter below-canopy light exposure and understory vegetation biodiversity (Frenne 2023). Leaf angle can rapidly change to excessive light and heat, and can alter leaf-to-canopy energy balance and water loss (Yang *et al* 2023). Leaf angle and its changes at the site level are relatively understudied as its measurements are often labour intensive, although recent studies have used laser scanners instead of labour measurements of leaf morphology (Puttonen *et al* 2016). Rapid changes of leaf angle is also complicated to monitor from space because of the lack of frequent satellite overpass or differences in solar zenith angle (Yang *et al* 2023). Soybean and some desert plants can change their leaf angle by 60 degrees during a day to find the optimal strategy for photosynthesis, indicating the potential for acclimation and adaptation of vegetation structure to the changing environment (Kao and Forseth 1992). The change in leaf angle is jointly controlled by hormones and leaf water potential, with a reduction in leaf water potential corresponding to a loss of turgor. Turgor adjusts the leaf angle by the differential cell growth on two leaf sides, and can change leaf angle to be more vertical to reduce the heat and cool down the surface (Posada *et al* 2012). In terms of studies related to vegetation physiology, stomatal conductance occupies the largest proportion of the literature, followed by some functional properties such as water and light use efficiency, and then by the action of Rubisco, leaf water potential, electron transport rate, and maximum photosynthetic rate, and xylem and root hydraulics.

4. Observing vegetation structure and physiology

This section includes an overview of common satellite and field measurements to monitor vegetation structure and physiology. Traditional field or laboratory measurements to assess vegetation physiological characteristics, such as photosynthetic carbon assimilation and Vcmax, require tools to measure net carbon exchange (leaf cuvettes or whole-plant chambers) and build empirical response curves of CO_2 exchange to different environmental conditions (Field *et al* 1982, Collatz *et al* 1991, Bernacchi *et al* 2001). Since 2000, eddy covariance technique has become a great tool to measure net carbon and water exchange at the ecosystem scale (Baldocchi 2003), from which is possible to calculate, with some limitations, ecosystem scale analogous of physiological properties (e.g. Knauer *et al* 2018). The leaf water potential can be measured in multiple ways, such as the pressure chamber method (Kao and Forseth 1992, Pineda-García *et al* 2016). By equilibrating the water potential of a detached leaf with known pressure inside a sealed chamber, one can measure leaf water potential. By collecting samples of stems and roots before dawn, one can measure root or xylem conductance by the water flow and the pressure gradient in the laboratory (Cinnirella *et al* 2002, Pineda-Garcia *et al* 2016). Sapflow measurements have been available with a broad bioclimatic coverage to track transpiration and can help to infer physiological changes at the single plant scale (Cammalleri *et al* 2013, Poyatos *et al* 2020).

Traditional ways are able to assess vegetation structural characteristics, such as hand-held inclinometer or protractor measuring leaf angle and ceptometers, while hemispherical cameras, or optical sensors measuring LAI through radiative transfer model inversion (Yan *et al* 2019, Yang *et al* 2023). Recently, Airborne Laser Scanning systems can also measure these structural changes such as tree height with the advantage that it greatly reduces manual labour (Potapov *et al* 2021, Yang *et al* 2023). Vegetation biomass is often estimated by inventory studies relying on allometric relationships between diameter at breast height, tree height, and standing biomass (Barford *et al* 2001, Teobaldelli *et al* 2009). There are also site-level measurements of vegetation structural dynamics using airborne remote sensing or near-surface sensors. A recent observational platform gathers long-term observations that monitor 3D canopy structure from LiDAR measurements from airborne remote sensing, the National Ecological Observatory Network at the eddy covariance, canopy level (Kampe *et al* 2010). In addition, phenoCam experiments can also be installed on top of eddy-covariance towers and provide greenness measurements for phenological and structural monitoring (Richardson *et al* 2018, Thapa *et al* 2021).

Vegetation structural and functional changes at a global scale can be measured by space-borne remote sensing, while vegetation physiology can only be inferred with additional information. To observe structural and functional changes, from short to long wavelengths, remote sensing provides multiple opportunities from visible, near-infrared, shortwave-infrared (SWIR), thermal-infrared, and microwave (e.g. Ku, X, C, L, and P) bands. From optical remote sensing, Zeng *et al* (2022b) summarized commonly used greenness indices, such as: normalized

difference vegetation index (NDVI), enhanced vegetation index, near-infrared reflectance of terrestrial vegetation (NIRv), and kernel NDVI. The normalized difference water index based on the near-infrared and SWIR bands is used to monitor moisture conditions of the land surface such as vegetation water content, a mixture of vegetation structure and physiology (Jackson *et al* 2004, Gu *et al* 2008, Alkama *et al* 2023 preprint). These are essentially based on two spectral bands in the red and near infrared domains that are readily measured by common Earth Observation satellites, and they consist of different mathematical combinations of these bands to bring forward their capacity to represent green vegetation. Another approach to extract information from optical remote sensing data is to derive biophysical variables, such as LAI that represents green leaf area per unit horizontal ground surface area (Yan *et al* 2019). LAI is typically retrieved from the optical remote sensing reflectance through the inversion of radiative transfer models, and model parameterisations are previously calibrated against field or lab measurements. LAI can improve the representation of vegetation structure in dense canopies where greenness indices are clearly saturated, but LAI also has a potential of a saturation due to model uncertainties and the complexity of canopy architecture (Yan *et al* 2019). Long-term records of these indices or variables are possible but suffering from systematic noise from e.g. shifts of satellite orbits, so additional methods and algorithms are developed to harmonise and calibrate data (Fang *et al* 2019). In addition to vegetation greenness and LAI, vegetation chlorophyll content can also provide structural information. Vegetation chlorophyll content can also be retrieved through the radiative transfer models but requiring medium-to-high spectral resolutions. These bands can be available from satellite instruments such as medium resolution imaging spectrometers (MERIS) or Sentinel-2 (Muramatsu 2019, Xu *et al* 2022). From microwave remote sensing, Radar and LiDAR can complement observations of canopy density by characterizing horizontal and vertical aspects of vegetation structure and biomass. Global Ecosystem Dynamics Investigation installed LiDAR Altimeters aboard the International Space Station to observe the 3D distribution of branches and leaves and vegetation canopy height from 2019 (Dubayah *et al* 2020), providing important information about the effect of management on vegetation height and structure (Ceccherini *et al* 2023). Vegetation optical depth (VOD) in the microwave wavelength range measures how much vegetation water content attenuates microwave signals, so that VOD is influenced by above-ground biomass and the relative water content per unit of biomass (Zhang *et al* 2019), with higher frequency reflecting more the biomass of leaves and canopy whereas lower frequency reflecting more the biomass of stems and branches (Saatchi *et al* 2000, Konings *et al* 2021a).

VOD observations which are applicable for long-term and global monitoring are typically from scatterometers and radiometers with relatively coarse spatial resolutions of 25–50 km (Du *et al* 2017, Konings *et al* 2021a). High spatial resolution synthetic aperture radar (SAR) and laser measurements can enhance these coarse observations. Examples include the laser-based ICESat-2 (Ice, Cloud, and land Elevation Satellite-2) and the planned NASA-ISRO SAR mission (NISAR). These methods offer the ability to quantify biomass and vegetation water content at a plot scale (tens of meters). However, they have limitations due to less frequent revisits and regional coverage (Silva *et al* 2021). The joint consideration of observations or products of different sensors allows the quantification of physiological activities of vegetation at multiple temporal and spatial scales and with improved accuracy. Other vegetation structural observations at the large scale such as leaf angle and below-ground biomass are less understood due to the lack of global observations.

In terms of monitoring vegetation functions, solar-induced chlorophyll fluorescence (SIF), which is a weak electromagnetic signal in the red to far-red spectrum (i.e. 650–800 nm) emitted by chlorophyll molecules, has shown a strong positive near-linear relationship with measured GPP at the ecosystem level (Frankenberg *et al* 2011, Joiner *et al* 2011, Doughty *et al* 2019). SIF can help to estimate GPP at the ecosystem to global scales as both are largely driven by incoming light, and more precisely by the absorbed photosynthetic active radiation (APAR). However, the relationship between GPP and SIF deteriorates under environmental stress. To better understand the relationship between SIF and tower-measured GPP, a high spatio-temporal-resolution SIF product is needed. The TROPOspheric Monitoring Instrument SIF (TROPOMI SIF) onboard the Sentinel-5p satellite has been available since 2018 with a better spatio-temporal resolution compared to other commonly-used SIF products which have longer temporal archives. TROPOMI SIF has a spatial resolution at approximately 0.1 ° and a temporal resolution at near-daily with a global coverage (Köhler *et al* 2018). So far, researchers have investigated the SIF-GPP relationship with several focuses: (i) the decoupling of APAR with SIF and GPP (Miao *et al* 2018, Yang *et al* 2018, Wieneke *et al* 2018, Dechant *et al* 2020), (ii) confounding effect of canopy structure (e.g. leaf angle) and leaf biochemical properties (e.g. chlorophyll a&b, carotenoids) (Migliavacca *et al* 2017, Xu *et al* 2021, Hwang *et al* 2023, Wang *et al* 2023a) (iii) the non-linear relationship between the quantum efficiency of fluorescence, photosynthesis and non-photochemical quenching (NPQ) (van der Tol *et al* 2014, Martini *et al* 2022, Wieneke *et al* 2022). Further analyses use hyperspectral remote sensing to study NPQ and its link to the xanthophyll activity by

using the Photochemical Reflectance Index (Gamon *et al* 1997, Chou *et al* 2017). Independent from SIF, Land surface temperature (LST) from the thermal-infrared remote sensing is mechanistically linked with the effect of vegetation evaporative cooling, contingent upon specific roughness and albedo characteristics (Farella *et al* 2022). Moderate Resolution Imaging Spectroradiometer (MODIS) LST provides global coverage and two images every day. Enhanced process understanding is enabled by sub-daily data which allows to resolve and study diurnal variability. This is possible with LST from the ECOSTRESS and SIF from OCO-3, mounted on-board of the International Space Station, which does not have a sun-synchronous orbit and can thus provide information of vegetation functioning at various different moments of the day, albeit not for every day and only for a limited spatial coverage (Fisher *et al* 2020, Taylor *et al* 2020).

As introduced above, large-scale vegetation physiology cannot be directly monitored from space-based remote sensing. We therefore advocate to disentangle vegetation physiology from structure at the large scales by several ways: (i) applying a simple operation between remote sensing products. For example, plant physiological information can be inferred from the ratio between SIF and the canopy structure-related near-infrared reflectance of vegetation multiplied by the incoming sunlight (NIRvP; Dechant *et al* 2022; Zeng *et al* 2022a), or the ratio between midday VOD and pre-drawn VOD (Konings and Gentine 2017, Zhang *et al* 2019, Konings *et al* 2021b). (ii) Traditional statistical methods or Machine learning algorithms can be used to disentangle vegetation physiology from overall vegetation functions, but certain assumptions are needed. For example, the physiological change can be inferred from an analogue of instantaneous hydro-meteorological contributions on the functional change (Li *et al* 2023a); Or physiological and structural changes can be partitioned from different frequency of data variations (Biriukova *et al* 2021). (iii) Radiative transfer modelling can estimate vegetation physiological parameters (e.g. estimating light use efficiency and producing MODIS GPP; or Soil Canopy Observation of Photochemistry and Energy flux, SCOPE; van der Tol *et al* 2009, Biriukova *et al* 2021). (iv) Data assimilation techniques can also infer vegetation physiology (e.g. estimating a global pattern of Vcmax based on TROPOMI SIF and MERIS chlorophyll content data assimilation; Chen *et al* 2022). Large-scale detection of spatial or temporal patterns in vegetation physiology has only been partially investigated, while current and near-future satellite observations offer great potential for investigating them using the approaches outlined above.

5. Environmental drivers on vegetation structure and physiology

The main environmental drivers of vegetation response are CO_2, water-related drivers (i.e. soil moisture, precipitation), energy-related drivers (i.e. temperature, radiation), vapour pressure deficit (VPD), nutrients (i.e. nitrogen, phosphorus) and wind speed. Figure 4 summarises the literature referring to specific environmental drivers on vegetation. Overall, temperature, precipitation, nutrients, and wind are commonly studied drivers of vegetation structure, whereas temperature, CO_2, radiation, and nutrients are commonly studied drivers of vegetation physiology. Different environmental drivers are relevant for vegetation types with different fractions of papers investigating them. Apart from temperature, water-related drivers are the main focus of research on grass and shrub ecosystems, while CO_2, radiation and nutrients are often studied in forest and crop ecosystems, when accounting for both vegetation structure and physiology. The results are consistent with the global patterns of water- or energy-related controls on vegetation from previous literature (Nemani *et al* 2003, Denissen *et al* 2020). Root-zone soil moisture is the dominant driver of vegetation structure and physiology in water-limited ecosystems such as the Mediterranean, Australia, and southern North America, whereas temperature and incoming light are dominant drivers in energy-limited regimes such as boreal and pan-tropical ecosystems (Forkel *et al* 2015, Stocker *et al* 2018, Walther *et al* 2019, Li *et al* 2021). Wind's impact on forest structure has been extensively researched, as it governs the microclimatic conditions within forests, and intense winds can cause damage to tall trees (Magnabosco *et al* 2018). Nutrients are often studied in croplands, as the use of nutrient fertilisers strongly increases photosynthetic rate and crop yields (Deng *et al* 2006, Mahajan *et al* 2012, Walker *et al* 2014).

In general, the relative importance of environmental drivers in regulating vegetation dynamics is consistent with the existing number of papers that have investigated the relevant drivers (figure 4). Less than one in ten of the literature has investigated more than three environmental variables together or considered non-linearity between environmental drivers and vegetation responses (not shown). We note that when investigating the importance of hydro-meteorological drivers on vegetation structural or physiological changes, proper consideration of their non-linear interactions (Stocker *et al* 2018, 2019, Li *et al* 2022) and comprehensive consideration of potential hydro-meteorological variables (Novick *et al* 2016, Denissen *et al* 2020, Li *et al* 2021, Fu *et al* 2022a) can help to more accurately quantify their
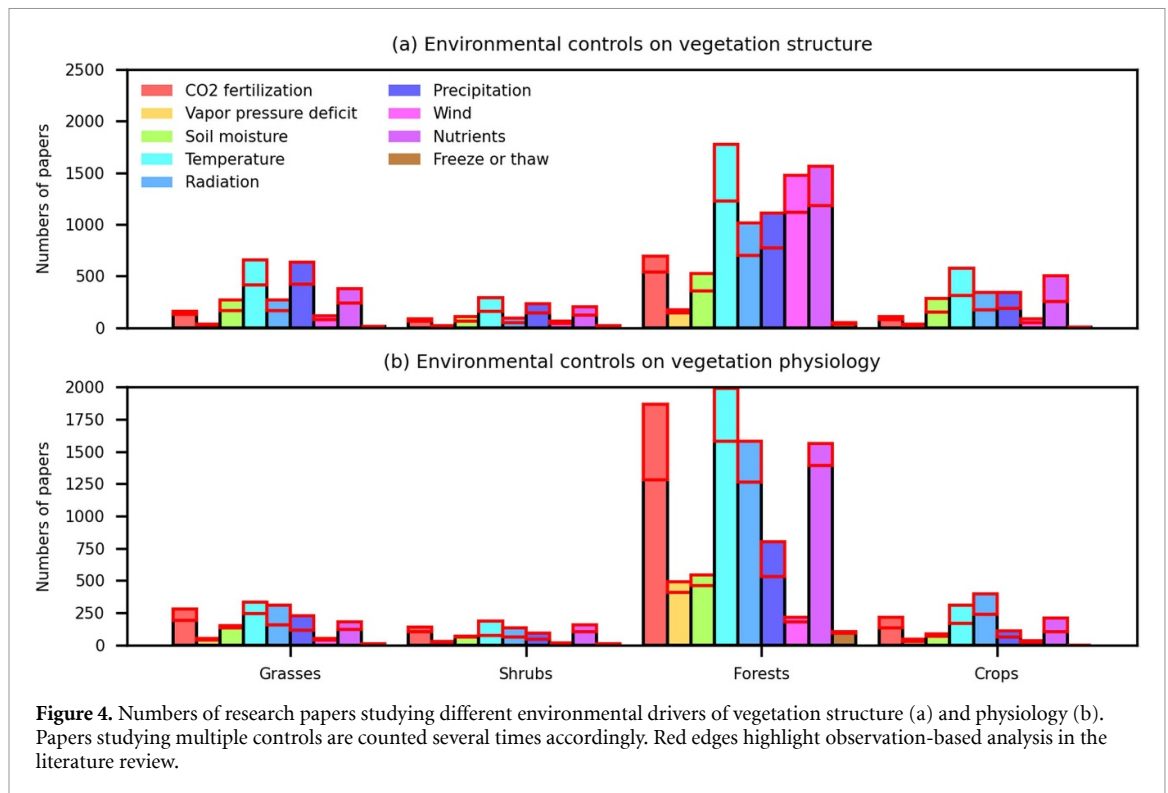
Figure 4. Numbers of research papers studying different environmental drivers of vegetation structure (a) and physiology (b). Papers studying multiple controls are counted several times accordingly. Red edges highlight observation-based analysis in the literature review.

relative importance and vegetation response functions to them.

5.1. Vegetation response to environmental changes

The influence of different environmental drivers on vegetation structure and/or physiology are discussed in details as follows across inter-annual to diurnal time scales. Physiological or structural acclimation to temperature has been found for photosynthesis and respiration at the inter-annual scale, e.g. increased optimum temperature of photosynthesis and respiration under global warming (Niu *et al* 2012). The CO_2 fertilisation effect on vegetation structure and physiology is often observed at longer time scales. The CO_2 fertilisation effect refers to the increasing atmospheric CO_2 that enhances the efficiency of photosynthetic uptake and water use (Field *et al* 1995). In terms of the CO_2 effect on vegetation physiology, direct evidence from Free-air CO_2 enrichment (FACE) experiments, and indirect evidence from isotope (Battipaglia *et al* 2013), ice-core, eddy-covariance, and tree ring measurements suggest that CO_2 fertilisation could increase leaf-to-canopy photosynthetic capacity and intrinsic water use efficiency (Walker *et al* 2021), because of an increased gradient between leaf surface and intercellular CO_2 concentration. The response of transpiration to increased atmospheric CO_2, however, differs across regions, related to water-use strategies of the respective vegetation and the availability of water, energy and nutrients (De Kauwe *et al* 2013, Gentine *et al* 2019, Walker *et al* 2021). In terms of the CO_2 effect on vegetation structure, CO_2 fertilisation may promote vegetation canopy density

and above-ground biomass (Zhu *et al* 2016), but the marginal benefit can be reduced with saturated CO_2 levels (Wang *et al* 2020). Many regions show vegetation greening due to CO_2 fertilisation, while some other regions show vegetation browning due to CO_2 or other climate factors (Zhu *et al* 2016, Chen *et al* 2019a). CO_2 fertilisation effects differ across ecosystems which can be related to different limitations of plants to the availability of soil water and nutrients (Wang *et al* 2020, Jiao *et al* 2021). There are also allometric increases due to CO_2 fertilisation effects in specific vegetation structural characteristics. Elevated CO_2 consistently decreases specific leaf area (leaf area divided by leaf biomass), but different site experiments detect different changes in leaf biomass and leaf area (De Kauwe *et al* 2014). Previous research has also examined trends in some emerging ecosystem properties at large scales, such as water use efficiency, although CO_2 fertilisation effects on large-scale plant physiology need to be better understood. The results of water use efficiency are controversial because they are data and scale-dependent compared to intrinsic water-use efficiency (defined as the ratio of net photosynthetic rate to stomatal conductance) which shows an increasing trend due to CO_2 fertilisation over decades (Frank *et al* 2015, Mathias *et al* 2021).

At the intra-annual scale, a multitude of hydro-meteorological variables regulate vegetation structure and physiology. Temperature, incoming light, and water availability dominantly regulate enzyme activities, electron transport rate, and maximum photosynthetic rate (Huang *et al* 2019, Luo and Keenan

2020). VPD and soil moisture are essential drivers that control vegetation physiology such as stomatal conductance and they are significantly decoupled at the hourly to weekly timescales (Novick *et al* 2016). Soil freezing and thawing, despite being the subject of relatively few research studies, is another important abiotic factor influencing vegetation dynamics. Recent advancements in passive microwave remote sensing, have facilitated its applicability for studying its impacts on vegetation physiology, greenness, and phenology, as highlighted by Kim *et al* (2017). Particularly notable are its effects on soil temperature, moisture, and microbial activity, which in turn exert significant influence on vegetation dynamics, especially in high latitude or high altitude regions such as permafrost areas, as underscored by Wang *et al* (2022). Furthermore, severe freezing events can lead to short-term damage to vegetation, resulting from freezing injury and negatively affecting vegetation physiology (Bao *et al* 2017). Daily reductions in canopy conductance and maximum photosynthetic assimilation rate are associated with increases in VPD and also with decreases in soil moisture when soil moisture is already low (Fu *et al* 2022a). Increases in VPD due to global warming also have contrasting impacts on vegetation photosynthesis and transpiration at different times of the day. For example, photosynthesis in Amazon rainforest is promoted by increases in VPD in the morning but is reduced in the afternoon related to diurnal changes of leaf water potential (Zhang *et al* 2023).

5.2. Vegetation response to climate extremes

Vegetation response to climate and weather extremes can vary according to the physiological and structural characteristics of the vegetation and the type of extremes. Climate and weather extremes include droughts, heat waves, cold spells, heavy precipitation and severe storms. The impact of these extremes on physiological characteristics is often more rapid than on structural characteristics. For example, warm and dry spells can easily cause stem dehydration but do not directly reduce respective biomass and growth (Salomón *et al* 2022). In high-elevation evergreen ecosystems like the conifers found on Niwot Ridge, Colorado, there's a noticeable decrease in photosynthetic activity during cold spells. This is associated with a decrease in proteins for photosynthetic reaction centers and an increase in photoprotective pigments, even as the vegetation retains its green appearance (Magney *et al* 2019). Light use efficiency determines how much light that leaf chlorophyll absorbs can be used for photosynthesis and can consequently increase carbon assimilation and biomass. Light use efficiency is more sensitive to soil moisture stress than large-scale structural properties such as canopy density (Stocker *et al* 2019).

We focus on more details about vegetation responses to drought events below, which are becoming more intense and frequent across the globe (Canadell *et al* 2021). Observational evidence shows that vegetation stomata can respond rapidly to increases in atmospheric drought (represented by high VPD), which is associated with guard cell regulation, when water supply, such as from the soil, is insufficient (Novick *et al* 2016, Liu *et al* 2020, Fu *et al* 2022a). When VPD increases, stomatal conductance, maximum photosynthetic rate, GPP and transpiration decrease. Coinciding with VPD drought, soil moisture drought often lead to similar changes of vegetation physiology, but the biogeochemical vegetation response is not the same (Carminati and Javaux 2020). Soil moisture drought can strongly affect the conductance of the rhizosphere and trigger the production of hormones such as ABA. The degree of change in stomatal conductance then depends on the sensitivity of the plant to hydraulic and hormonal signals. In terms of vegetation structural traits, field observations suggest that leaf angle and shape can change relatively quickly in response to drought (Yang 2023), compared to other traits that require the accumulation of non-structural carbohydrates and therefore take longer to manifest respond. The effects of drought on canopy density are often detrimental in mainly water-limited regions, but can actually be beneficial in energy-limited regions. An increasing number of recent studies on a global scale support that canopy density in water-limited ecosystems shows negative changes under soil moisture or atmospheric drought, which are distinct from changes in canopy density in energy-limited ecosystems (Zhao *et al* 2022, Hoek van Dijke *et al* 2023, Li *et al* 2023a, 2023b). Increases in canopy density in energy-limited ecosystems may be related to potentially deep rooting systems (Stocker *et al* 2023), maintained groundwater availability under soil moisture drought (Mu *et al* 2021), increases in light illumination and reductions in waterlogging (Ohta *et al* 2014), and the emergence of new leaves during drought-associated sunny weather (Janssen *et al* 2021). More research on the relative roles of these drivers is needed to further understand the dominating mechanisms of drought-induced divergent structural changes.

The direct impact of drought is only one part of its impacts on vegetation ecosystems, while additionally there are also drought legacy effects that are relevant to the stability of vegetation ecosystems. Drought legacy effects thereby refer to changes in the vegetation response to climate which last beyond the actual drought period (e.g. decreased photosynthesis for the same meteorological conditions after the drought compared to before the drought). Previous studies have mostly investigated drought legacy effects in terms of individual physiological or structural traits, such as stomatal conductance (Virlouvet *et al* 2015),

wood density (Corcuera *et al* 2004), xylem conductance (Hacke *et al* 2001), ring width index (Anderegg *et al* 2015), GPP (Yu *et al* 2022), or tree mortality (Anderegg *et al* 2013). Multiple lines of evidence show that the legacy effects of drought on vegetation depend on vegetation types and drought severity, with vegetation being more susceptible to embolism under more severe drought which then leads to the slowest recovery (Anderegg *et al* 2015, Yu *et al* 2022). Loss of non-structural carbohydrate due to drought-reduced photosynthesis can affect vegetation growth for several years. As a consequence of the reduced vegetation functioning and resilience following drought legacy effects, disturbances such as pests and pathogens can more easily harm vegetation. A direct comparison of drought legacy effects on different structural and physiological characteristics is lacking but should be a focus of future research, as is key to guiding ecosystem management and to maintaining the overall stability and resilience of ecosystems.

6. Regulation of the global carbon and water cycles through vegetation

Vegetation structure and physiology play essential roles in regulating the global carbon and water cycles (figure 5). The terrestrial water cycle encompasses precipitation from the atmosphere, evaporation to the atmosphere and runoff flow to reservoirs and the ocean, and terrestrial water storage (including interception, snow, soil and bedrock moisture, groundwater, and some other water components). Among these water cycle components, evaporation is fundamental to balancing available terrestrial freshwater storage for human activities such as irrigation, and is also fundamental to ecosystem services such as evaporative cooling (Zeng *et al* 2018, Pan *et al* 2020).

Vegetation structure regulates evaporation through several direct and indirect processes. Changes in LAI or vegetation fractional cover directly affect interception and transpiration, but they also alter surface albedo with higher albedo reducing the later energy availability for evaporation (Betts *et al* 1997, Forzieri *et al* 2017, 2020). Tree ecosystems, compared to grasses or shrubs, increase the surface roughness and turbulence so that microclimate changes feed back to the water cycle (Zhang *et al* 2016, Duveiller *et al* 2018, Piao *et al* 2020). Both the above-ground structure and the root structure can indirectly modulate evaporation. Increases in root biomass promote the rate of precipitation infiltration into the soil and prevent soil erosion, enhancing soil water holding capacity and relieving the risk of floods and landslides and thus land degradation (Cui *et al* 2019). Therefore, the root structure contributes to the stability of the water cycle. Vegetation greenness and evaporation are enhanced by warm temperatures in the early growing season, leading to an early decline in soil water availability and groundwater recharge, which then feeds back to soil water deficit in dry seasons when precipitation is not compensating (Lian *et al* 2020).

Vegetation physiology, such as stomatal conductance, often directly influences evaporation and soil moisture, but regulates runoff and atmospheric moisture more indirectly via changes in evaporation (Zhang *et al* 2016). Plant hydraulic traits determine their water saving strategies under drought or heat waves, with conservative plants closing or partially closing stomata to reduce evaporation until the next precipitation event. Therefore, the high resistance of vegetation to drought or heat waves reduces mortality risks and maintains the other ecosystem services such as atmospheric water demand and runoff recharge (Teuling *et al* 2010, Li *et al* 2023b).

The terrestrial carbon cycle involves processes of carbon uptake through vegetation photosynthesis, carbon loss through respiration, and carbon storage e.g. above- and below-ground biomass. Vegetation structural changes (e.g. greening) driven by atmospheric CO_2 increases and climate change benefit the land carbon sink. Increases in LAI contribute 12.4% to the terrestrial carbon sink during 1982–2016 (Chen *et al* 2019b). Over the last century, increased vegetation greenness and also photosynthesis have doubled the land carbon sink, contributed by tropical forests largely due to CO_2 fertilisation effects, by boreal forests due to elevated temperature, and by agricultural intensification due to human land-use management (Chen *et al* 2019a, Piao *et al* 2020, Ruehr *et al* 2023). It has been argued about the potential of decline in the land carbon sink when considering additional physiological stress that downregulates carbon assimilation under climate extremes (Stocker *et al* 2019). Warm temperature increases light use efficiency through increases in Rubisco activities and electron transport rate, but some vegetation reduces their photosynthetic efficiency under warming as they frequently experience temperature beyond their optimal ranges (Huang *et al* 2019). There are also other physiological or biophysical responses to climate change that increase land carbon emissions. The reduced peak photosynthetic capacity can be found due to excessive water and nutrient consumption by warming-induced vegetation growth in the early and middle growing seasons (Zani *et al* 2020, Zhang *et al* 2021, Vitasse *et al* 2021, Wang *et al* 2023b). Accumulated vegetation biomass enhances plant and soil respiration, and global warming accelerates the decomposition of soil organic carbon through microbial processes (Terrer *et al* 2021). Ecosystem disturbance such as pest and pathogen attack and fires that frequently occur in recent decades also increases the risk of land carbon emissions (Reichstein *et al* 2013, Williams *et al* 2013, Bastos *et al* 2023).

As discussed above, the increase of the land carbon sink is mainly driven by increased temperature and atmospheric CO_2, and other human-climate
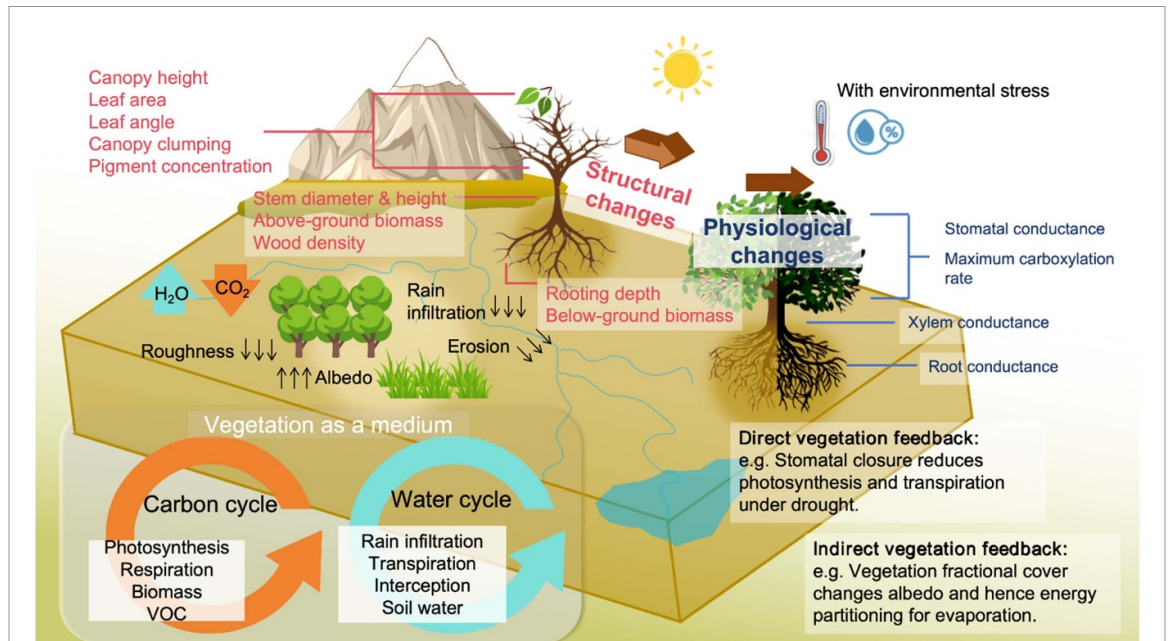
Figure 5. Characteristics of vegetation structure and physiology and their regulation on the global carbon and water cycles. VOC: volatile organic compounds.
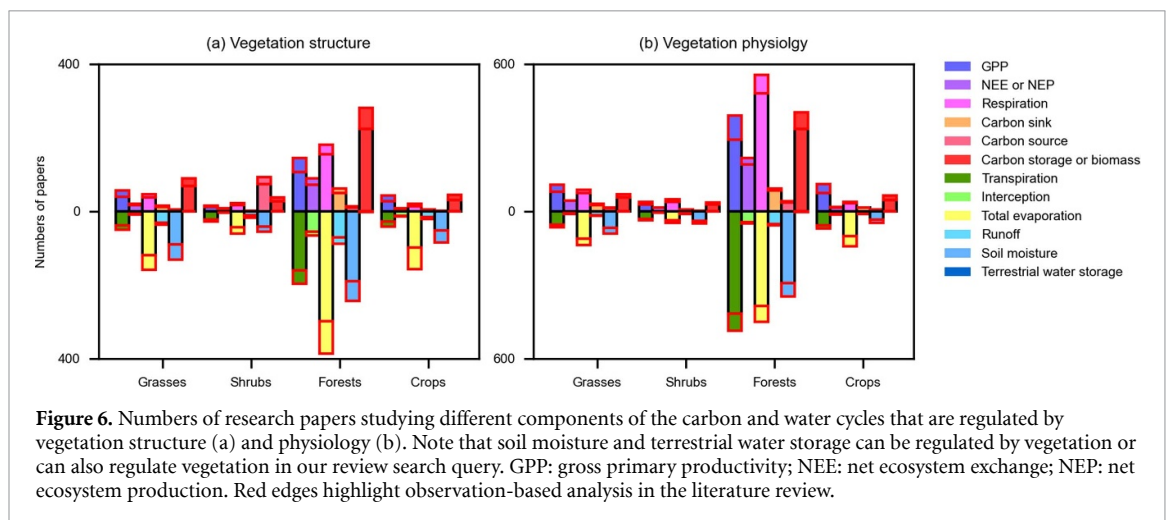

Figure 6. Numbers of research papers studying different components of the carbon and water cycles that are regulated by vegetation structure (a) and physiology (b). Note that soil moisture and terrestrial water storage can be regulated by vegetation or can also regulate vegetation in our review search query. GPP: gross primary productivity; NEE: net ecosystem exchange; NEP: net ecosystem production. Red edges highlight observation-based analysis in the literature review.

drivers, but vegetation structural or physiological adaptations can modulate the effect of these drivers on the carbon cycle (Alkama *et al* 2023 preprint). Droughts and heat waves are becoming more frequent and intense in the past three decades. Accumulated drought effects on vegetation, such as plant xylem embolism and hydraulic failure, can reduce biomass and ecosystem stability to the next climate extremes or disturbances (McDowell *et al* 2008, Bastos *et al* 2023). Human-induced reductions of vegetation biodiversity and landscape heterogeneity also affect ecosystem stability to withstand climate extremes and disturbances (Fuhlendorf *et al* 2006, Beckmann *et al* 2019). For example, wildfires are likely to spread more easily where there is a homogeneous and dense distribution of dry woody or herbaceous vegetation (e.g. continuous fuel, Fuhlendorf *et al* 2006, Loepfe *et al* 2010). Insect outbreaks,

similarly, can be more prolonged when plant types with different resistance are not well mixed in space (Klapwijk *et al* 2018).

Figure 6 displays the numbers of research papers that investigate the regulation of the global carbon and water cycles through vegetation structure and physiology. Vegetation biomass is mostly often studied in the topic of the carbon cycle, followed by GPP and respiration, and then the quantification of land carbon sink or source. In terms of the water cycle, evaporation is the most-often studied, followed by soil moisture, transpiration, runoff, interception, and terrestrial water storage.

7. Discussions and conclusion

Overall, we find that vegetation structural characteristics in previous studies that focus

on vegetation-climate interactions at the large scale often refer to vegetation greenness indices or LAI. However, other characteristics, such as the consideration of vertical and horizontal canopy and stem architecture, leaf angle distribution, vegetation height, and the below-ground structure, and their regulation on the land carbon sink and land evaporation, are poorly studied at the large scale. Vegetation physiological characteristics at the large scale are not easily accessible from observations, but can be inferred from remotely-sensed vegetation functions and structure that are increasingly becoming available. More exploration of large-scale physiological responses to climate change and validation against site measurements are urgently needed, as it is part of the key to reconstruct the past and predict the future functional performance of vegetation. We hence suggest prioritizing the agenda of monitoring multifaceted vegetation structure and functions, and analysizing vegetation physiology at the ecosystem-to-global scales to better understand vegetation processes, drivers, and feedback to the global water and carbon cycles.

There are several key scientific questions that need to be answered in the agenda. Firstly, when and where do large-scale vegetation structural and physiological changes differ with each other? Previous studies that compare vegetation structural and physiological changes reveal a strong similarity between vegetation structure and physiology in terms of global spatial patterns, while the temporal decoupling is often found at different time scales. Decoupled physiological and canopy structural responses are found at sub-weekly scales during severe drought events and at interannual scales during growing seasons (Magney *et al* 2019, Hu *et al* 2022, Li *et al* 2023a). In wet or cold regions, the decoupling is more readily apparent compared to dry or warm regions. This is likely due to the heightened uncertainties associated with monitoring vegetation canopy structure, considering issues such as saturation or cloud interference in vegetation indices (Morton *et al* 2014, Doughty *et al* 2019), or related to the frequent downregulation of vegetation performance in response to environmental stress (Magney *et al* 2019, Li *et al* 2023a). Upcoming missions such as the ESA Biomass mission, NASA's NISAR mission, GNSS Interferometric Reflectometry (GNSS-IR)-based vegetation observation, and tomographic SAR will help to improve the characterisation of vegetation structure, functions and physiology. High spatio-temporal resolution optical-infrared and SAR data hold great promise for overcoming current limitations associated with cloud cover and spectral saturation. Future research endeavors should extensively utilize these newly developed products and advance the field by employing more sophisticated modeling techniques to integrate multi-stream data.

Secondly, to what extent can state-of-the-art space-borne remote sensing observations reveal changes in vegetation physiology? SIF has recently been widely studied due to its relationship with the light reactions of photosynthesis and, consequently, with GPP. However, the extent to which SIF reflects vegetation physiological signals still needs to be better quantified, but the task is challenging due to the weak retrieved SIF signal, which is easily affected and confounded by vegetation structural complexity and satellite geometry (Köhler *et al* 2018, Doughty *et al* 2019). Tower-measured and recently satellite-observed carbon and water fluxes (e.g. atmospheric column averaged CO_2 dry air mole fraction; Eldering *et al* 2017) can complement vegetation functional estimates and advance the inference of physiological parameters (e.g. Wolf *et al* 2006, Knauer *et al* 2018, Migliavacca *et al* 2021). Other examples of remote sensing capabilities in reflecting physiological signals, such as LST, have often been studied because it is a response variable of evaporative cooling by vegetation. LST changes rapidly not only due to changes in transpiration but also due to meteorological and aerodynamic conditions between the land surface and the boundary layer (Panwar *et al* 2020, Fu *et al* 2022b, Green *et al* 2022, Panwar *et al* 2022). Future studies need to better account for meteorological or aerodynamic conditions in confounding the physiological signals of LST or SIF to more accurately estimate plant physiology.

Monitoring multiple vegetation characteristics at large scales, rather than simplifying them into two types, structure and physiology, is a challenge for satellite remote sensing, e.g. structural dynamics involves changes in LAI but also rapid changes to leaf angle. On the other hand, site measurements monitor multiple vegetation structural or physiological characteristics, e.g. eddy-covariance carbon or energy fluxes, 3D vegetation structure from ground-based laser scanning (Calders *et al* 2023), vegetation height from airborne LiDAR, transpiration estimated using harmonized sap-flux measurements such as SAPFLUXNET (Poyatos *et al* 2020), leaf water potential measured in the laboratory, etc. A third step on the agenda is to leverage site-level observations and satellite remote sensing to advance the understanding of vegetation response to climate change at large to global scales. One simple way is to investigate multi-stream data using traditional statistics or machine learning algorithms, but different sources of data are often mismatched in terms of spatio-temporal resolution and coverage or biased by their unique systematic uncertainties. Cloud cover or changes in orbit geometry can confound optical remote sensing signals (Morton *et al* 2014, Doughty *et al* 2019, Zeng *et al* 2022b). Satellite signals from multi-weekly or monthly half-degree data are often a mixture

of changes in vegetation structure and physiology. Long-term remote sensing records since the 1980s of vegetation greenness and since the 1990s of VOD from different orbits suffer from a mismatch in frequencies (Jiang *et al* 2017). *In-situ* measurements with long-term observations are also easily interrupted by the experiment deterioration (Walker *et al* 2021). Future investments in monitoring global or large-scale vegetation at fine spatiotemporal resolutions (e.g. to match the footprint and diurnal dynamics of eddy towers) are therefore needed to establish better empirical relationships between satellite and ground measurements (Emmerik *et al* 2015, Weiss *et al* 2020, Zhang *et al* 2023). These state-of-the-art site and satellite measurements may also open new avenues for integrating multi-source observations into data assimilation framework to better constrain biophysical and physiological processes (Luo *et al* 2011, Smith *et al* 2020), and may provide more accurate parameters for land surface/earth system simulations (Ukkola *et al* 2016, Trugman *et al* 2018) and for reconstructing or harmonising tasks to produce long-term satellite-based vegetation products (Zhang *et al* 2018, Moesinger *et al* 2020).

Global vegetation structure and physiology have changed over time in the past, and they will continue to do so in the future under a warmer and more CO_2-rich atmosphere. Although vegetation greenness is on the rise in numerous regions globally due to increasing temperatures, elevated atmospheric CO_2 levels, and other anthropogenic factors (Donohue *et al* 2013, Zhu *et al* 2016, Chen *et al* 2019b), the advantageous effects of climate change seem negligible in areas characterized by limited nutrient supply and water availability (Wang *et al* 2020, Winkler *et al* 2021). Water limitation is dominant in semi-arid and arid areas, where the relationship between vegetation greenness and soil water availability has become stronger over the past 30 years and will continue to become stronger in future scenarios due to increased fractions of water-limited regimes (Jiao *et al* 2021, Denissen *et al* 2022). With more frequent and intense droughts and heat waves over these regions, certain degrees of soil depletion could lead to an amplified reduction in vegetation greenness (Li *et al* 2022, Zhang *et al* 2022). In future studies, there is a critical need to more accurately attribute and comprehend the mechanisms driving changes in vegetation structural and physiological properties. Additionally, studies should address a fundamental question regarding the temporal variation of different structural and physiological variables of vegetation. With the discussed data and methodological advantages, this topic is primed for comprehensive investigations on large scales.

In summary, we provide a means or conceptualisation for separating vegetation structure and physiology. We review the scientific evidence that addresses the responses of vegetation structure and physiology to climate change, including different vegetation morphologies, plant traits related to water and nutrient transport and photosynthesis, etc. Although vegetation structure and physiology interact and their dynamics are largely coupled, their decoupled responses to environmental stress cannot be ignored and need to be better understood across a wide range of ecosystems. Finally, we recommend a more comprehensive use of satellite remote sensing and *in-situ* measurements for a holistic diagnosis of global vegetation health under climate change. Comprehensive vegetation monitoring can help to better estimate land carbon sink and land evaporation, and guide land management to adapt to climate change.

Data availability statement

No new data were created or analysed in this study.

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Author contributions

W L conceived the study with the support of R O and G D. All authors provided valuable comments on the entire manuscript.

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