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Limited role of soil texture in mediating natural vegetation response to rainfall anomalies

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Supplementary material for this article is available online

Abstract

Evidence suggests that the response of rainfed crops to dry or wet years is modulated by soil texture. This is a central tenet for certain agronomic operations in water-limited regions that rely on spatial distribution of soil texture for guiding precision agriculture. In contrast, natural vegetation in climatic equilibrium evolves to form a dynamic assemblage of traits and species adapted to local climatic conditions, primarily precipitation in water-limited regions. For undisturbed landscapes, we hypothesize that natural vegetation responds to rainfall anomalies irrespectively of local soil texture whereas rainfed crops are expected to respond to texture-mediated plant available water. Earth system models (ESMs) often quantify vegetation response to drought and water stress based on traditional agronomic concepts despite fundamental differences in composition and traits of natural vegetation and crops. We seek to test the hypothesis above at local and regional scales to differentiate natural vegetation and rainfed crops response to rainfall anomalies across soil types and better link them to water and carbon cycles. We employed field observations and remote sensing data to systematically examine the response of natural and rainfed cropped vegetation across biomes and scales. At local scales (field to ∼0.1 km), we used crop yields from literature data and natural vegetation productivity as gross primary productivity (GPP) from adjacent FLUXNET sites. At regional scales (∼10^2 km), we rely exclusively on remote-sensing-based GPP. Results confirm a lack of response of natural vegetation productivity to soil texture across biomes and rainfall anomalies at all scales. In contrast, crop yields at field scale exhibit correlation with soil texture in dry years (in agreement with conventional agronomic practices). These results support the hypothesis that natural vegetation is decoupled from soil texture, whereas rainfed crops retain dependency on soil texture in dry years. However, the observed correlation of crops with soil texture becomes obscured at larger scales by spatial variation of topography, rainfall, and uncertainty in soil texture and GPP values. The study provides new insights into what natural vegetation's climatic equilibrium might mean and reveals the role of scale in expressing such sensitivities in ESMs.

1. Introduction

Precision agriculture aims to provide spatially resolved application of water and other inputs (fertilizers, agrochemicals) based on differences in crop response to local soil texture and topography (Jiang and Thelen 2004). These empirically based tenets also guide the design of irrigation systems and their management (Holzapfel *et al* 2015, Valdivia-Cea *et al* 2017). Agronomic experience is replete with examples showing the centrality of soil texture in controlling drainage, water redistribution, and soil aeration, which play a key role for crop productivity (e.g. Travlos and Karamanos 2006, Obia *et al* 2018). Evidence shows that variations in soil texture and topography influence yield variability at the field

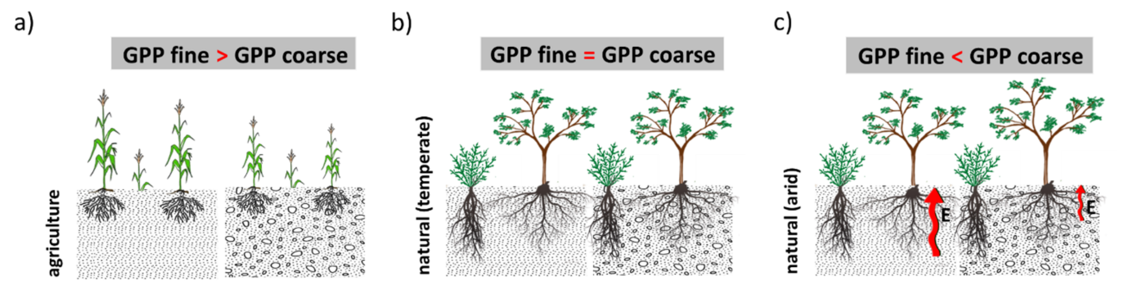

Figure 1. Conceptual diagram to describe the response of crop and natural vegetation to dry years as a function of soil texture. (a) In anomalous dry years, more water can be retained in fine textured soils, resulting in larger crop yield (GPP) compared to coarse textured soils. (b) In contrast, natural vegetation in temperate regions is insensitive to soil texture because of selection of traits that are adapted to the local climate. (c) Productivity of natural vegetation in arid regions is larger in coarse than in fine textured soils due to the 'inverse texture effect' (the thickness of soil layer with bare soil evaporation (E) is much thinner in coarse soil; rainfall water percolates below this layer and can be used by plant roots.).

scale (Manoli *et al* 2015, Fang and Su 2019, Neupane and Guo 2019), particularly in rainfed agriculture during dry years when soil water storage and plant available water are strongly affected by local soil texture (figure 1(a)). For example, Fang and Su (2019) showed that, in dryland agriculture, crop productivity was reduced and nitrogen losses were increased in sandy soils compared to loamy soils that exhibit lower rates of internal drainage and higher field capacity. Similarly, Roncucci *et al* (2015) have shown that the crop yield in silty clay loam soils was higher than in sandy loam during an anomalous dry year in a Mediterranean environment. In contrast to crop textural response in dry regions, crops grown in fine-textured soils in temperate regions exhibit yield losses in wet years due to water logging (Najeeb *et al* 2015).

In addition to soil textural effects, other geomorphic and biochemical processes (e.g. topography, physical and chemical weathering, biological activity, water flow patterns) may affect crop response at a specific location in the landscape (Hallema *et al* 2016, Ayoubi *et al* 2021). The variation (spatial and temporal) in such physical and chemical processes is often considered during crop placement at the field scale (Thelemann *et al* 2010). Matinez-Feria and Basso (2020) differentiated between stable and unstable zones (stability with respect to yield variation over time) and showed that soil type is the leading factor explaining spatial variability in stable zones but not in unstable zones, where weather and landscape position control spatial yield variations.

While the sensitivity of agricultural crop productivity to soil texture and topography has been confirmed in numerous studies, the relationship between natural vegetation productivity and soil texture remains sketchy. Studies have reported the so-called 'inverse texture effect', namely higher vegetation productivity of coarse textured soils compared to fine textured ones in arid regions (Noy-Meir 1973) and during dry years for specific biomes and plant species (Lane *et al* 1998, Fernandez-Illescas *et al* 2001, Strohbach *et al* 2014). The inverse texture effect in dry regions is related to higher bare soil evaporation losses in fine textured soils compared to coarser soils. In fact, for coarse textured soils, only a thin layer contributes to bare soil evaporation and rainfall water percolating to larger depths is protected from evaporation but can be used by the deeper plant roots (see figure 1(c)).

Studies have often attributed variations in natural vegetation productivity to climatic factors and disturbances (Chmielewski and Rötzer 2001, Abera *et al* 2018) and less to soil factors (texture). Imbach *et al* (2012) estimated that the leaf area index (LAI) in Mesoamerica might decrease by 77%–89% (depending on climate change scenarios) with natural vegetation shifting from humid to dry types. Liu *et al* (2019) observed negative effects of high summer temperature on gross primary productivity (GPP) in arid regions, resulting in enhanced aridity stress on productivity under global warming.

The assemblage and traits of natural vegetation in equilibrium with climatic conditions often exhibit specific adaptation to regional rainfall patterns. For example, Fisher *et al* (2007) found that deeper roots in tropical regions alleviate limitations to transpiration relative to shallow-rooted crops. Gentine *et al* (2012) confirmed the key role of deeper root zones in a semi-arid catchment with deep-rooted vegetation, which is better suited for coping with water stress. These findings support the hypothesis by Troch *et al* (2009) that a region's natural vegetation is adapted to local climate variability by utilizing the largest proportion of available soil moisture. Furthermore, according to Green *et al* (2019), the capacity of continents to act as future carbon sinks critically depends on the nonlinear response of carbon fluxes to soil moisture and on land–atmosphere interactions.

Motivated by these observations, we hypothesize that, unlike rainfed agricultural crops (monoculture), natural vegetation is well adapted to local climate variability by responding to climatic variables (rainfall) irrespective of local soil texture, particularly in anomalously dry years (see sketch in figure 1(b)). We emphasize that natural vegetation responds to rainfall anomalies in terms of ecosystem GPP, however, this response exhibits lower sensitivity to soil texture than shown by rainfed crops under similar conditions. To test the hypothesis, we compare natural vegetation and crop response to rainfall anomalies and soil texture at different spatial and temporal scales and resolution. At large scales ($\sim 10^2$ km) and coarse resolution, confounding factors such as rainfall regional variability, landscape features and topography, and uncertainty in soil and vegetation maps will gradually obscure the nuanced relations hypothesized in this study.

The specific objectives of this study are:

(a) To evaluate the sensitivity of natural vegetation and crop productivity to soil texture across different biomes and at different spatial scales,
(b) To quantify the effect of rainfall anomalies (dry and wet years) on vegetation productivity as a function of soil texture,
(c) To quantify the effect of other environmental variables (i.e. topography and rainfall) on the sensitivity of vegetation productivity to soil texture at regional scale.

2. Material and methods

In this study, we link productivity of vegetation with soil texture, rainfall, and topography. Depending on the spatial scale and data resolution, we conducted three different analyses focusing on (a) sensitivity of productivity to soil texture, (b) sensitivity to rainfall amount, and (c) effects of spatial variation. We distinguished between natural vegetation and rainfed agricultural crops and we collected data from different sources and climatic regions (temperate and arid) as detailed below.

2.1. Data sources

2.1.1. Productivity of natural vegetation and rainfed agricultural crops

We use GPP as a representative metric for both crop yield and natural vegetation productivity. GPP was estimated at two different scales (local scale and regional scale). Note that we conducted this study in temperate and arid climatic regions and the climatic classification was based on the Köppen–Geiger climate zone map (Rubel and Kottek 2010, Hamel *et al* 2017).

2.1.1.1. Local scale

At local scale (field to $\sim$0.1 km), we used crop yields from literature data and GPP from adjacent FLUXNET sites (https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/). To quantify agricultural productivity for various sites at local scale for different climatic zones, we selected wheat crop studies (listed in table S1 available online at stacks.iop.org/ERL/17/034012/mmedia) and only considered conventional yield (in agreement with conventional agronomic practices such as tillage, large inputs of pesticides and mineral fertilizers). For both crop yield and natural vegetation (listed in table S2), the dry and wet year GPP was extracted from time-series data.

2.1.1.2. Regional scale

For the regional scale analysis, remote sensing based GPP (hereafter referred to as 'regional scale GPP') was extracted from MODIS (Moderate Resolution Imaging Spectroradiometer) at spatial resolution of 0.5 km (https://modis.gsfc.nasa.gov/data/dataprod/mod17.php). We note that, unlike natural vegetation, agricultural crops are rainfed or irrigated and we used maps published by Biradar *et al* (2009) to distinguish between rainfed and irrigated crops. The relationship between soil texture and crop yield could be obscured by combining data from different crops, so we differentiated across different crop types. To this purpose, we used land use/land cover information from MODIS (https://modis.gsfc.nasa.gov/data/dataprod/mod12.php) to identify agricultural lands and classified different crops using cropland data layers (https://nassgeodata.gmu.edu/CropScape/). In this study, we used corn for arid regions and corn and soybean for temperate regions. The crop is usually harvested in 6–8 months depending on the crop type. Hence, GPP was evaluated based on the crop period (time between sowing and harvesting)—we extracted this information from USDA-Nass (1997, https://swat.tamu.edu/media/90113/crops-typicalplanting-harvestingdates-by-states.pdf).

2.1.2. Soil texture information

We used sand content within the top 0–30 cm to quantify soil texture. Consideration of deeper depths did not affect the inferences, as no significant change in sand content was found in global maps as deeper layers were considered (see sand content distributions in figure S1). In most cases, sand content was extracted from the global maps of SoilGrids at a spatial resolution of 0.25 km (Hengl *et al* 2017, https://soilgrids.org/). In SoilGrids, the sand content is estimated using machine learning algorithms trained with a large data set and considering various maps of environmental covariates collected by remote sensing. For the analysis on the temporal change of GPP as a function of soil texture, we used measured soil texture data obtained from Batjes *et al* (2020). The soil textural class information was extracted using the USDA-NRCS (Natural Resources Conservation Service) soil texture calculator (www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2_054167).

2.1.3. Rainfall and temperature effects

To study the sensitivity of vegetation productivity to rainfall, we defined dry years as those years with

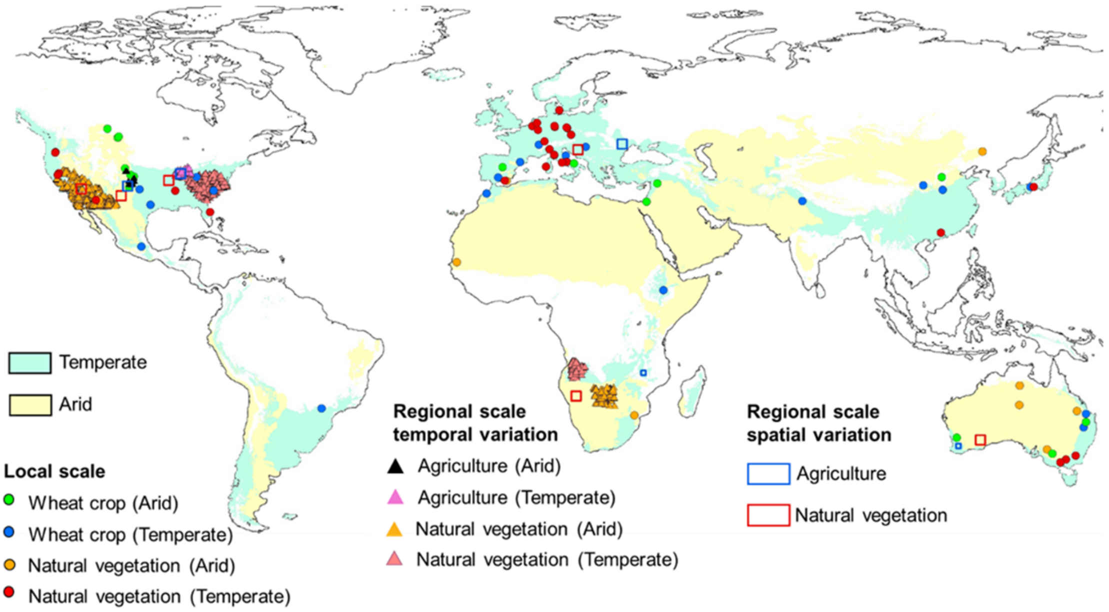

Figure 2. Spatial distribution of study sites to determine soil texture-vegetation relationships for natural vegetation and agricultural crops. Three types of studies are distinguished with respect to underlying data source and spatial scale. At the 'local scale', the productivity of a site was measured locally (not by remote sensing). For analysis on temporal variation ('regional scale—temporal variation'), the change of remotely sensed GPP with time was quantified for different soil textural classes. Lastly, the effect of spatial variation of environmental factors on soil texture vegetation relationship was analyzed ('regional scale—spatial variation').

annual rainfall amount below 80% of the long-term average rainfall and wet years as those with annual rainfall amount above 120% of the long-term average rainfall (Kumar *et al* 2013). For the case of several years fulfilling these criteria, we chose the year with lowest rainfall amount as 'dry year' and highest rainfall amount as 'wet year'. Daily rainfall values were obtained from MSWEP (Multi-Source Weighted-Ensemble Precipitation) V2 (Beck *et al* 2019) with spatial resolution of 10 km and converted to yearly data to differentiate between dry and wet years. We have used the annual CHELSA (Climatologies at high resolution for the earth's land surface areas) temperature data (Karger *et al* 2017) to study temperature relations with rainfall and potential effects on GPP.

2.1.4. Topography

To quantify the effect of different topographic attributes on vegetation productivity, we used digital elevation models obtained from 'GTOPO30' (Miliaresis and Argialas 1999) with a horizontal grid spacing of 30 arc seconds (≈1 km).

2.2. Three approaches to quantify soil texture—vegetation relationships

The quantitative relationship between vegetation productivity and soil texture can be obscured by uncertainties in the underlying global maps (MODIS and SoilGrids) and variations of other environmental factors (e.g. climate and topography). To distinguish between the effects of such factors we conducted three types of analysis (see figure 2).

2.2.1. Local scale (field scale) GPP

Directly measured GPP (not based on remote sensing) from the literature for crop yield and FLUXNET data for natural vegetation were collected from several continents. For crop yield in arid and temperate regions, 15 and 23 sites were used, respectively. For natural vegetation, 11 and 30 sites were selected for arid and temperate sites, respectively. Soil texture information was estimated using SoilGrids.

2.2.2. Regional scale—temporal variation

Vegetation productivity is expected to change in time with rainfall amount. The temporal variation of productivity (deduced from MODIS) with rainfall for different soil textural classes was determined for some regions in USA and Africa. The measured soil texture information provided by Batjes *et al* (2020) was used for this analysis. The number of samples used for this study for agriculture and natural vegetation is provided in table S3.

2.2.3. Regional scale—spatial variation

To compare soil texture-vegetation relationships for natural vegetation and crops in the same region, a total of 11 regions was selected in which six regions belong to natural vegetation and five to agricultural land. We chose nearby squares of 250 × 250 km size from both vegetation types (natural and crop) in the same climatic region to allow comparison between crop and natural vegetation. While for the USA it

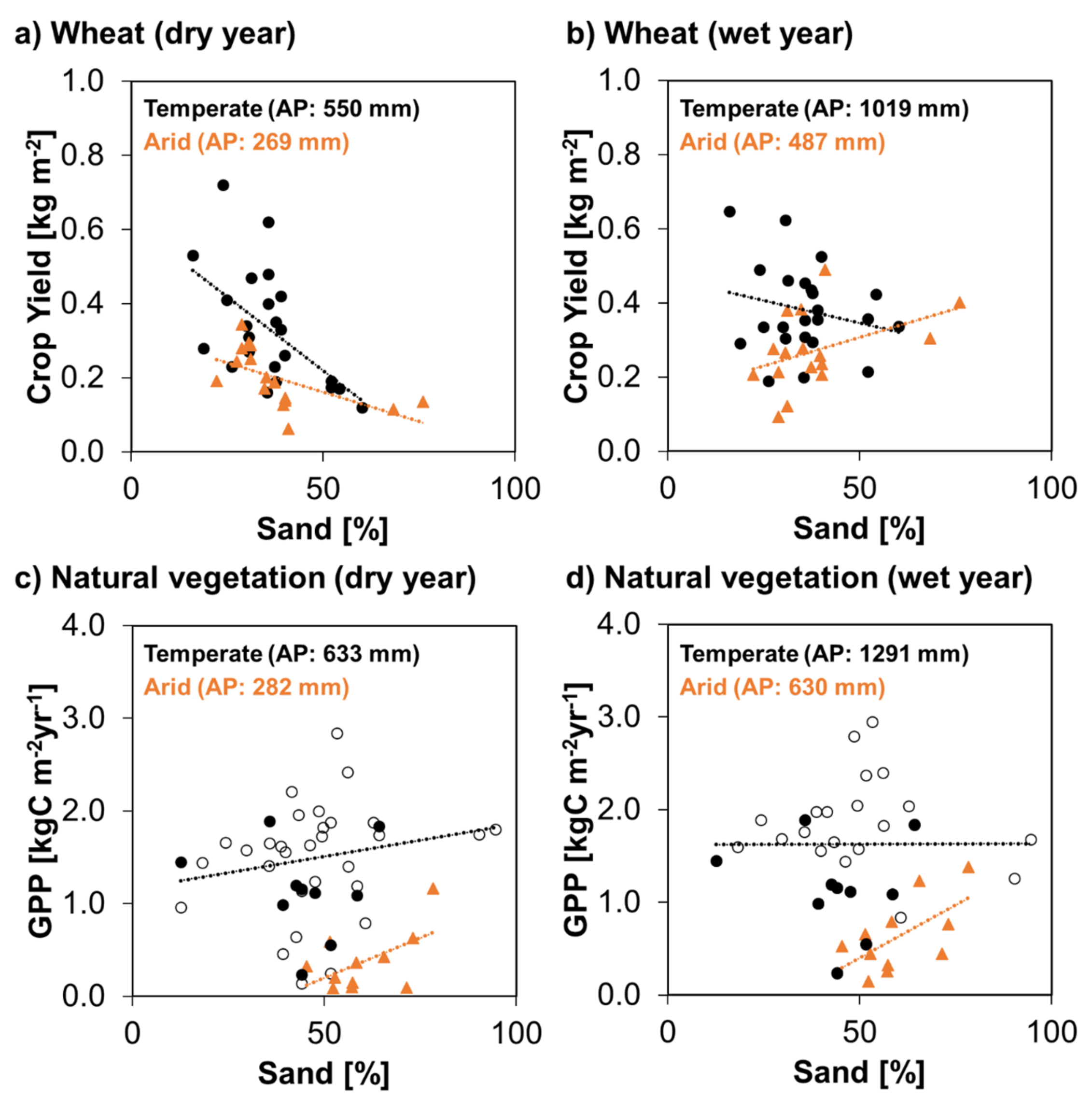

Figure 3. Relationship between sand content and vegetation productivity measured directly ('locally') in the field. Only in the case of crops in dry years (a), the expectation of decreasing crop yield with increasing sand content was observed for both arid and temperate climates. (b) For wet years, the negative trend is less distinct for crops in temperate and slightly positive in arid climates. The coefficients of determination (R^2) of 0.32 (p-value 0.005) and 0.33 (p-value 0.01) for temperate and arid climate in dry year, are higher than those obtained for wet year (0.05 (p-value 0.31) and 0.17 (p-value 0.09) for temperate and arid, respectively). In contrast to agricultural crops, natural vegetation showed a positive trend with increasing sand content during both dry and wet years for arid regions with R^2 of 0.30 (p-value 0.07) and 0.37 (p-value 0.04), respectively (c) and (d). Note that black empty circles represent the GPP from the forest sites and black dots from grassland and scrublands (the lack of correlation was evaluated with grassland samples only, but the forest samples were included to highlight the missing correlation). AP represents the annual precipitation.

was possible to find nearby squares of 250 × 250 km size, for other continents squares of natural vegetation and crops were more separated and smaller (125 × 125 km). Each square contains up to 2.5×10^5 pixels of 0.5 × 0.5 km size in 250 × 250 km^2 (0.6×10^5 pixels for 125 × 125 km^2) with sand fraction and GPP deduced for each pixel from remote sensing products (MODIS and SoilGrids).

3. Results

3.1. Local scale: GPP sensitivity to soil texture in water limited conditions

An important tenet in agronomic operations is the decreasing water holding capacity with increasing sand content and the corresponding expectation of decreasing crop yield under water-limited conditions (He *et al* 2014, Zipper *et al* 2015). By collecting and analyzing measured crop yield data at the field scale around the globe, we show (figure 3(a)) that the expected trend of decreasing crop yield with increasing sand content was found in both arid and temperate climates. Crop yield is more sensitive to soil texture during dry years (figure 3(a)) compared to wet years (figure 3(b)) for both arid and temperate climates (note that the analysis was performed using data from the very same field sites for wet and dry years). This statement is based on the larger coefficient of determination (R^2) of 0.32 (p-value 0.005)

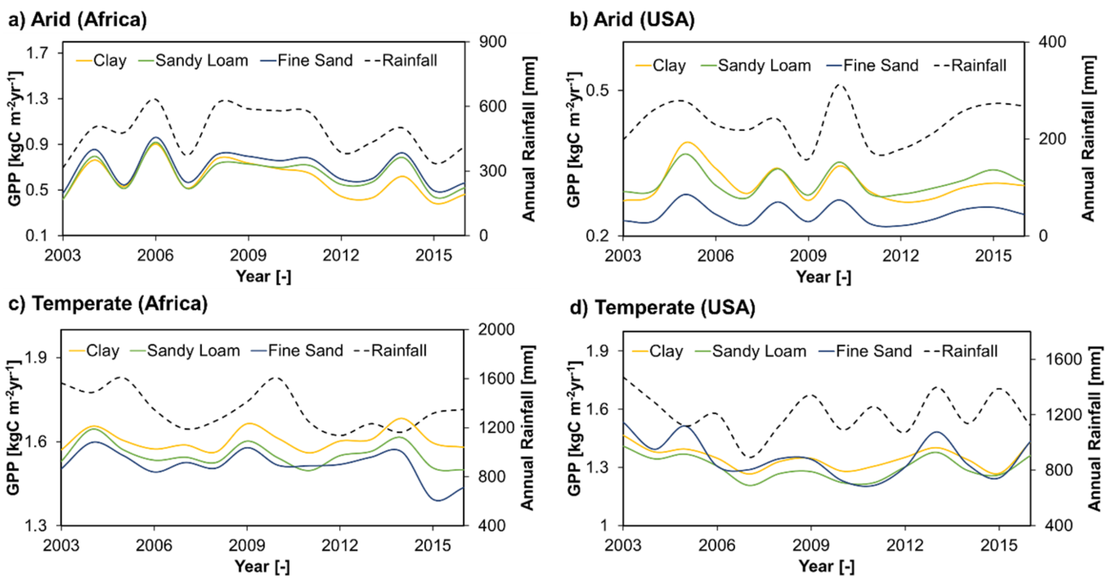

Figure 4. Time series of GPP (natural vegetation) and rainfall for different soil textures. Panels (a) and (b) show results from arid regions, (c) and (d) from temperate regions. Especially in arid regions, the fluctuations of rainfall and GPP are synchronized, with GPP increasing with rainfall amount.

and 0.33 (p-value 0.01) for temperate and arid climate in dry year, compared to 0.05 (p-value 0.31) and 0.17 (p-value 0.09) for wet year. In contrast to the findings for agricultural crops, no significant correlation was found between natural vegetation GPP and sand content for both dry and wet years for temperate conditions (figures 3(c) and (d)). However, in arid climates, natural vegetation showed a positive trend with increasing sand content during both dry and wet years with R^2 of 0.30 (p-value 0.07) and 0.37 (p-value 0.04), respectively. This increase of GPP with sand content is related to the 'inverse texture effect', in which case infiltrated rainwater becomes protected from surface evaporation and can thus be used by plant roots. At the basis of this phenomenon is the hydraulic decoupling and cessation of capillary pumping to supply evaporation that occurs at shallower depths for coarse textured soils according to their evaporation characteristic depth (a property that can be predicted from soil hydraulic properties) proposed and tested by Lehmann *et al* (2008). The values of this decoupling depth vary from 0.1 m in sand up to 1 m in silt-loam soils. In contrast to crops, root systems of natural vegetation are adapted to use the rainfall water that becomes protected from bare soil evaporation.

In summary, from the local scale analysis, the expectations of (a) reduction in crop yield in sandy soils and (b) inverse texture effect for natural vegetation were both confirmed. It can be assumed that, for all the sites used in this analysis (collected from several continents), topographic effects do not obscure the expected texture-vegetation relationship as all sites lay on flat areas. Regarding the sensitivity of GPP on rainfall amounts for dry and wet years (see table S1), the crop yield increased from dry to wet year by 30% and 80% for crops in temperate and arid regions, respectively. For natural vegetation (table S2), the increase was minor (20%) for temperate regions but much higher (>100%) for arid climates.

3.2. Regional scale—GPP sensitivity to rainfall across different soil types

To show the effect of changing rainfall on GPP more systematically than in the previous section (where we looked at the difference between wet and dry years at local scale), we analyzed time series of GPP and rainfall for different soil textural classes (see figures 4 and 5). The time series plots of natural vegetation GPP show high sensitivity to rainfall in arid climate for all soil textural classes (figures 4(a) and (b)). As shown in table 1, the positive correlation between GPP and rainfall was stronger for coarse textured soils. In temperate regions, the correlation between GPP and rainfall was weaker (see figures 4(c), (d) and coefficients in table 1) and higher in fine compared to coarse textured soils. Note that, in the supplementary information, we compare time series of natural vegetation GPP with mean annual temperature across different soil textures (figure S4 and table S4). Results show a negative correlation between GPP and temperature for all biomes. These relations are linked to a negative correlation of temperature with annual rainfall in many biomes (Nzabarinda *et al* 2021, Onyutha *et al* 2021), and the potential for increased evaporative losses in hot years (that reduce plant available soil water).

In contrast to natural vegetation, rainfed crop productivity was less correlated to rainfall as shown in figure 5 and table 1 (and to temperature, see

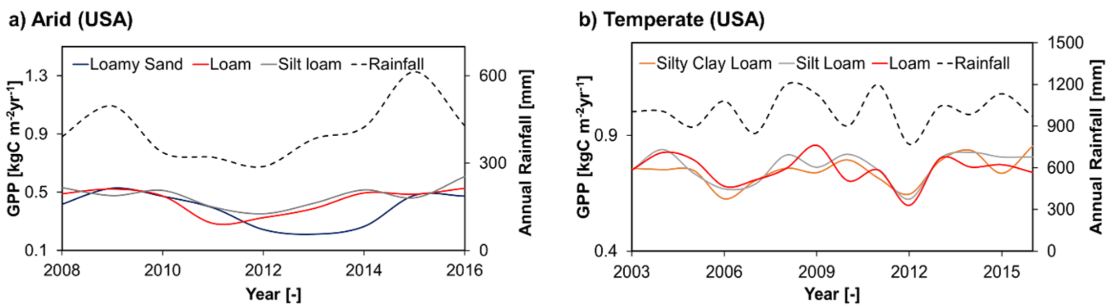

Figure 5. Time series of GPP (crop) and rainfall for different soil textures for arid (a) and temperate (b) regions. Compared to the case of natural vegetation presented in figure 4, the GPP and rainfall trends are less correlated. Note that the time series in (a) is shorter than those in panel (b) and in figure 4 due to limited data available.

Table 1. Correlation between rainfall amount and GPP for various soil textural classes and regions. Natural vegetation is more sensitive to changes in rainfall amount (higher R^2 values) compared to agricultural crops.

	Natural vegetation (R^2)				Crop (R^2)	
Texture	USA_Arid	Africa_Arid	USA_Temp	Africa_Temp	USA_Arid	USA_Temp
Silty clay	0.24	0.56	0.50	—	—	0.00
Silty clay loam	0.36	—	0.49	—	—	0.07
Silt loam	0.50	—	0.50	—	0.10	0.19
Clay	0.43	0.82	0.17	0.006	—	—
Clay loam	0.44	0.79	0.28	0.08	—	0.25
Loam	0.34	—	0.39	—	0.40	0.03
Sandy clay	0.34	0.80	0.20	0.12	—	—
Sandy clay loam	0.69	0.78	0.25	0.02	—	—
Sandy loam	0.61	0.75	0.24	0.01	0.37	0.09
Loamy sand	0.68	0.77	0.11	0.02	0.24	—
Sand	0.59	0.78	0.11	0.01	—	—

figure S5). We observed no clear trend with respect to soil textural classes (higher correlations for loamy soils were obtained for arid regions but the number of soil classes and years are too small to be significant).

As a main finding from this analysis, we state that natural vegetation is more sensitive to rainfall variations (i.e. it can adapt more effectively to rainfall amount) compared to agricultural crops (especially in water-limited regions). We further note that correlations between rainfall amount and GPP for natural vegetation of the arid region in Africa are stronger than that of the arid region in the USA (table 1), reflecting a heterogeneity in space in the analyzed relationships.

3.3. Regional scale—effects of uncertainty and spatial variability on the soil texture-vegetation relationship

At the local scale, using accurate GPP measurements in the field, we found (a) decreasing crop yield with increasing sand content during dry years because of water limitations and (b) evidence of inverse texture effect for natural vegetation in arid regions. All sites were on flat area so we could neglect any topographic effects (in terms of flow convergence/divergence) on local water availability. At regional scale, collecting information from pixels of 0.5 × 0.5 km within a region of 250 × 250 km in size, environmental conditions, water flow, and soil formation processes may be more diversified for the various pixels due to heterogeneities in topographic and environmental properties. In addition, GPP and soil texture are not measured directly but deduced from remote sensing and machine learning. Both effects (spatial variability and uncertainty of GPP and sand content values) may obscure the trends observed at the field scale.

The relationship between GPP and sand content for various squares of 250 × 250 km is shown in figure 6 for wet and dry years for various regions worldwide. For all sites and both climatic regions (arid and temperate), GPP increased from dry to wet years. For natural vegetation in arid areas (figure 6(a)), no correlation between GPP and sand content was observed in USA, while a slight positive trend was observed in Australia. Likewise, no correlation with soil texture was found for rainfed crops in USA (figure 6(b)) in contrast to the findings at the local scale. Additionally, in temperate regions, no significant relationship between GPP and sand content was observed for both natural vegetation (figure 6(c)) and agricultural crops (figure 6(d)).

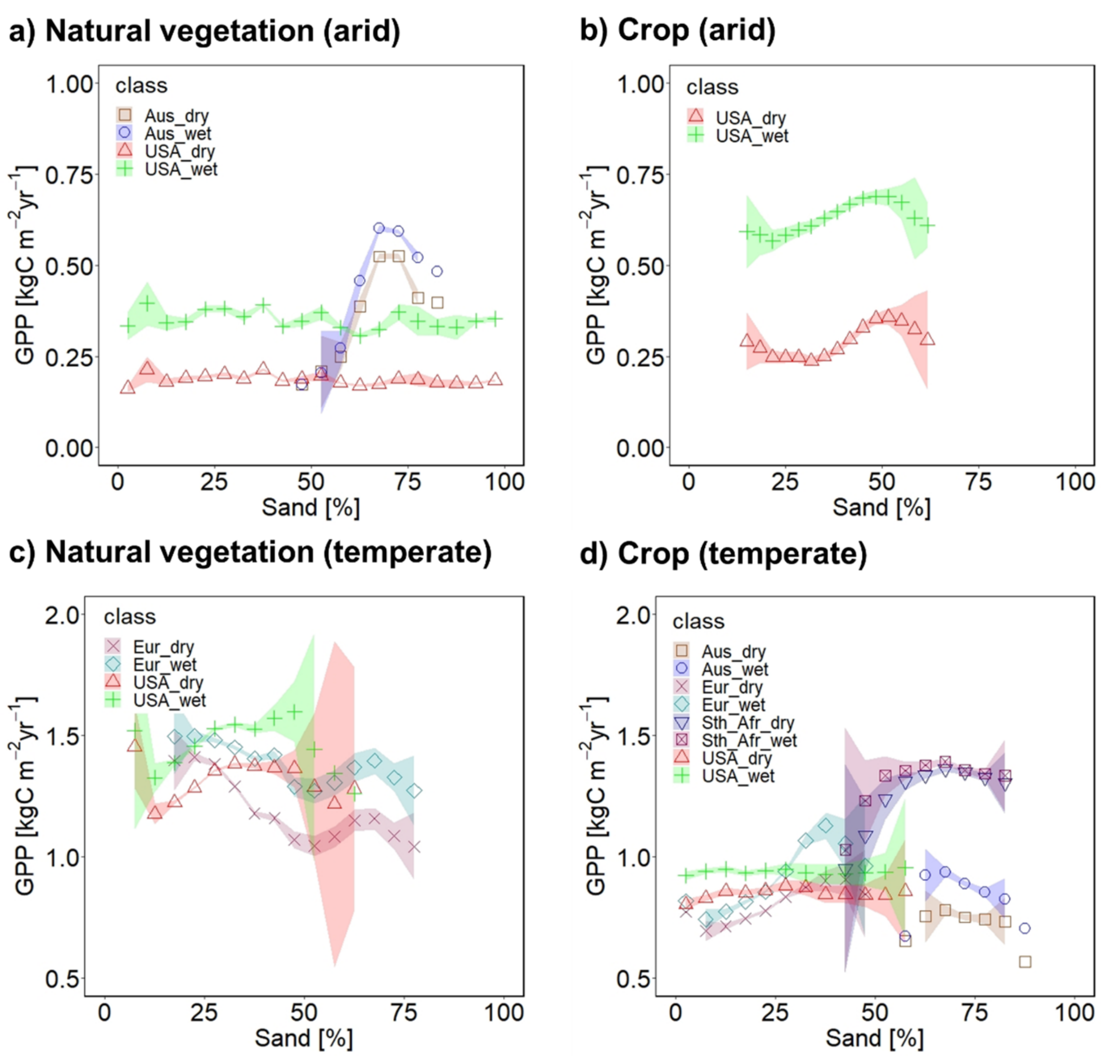

Figure 6. Relationship between GPP and soil texture (sand content) during dry and wet years for various regions of 250 × 250 km size (125 × 125 km for Australia and South Africa). The symbols show the average GPP (binned for a certain range of sand fraction) and the shading represents the standard deviation. GPP and sand content were determined for pixels of 0.5 × 0.5 km in size. Agricultural productivity (GPP) at a regional scale (b) and (d) does not show the same textural effect observed at the local (field) scale (figure 3) for both climatic regions. No trend of GPP with sand content can be found for natural vegetation (a) and (c). However, the impact of rainfall is evident in all figures as mean values increased during the wet year.

The lack of correlation between GPP and sand content can be explained by the different environmental conditions in the various pixels of 0.5 × 0.5 km size within a region of 250 × 250 km, as shown in figure 7. Results exhibit high variability in rainfall and topographic slope for similar sand contents. This implies that (a) high variability in climatic and topographic factors can partly suppress soil texture effects at the regional scale and (b) natural vegetation shows higher sensitivity to variations in rainfall than to variability in soil texture. We performed a similar analysis at a smaller scale of 25 × 25 km (see text S1 and figure S2), where we found a higher correlation between soil texture and GPP due to a decrease in the extent of confounding environmental factors (note that for a 25 × 25 km square, a maximum of 2500 pixels of 0.5 × 0.5 km size can be used to plot the vegetation texture relationship). At this smaller scale (25 × 25 km), the response of agricultural crops across different soil textures was higher (more pronounced) for anomalously dry than for wet year (see table S5), whereas no significant difference was observed between dry and wet years for natural vegetation across different soil textures.

A different confounding factor for the obscured textural effects at large scales is the increase in uncertainty in estimated GPP values and soil texture data deduced from remote sensing products. For example, we tested the accuracy of SoilGrids data by comparing direct soil texture measurements and SoilGrids data for the sites we used for the regional scale analysis in USA and Africa (see figure S3). The correlation coefficient between SoilGrids and soil profile measured sand content was 0.67 with a root mean square error of 16%. Figure S6 shows the narrower distribution of sand content obtained with SoilGrids compared to directly measured data implying loss of soil

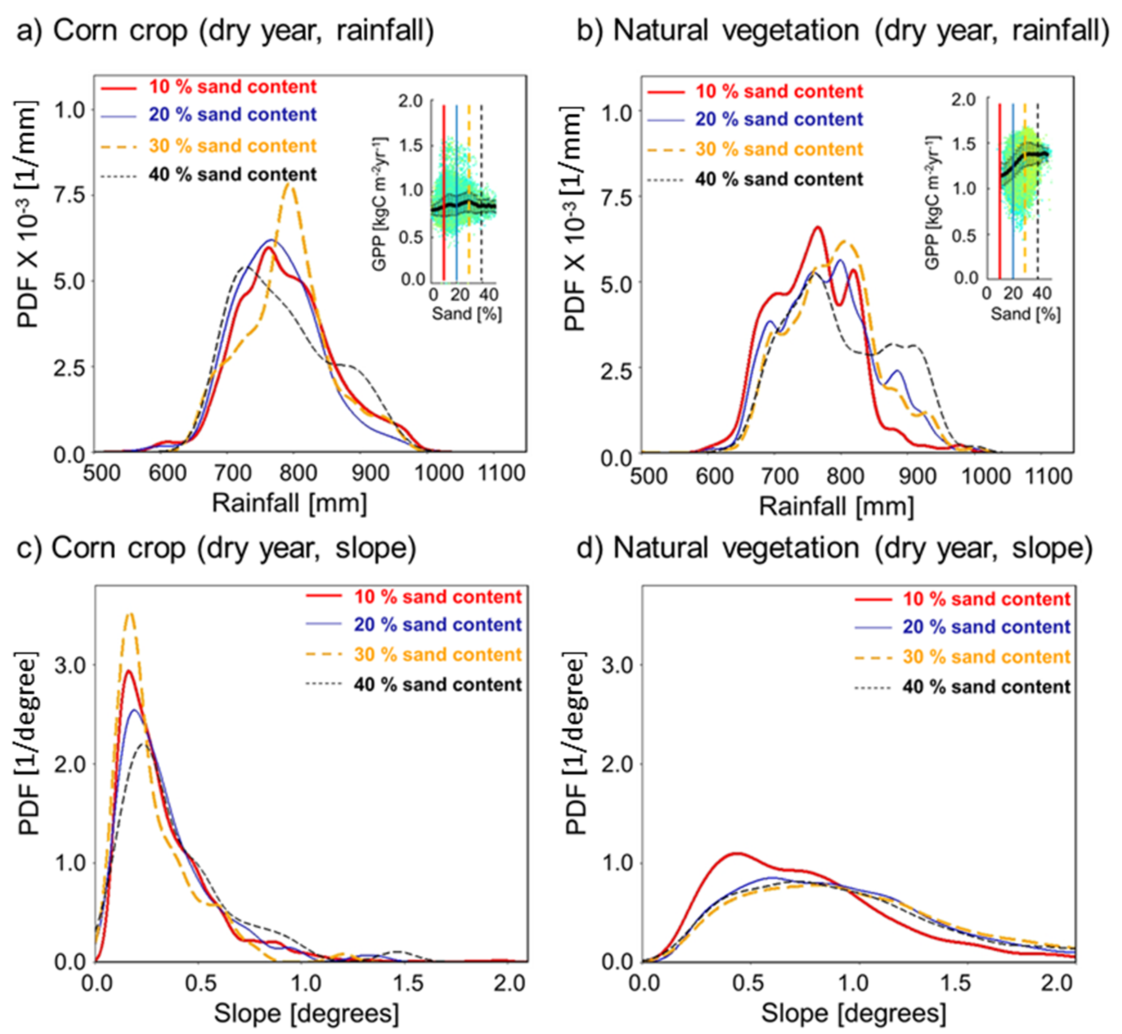

Figure 7. Variability of (a) and (b) climatic (rainfall) and (c), (d) topographic (slope) factors at regional scale (250 km × 250 km). Panels (a) and (c) show the probability density functions (PDFs) for agriculture (dry year) at various sand contents, while panels (b) and (d) show the PDFs for natural vegetation (dry year). Slope and rainfall showed high variation for the same sand content, possibly obscuring the soil texture effects revealed at the local scale.

information with spatial interpolation. We also estimated the correlation between measured FLUXNET and MODIS-based GPP values for the locations used in this study (see figure S7) and found a correlation coefficient below 0.6 with a trend of underestimating GPP values using MODIS.

4. Discussion

4.1. Natural vegetation is adapted to local climate variability

At local scale (field to ~0.1 km), we found that rainfed crops exhibited sensitivity to soil texture for all climatic regions, particularly during anomalously dry years. Similar results related to rainfed crops were reported in other studies (e.g. Fang and Su 2019, Neupane and Guo 2019). In contrast to crops, no sensitivity to soil texture was found for natural vegetation in temperate regions. While natural vegetation is less sensitive to soil texture, it is more sensitive to annual rainfall amount (and temperature) compared to agricultural crops. The analyses presented at all scales indicate that natural vegetation is optimally adapted to local climate and responds primarily to changes in rainfall amount. This finding is in agreement with Paschalis *et al* (2018) who showed that vegetation is in equilibrium with local climate and productivity (LAI) correlates with rainfall properties. While the focus of this study is on plant soil water availability as modulated by soil texture, temperature effects in certain regions cannot be ignored. Analyses summarized in table S4 delineate a sensitivity of natural vegetation to temperature primarily due to strong negative correlation between temperature and rainfall. Such negative correlation is expected in water-limited systems of arid regions in Africa with small rainfall amounts and high potential evaporation rates limiting productivity (Nzabarinda *et al* 2021, Onyutha 2021). In contrast to Africa, rainfall and temperature in arid regions of USA are not correlated. These results are similar to the findings of Misra et al (2012) and Portmann et al (2009) showing a weak correlation between precipitation and temperature for monsoon-controlled arid regions of the USA. For crops in temperate regions, GPP was neither correlated to rainfall nor to temperature (both are not limiting). In summary, for certain water-limited regions rainfall and temperature may be correlated (Africa) or uncorrelated (Western USA), thus affecting the correlation of GPP with temperature. The comparative studies reported here were conducted in geographically proxime regions with similar temperatures to avoid potential confounding effects of temperature on GPP.

An interesting and unintuitive observation in arid climate is the so-called 'inverse texture effect' (Noy-Meir 1973). In contrast to fine textured soils, evaporative losses from coarse textured soils occur from a relatively thin top layer determined by conditions for capillary flow continuity (Lehmann et al 2008). Not only this capillary flow characteristic depth for bare soil evaporation is relatively short in sandy soil (20–30 cm), but a larger fraction of infiltrating rainfall water rapidly percolates below this depth and becomes somewhat sheltered from surface evaporation (Lehman et al 2019).

The results of this study suggest that soil texture is not an effective indicator for natural vegetation GPP as compared to arable lands. Consequently, the parameterization of land surface and Earth system models (ESMs) concerning natural vegetation should not overemphasize soil texture information (a concept borrowed from agronomic practices). A possible pathway to model different sensitivities of natural vegetation and crops is to develop different water stress functions that consider the effective soil water volumes available to natural vegetation (an effective rooting depth weighted function). This is essential given the high spatial heterogeneity of plant rooting depths within biomes (Yang et al 2016). Similarly, Yang et al (2016) pointed out that, unlike rainfed crops, natural vegetation has deeper roots in regions where there is a longer dry season and water supply and demand are out-of-phase. Therefore, we propose the definition of water stress functions with respect to rainfall anomalies that account for natural vegetation specific traits and local biomes (arid vs. temperate), by considering for example larger volume of soil available in deep rooted and sparse vegetation. Additionally, well-developed and uninterrupted soil structure under natural vegetation may play an important role in decoupling natural vegetation from soil texture control compared to arable lands (Or et al 2021). The cumulative effects of biological activity under natural vegetation give rise to aggregation and accumulation of biopores disrupted in top layers of tilled (arable) lands. These differences may further reduce the mediating role of soil texture and reinforce vegetation reliance on climatic variables. Recent studies have emphasized the importance of incorporating soil structure information in soil parameterization of ESMs in contrast to reliance on soil texture information only (Fatichi et al 2020, Bonetti et al 2021).

4.2. Spatial variability and data uncertainties obscure the soil texture-vegetation relationship

At regional scales ($\sim 10^2$ km), the soil texture-vegetation relationship is obscured by the spatial variability of climatic and topographic variables and the uncertainty of the underlying information. By reducing the scale from 250 to 25 km, the spatial variability and its effect on the soil texture-vegetation relationship is less pronounced. At the smaller (25 km) scale, we could observe a sensitivity to soil texture for crops, with stronger correlations between sand content and GPP for dry years (text S1 and figure S2). This is in agreement with Guo et al (2012) who showed that yield and soil properties are more strongly related during dry seasons compared to wet ones. However, compared to the local scale, the soil texture vegetation relationship was less pronounced at a scale of 25 km. This 'fading' of the correlation may depend on the uncertainties of the GPP and soil texture data. In these regards, Baroni et al (2017) showed the impact of uncertainty of soil properties on the hydrological states and fluxes and they discussed how their correct characterization remains a crucial challenge especially over large areas. Zhao et al (2005) further reported a weak correlation between MODIS LAI and ground measurements that could lead to an inaccurate estimation of the fraction of photosynthetically active radiation.

5. Summary and conclusions

Plant growth and productivity depend on the amount of plant available soil water, which in turn is a function of climatic conditions (rainfall, temperature), soil properties, and specific plant traits. The reliable representation of water and carbon fluxes in ESMs hinges on the proper definition of relationships between climate, soil properties, and vegetation response. Presently, ESMs rely heavily on analogy with agronomical principles in representing vegetation response to drought and water stresses (Fisher et al 2007, Imbach et al 2012). The study evaluates differences between climate-adapted natural vegetation (via trait and species selection) by systematically examining the different responses of natural and rainfed cropped vegetation to rainfall anomalies across biomes and scales using field observations and remote sensing data. Results illustrate the relative insensitivity of natural vegetation to soil texture at all scales with the exception of the inverse texture effect in certain arid regions. In contrast, locally measured rainfed crop yield data revealed sensitivity to soil texture with decreasing crop yield for increasing sand content. However, at regional scales, no discernible sensitivity to soil texture was found for rainfed crops.

We examined the role of temperature on vegetation response (natural and rainfed crops) and found that for most biomes GPP was negatively correlated with temperature largely due to negative correlation between rainfall and temperature (enhanced evaporative water losses in hot years).

We attribute the loss of sensitivity to soil texture at large (regional) scales to confounding effects of spatial variations in topographic and climatic conditions and uncertainty of soil texture and productivity data. The lack of correlation between GPP and soil texture for natural vegetation offers certain opportunities to using mean soil parameter values for incorporating soil structure effects in soil hydraulic properties at scales relevant to ESMs (Bonetti *et al* 2021). The study suggests that ESMs can benefit from differentiating the representation of natural vegetation and crop response to water stress. While developing these novel water stress functions is beyond the scope of this study, we may consider the assembly of natural vegetation species and physiological traits (rooting depths, water use efficiency) in broadening the definition of natural vegetation water stress responses.

Data availability statement

The data that support the findings of this study are openly available in the SI document.

All data that support the findings of this study are included within the article (and any supplementary files).

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