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Geremew, Tenaw

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CHANGING SENSITIVITY OF DIVERSE TROPICAL BIOMES TO PRECIPITATION CONSISTENT WITH THE EXPECTED CARBON DIOXIDE FERTILIZATION EFFECT

TENAW GEREMEW[1*], ALEMU GONSAMO[2], WORKU ZEWDIE[1], PETRI PELLIKKA[3,4]

[1]Earth observation research division, Entoto Observatory & Research Center, Addis Ababa, 33679, Ethiopia.
[2]School of Earth, Environment & Society, McMaster University, Hamilton, Ontario, Canada
[3]Department of Geosciences and Geography, University of Helsinki, Helsinki, Finland
[4]State Key Laboratory of Information Engineering in Surveying, Mapping and Remote Sensing, Wuhan University, Wuhan 430000, China
**Corresponding author email: tenever4@gmail.com*

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ABSTRACT

Global environmental changes have implications for the terrestrial ecosystem functioning, but disentangling individual effects remains elusive. The impact of vegetation responses to increasing atmospheric CO_2 concentrations is particularly poorly understood. As the atmospheric CO_2 concentration increases, the CO_2 acts as a fertilizer for plant growth. An increase in atmospheric CO_2 reduces the amount of water needed to produce an equivalent amount of biomass due to closing or a narrowing of the stomata that reduces the amount of water that is transpired by plants. To study the impacts of climate change and CO_2 fertilization on plant growth, we analyzed the growing season sensitivity of plant growth to climatic forcing from alpine to semi-desert eco-climatic zones of Ethiopia for various plant functional types over the period of 1982−2011. Growing season 3rd generation Normalized Difference Vegetation Index of Global Inventory Modeling and Mapping Studies (NDVI) was used as a proxy of plant growth, while mean growing season precipitation (prec), temperature (temp), and solar radiation (sr) as the climate forcing. The sensitivities of plant growth are calculated as a partial correlation, and a derivative of NDVI with respect to prec, temp and sr for earliest and recent 15-year periods of the satellite records, and using a moving window of 15-year. Our results show increasing trends of plant growth that are not explained by any climate variables. We also find that an equivalent increase in prec leads to a larger increase in NDVI since the 1980s. This result implies a given amount of prec has sustained greater amounts of plant foliage materials over time due to decreasing transpiration with increasing CO_2 concentration as expected from the CO_2 fertilization effect on water use efficiency and plant growth. Increasing trends of growth in shallow-rooted vegetation tend to be associated with woody vegetation encroachment.

Keywords: Vegetation productivity, climate change, CO_2 fertilization, vegetation sensitivity, woody encroachment, Ethiopia, Tropics.

INTRODUCTION

Global environmental change, manifested by changing the concentration of greenhouse gases, rising temperature, changing precipitation patterns, and increasing frequency of extreme weather events (Gray & Brady, 2016), is posing one of the biggest challenges to our planet. Over the period between 1880 to 2012, global temperature has increased by 0.85 ^oC on average, and widespread rainfall extremes and variabilities were apparent, with more frequent drought appearing in regions that are already arid (IPCC, 2012). The continued increase in CO_2 concentration is also predicted to reach 730-1000 ppm by the end of this century (IPCC, 2012). The effect of the increasing CO_2 concentration on plants is generally believed to be positive in terms of increasing photosynthesis rate, decreasing water use, and increasing overall plant growth (Taub, 2015).

At the species level, the effect of such environmental changes extends to altering molecular functions, developmental processes, morphological traits, and physiology (Gray & Brady, 2016). Understanding the ecological implication of environmental change is necessary to increase the resilience and adaptability of society (Guan *et al.*, 2018). Our ability to forecast the fate of terrestrial ecosystems to future changes in climate relies largely on our ability to understand the responses of ecosystems to past environmental changes. Previous studies characterized the response of ecosystems to changes and variability's of climate using different methods including field experiments (Vogel *et al.*, 2012), earth system models (Medvigy *et al.*, 2009; Smith *et al.*, 2001), and models based on satellite observations and gridded climate datasets (Seddon *et al.*, 2016; Hilker *et al.*, 2014; Gonsamo *et al.*, 2016; Gonsamo *et al.*, 2021). The conclusions of these studies are equivocal (Vogel *et al.*, 2012; Yuan *et al.*, 2015; Walker *et al.*, 2021) and the mechanisms underlying such discrepancy in plant sensitivity to environmental change are less understood (Smith *et al.*, 2017). Terrestrial ecosystems are subjected to multiple confounding environmental factors at a time and the impact is often the net effect of them. The net effect of the climate forcing for example appears to vary depending on latitude, ecosystem types, nutrient availability, and land use and land management practices (Piao *et al.*, 2014).

New evidence is appearing that shows weakening relationships between interannual temperature variability and vegetation activity in the northern hemisphere where the temperature is the dominant factor that controls vegetation productivity (Piao *et al.*, 2014; Zeng *et al.*, 2013). While precipitation controls much of the terrestrial ecosystem in the tropics (Hilker *et al.*, 2014; Zeng *et al.*, 2013), plant growth sensitivity to precipitation under changing climate has not been studied systematically. Recent satellite-based observations show an increasing response of leaf area to soil moisture over time in all tropical drylands (Gonsamo *et al*. 2021). Precipitation affects soil moisture and nutrient availability and it is one of the most important limiting factors in vegetation growth and productivity in arid and semi-arid ecosystems (Huxman *et al.*, 2004; Schwinning & Sala, 2004). Previous studies suggest that vegetation in water-limited semi-arid and semi-humid regions might be adapted to drought and they are more resistant (Vicente-Serrano *et al.*, 2013). Contradictory to this, (Liu, 2013) suggests that resistance or slow responses might be a precursor to a more lasting or profound impact after a certain time lag. Increasing evidence of CO_2 fertilization effect compensating other climate forcing is also apparent in most vegetation across the globe. CO_2 fertilization effect was found to increase productivity in tropical forests through increased assimilation and light use efficiency (Yang *et al.*, 2016). Elevated CO_2 (eCO_2) reduces stomatal conductance and enforces the carbon demands for photosynthesis to be met early causing enhanced water use efficiency (eWUE) (Taub, 2015). This makes plants exposed to elevated CO_2 to be more resistant to drought/water stress. Significant increases in eWUE in a tropical forest in Africa were observed over the period 1982 – 2010, signifying their sensitivity to elevated CO_2 (Traore *et al.*, 2014). However, this effect varies depending on the photosynthesis process type in plants. C4 grasses which include tropical grasses showed little or no enhancement of growth to elevated CO_2 (Taub, 2015; Onofrio *et al.*, 2019). The same effect was also observed in temperate region C3 grasslands under extreme weather conditions (Obermeier *et al.*, 2016). Shrubs are also found to be quite resistant to long-term experimental warming and drought (Kroël-Dulay *et al.*, 2015).

Deep-rooted vegetation generally is considered to be less sensitive to climate variability in water-limited regions than shallow-rooted vegetation (Sala *et al.*, 2015), owing to the deep root system and adaptive water use strategy (Asbjornsen *et al.*, 2008; Eggemeyer *et al.*, 2009). Contrary to this, Darcy's law suggests that taller plants are becoming more vulnerable to temperature-induced changes in vapor pressure deficits (VPD) and the consequent effects on canopy water conductance and vegetation growth (McDowell & Allen, 2015), especially under enhanced warming in semi-arid and more extreme climate (Wu *et al.*, 2017).

To study the response of tropical vegetation to climate change and increasing CO_2 concentration, we analyze changes in the sensitivity of plant growth in the diverse vegetation types of Ethiopia ranging from alpine to semi-desert eco-climate zones. We use satellite observed greenness records as a proxy of plant growth to assess the response of different plant functional types (PFTs) to inter-annual mean growing season (GS) climate forcing. We hypothesize that under enhanced warming, the response of deep-rooted vegetation to CO_2 fertilization effect will increase offsetting the adverse impacts of climate change while shallow-rooted vegetation (shrubs and grasses) will be more resistant to elevated CO_2 concentration.

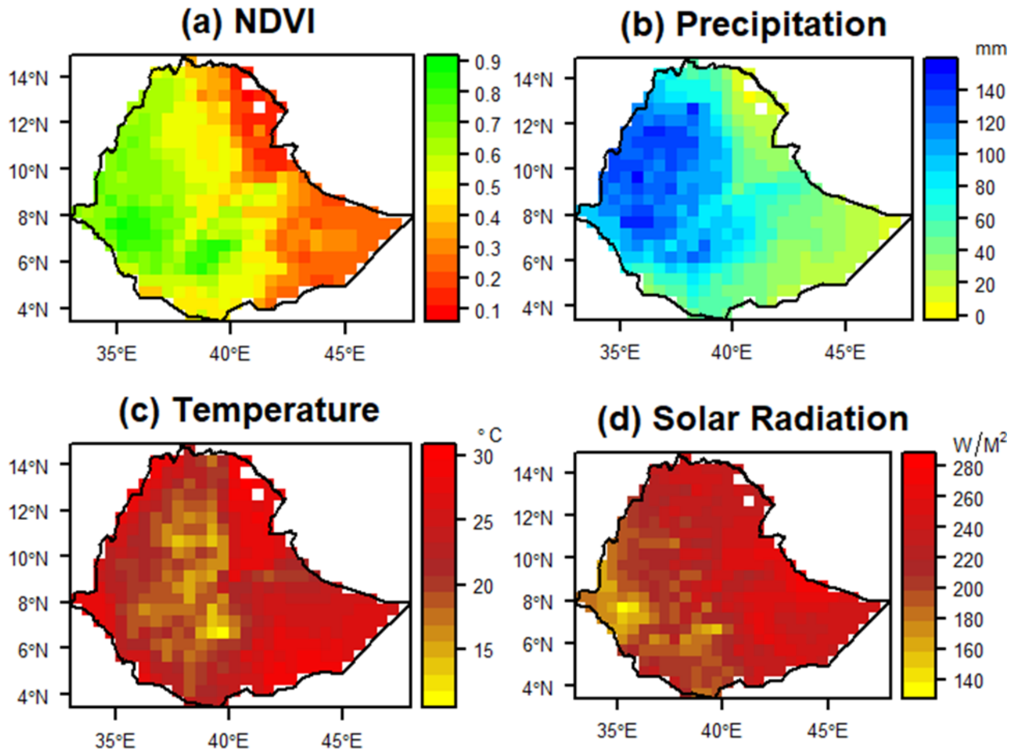
METHODS

Study area

Ethiopia constitutes diverse vegetation types ranging from alpine to semi-desert eco-climate zones with elevations ranging from 125 m below sea level in Danakil depression to central highlands on both sides of the rift reaching 4550 m above sea level at Ras Dashen. It lies between 3^{o}-15^{o}N latitude and 33^{o}-45^{o}E longitude. The vegetation can be summarized in four major PFTs, including evergreen broad-leaf trees (EBlT), deciduous broad-leaf trees (DBlT), shrub, and grasses. The evergreen broad-leaf trees found in the southwestern and southeastern highlands receive precipitation throughout or nearly throughout the year. Deciduous broad-leaf trees confined in the western lowlands of Ethiopia are seasonally dry forests that shade their leaves during the dry seasons in response to water stress. The shrubs and grasses are located in the southern and eastern lowlands of the country. The shrubs and grasses are part of the savannas in Africa and are characterized by low cation exchange capacity, very low phosphorus, and nitrogen (Solbrig & Medina, 1996). Evergreen broad-leaf trees are the most productive forest types followed by deciduous broad-leaf trees, grass, and shrubs, respectively. Deciduous broad-leaf trees and evergreen broad-leaf trees receive a comparable amount of growing season mean monthly precipitation which is about 110 mm. Shrub and grasses receive about 32 mm and 63 mm growing season mean monthly precipitation, respectively (Fig.1). Temperature and solar radiation are generally higher for the lowland vegetation. Evergreen broad-leaf trees, deciduous broad-leaf trees, shrub, and grasses receive a growing season mean monthly temperature of 18.9 ^{o}C, 21.97 ^{o}C, 25.9 ^{o}C, and 23 ^{o}C while the solar radiation is in the order of 179.5, 192.2, 241.45, and 226.94 W/M^2, respectively. The growing season mean monthly NDVI and climate datasets are presented in

Fig. 1. The elevation range and its impact on precipitation make Ethiopia a unique country in Africa to study climate change impacts on vegetation structure, growth, and photosynthesis.

Fig.1: Long-term growing season mean monthly NDVI (a), precipitation (b), temperature (c), and Solar radiation (d).



Data

Biweekly normalized difference vegetation index (NDVI) products from two sensors, i.e, the 8 km 3rd generation NDVI of Global Inventory Modeling and Mapping Studies (GIMMS NDVI3g) derived from the advanced very high-resolution radiometer (AVHRR) for 1982-2011. The GIMMS NDVI3g datasets were used to assess the response of vegetation to changes in climate in 1982-2011.The climate datasets considered include precipitation, temperature, and solar radiation. Except for the solar radiation data obtained from the National Center for Atmospheric Research (https://climatedataguide.ucar.edu), all the climate datasets were obtained from Climate Research Unit (CRU) TS 3.23 data sets, compiled by the Climate Research Unit of University of East Anglia (Harris *et al.*, 2014).

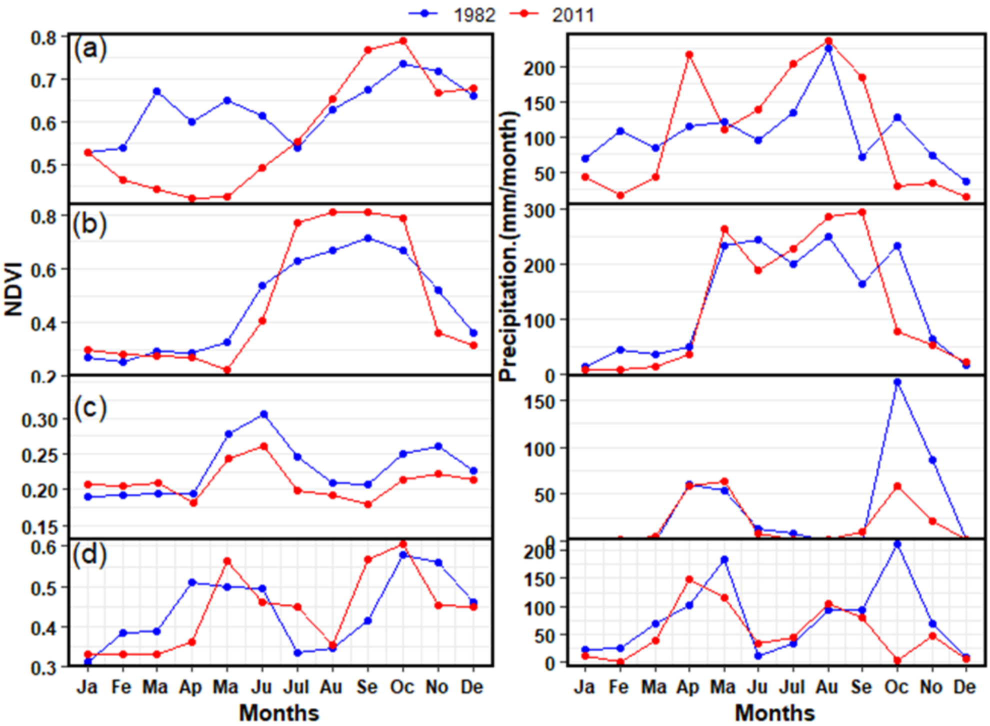
GIMMS NDVI3g dataset has been extensively corrected for various defects due to atmospheric contamination, orbital characteristics (e.g. navigational drift, satellite drift, solar zenith, and viewing angles), and sensor degradations (Tucker *et al.*, 2005). It has been successfully used in various vegetation monitoring studies including for assessing the sensitivity of vegetation to changes in climate from national to global scales (Guay *et al.*, 2014; Piao *et al.*, 2017; Gonsamo *et al*., 2016).

The biweekly GIMMS NDVI3g was spatially and temporally aggregated to have common spatial and temporal resolutions with the climate datasets to $0.5^0 \times 0.5^0$ and monthly values by taking the maximum of the biweekly observations, respectively. This was done after masking non-vegetated areas with pixels < 0.1 NDVI values, from all the observations.

Analysis

Ethiopia has different growing seasons both in unimodal and bimodal forms. Changes in the phenological cycles of vegetation are evident across different eco-regions of Ethiopia (Workie & Debela, 2018). The comparison of the monthly vegetation growth and precipitation also reveals changes in the growing season over time, particularly for the evergreen broad-leaf trees and grasses (Fig. 2).

Fig. 2: Comparison of monthly NDVI and precipitation seasonality across plant functional types in Ethiopia for the year 1982 and 2011 for evergreen broad-leaf trees (a), deciduous broad-leaf trees (b), shrub (c), and grass (d).



The determination of the growing season (GS) was made in two approaches to help elucidate the impact of plant functional types (PFTs) in plant-water relationship changes over time. The first approach was determined by aggregating the start and end of GS MODIS phenology products to each PFT. For the second method, we set thresholds from the seasonal greenness amplitude to determine the start and end of the GS (Piao *et al*., 2014). NDVI values between the seasonal greenness amplitude that is defined as a maximum monthly NDVI in a given year and NDVI values above 25 % and 50 % of the maximum monthly values are considered to be within the growing season. Based on the correlation between GS NDVI and climate, the method that yields a better correlation was adopted as an optimum method for GS determination. Based on this assessment, the 50 % threshold of the seasonal greenness amplitude was used to determine the GS. This method is robust since it dynamically determines the GS in such areas where there are diverse growing periods. As the start and end of growing seasons change due to climate change, this method captures the shift in these phases of the phenology. Then NDVI was aggregated by taking their means to get GS NDVI (GSndvi), a proxy for plant growth during the growing season. The respective GS climate data were also aggregated in the same way to form GS precipitation (GSprec), GS temperature (GStemp), and GS solar radiations (GSsr). Moreover, the analysis was repeated by aggregating all datasets by their annual mean.

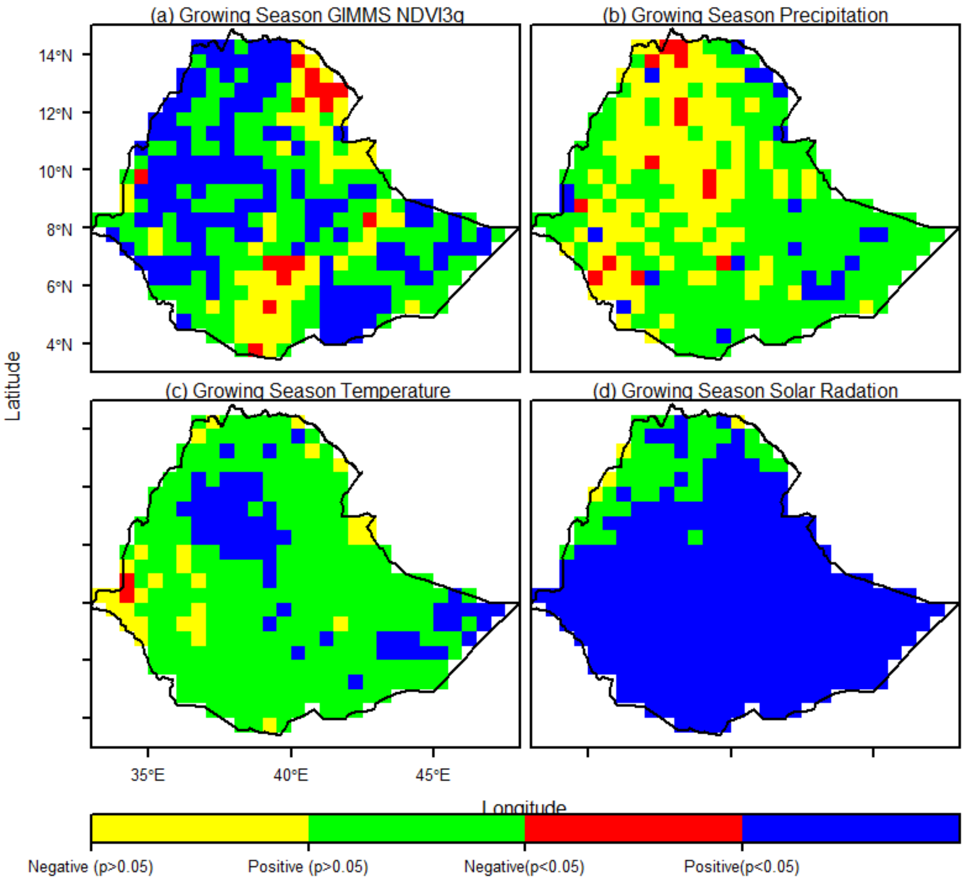
Partial correlation was applied to calculate the inter-annual sensitivity of vegetation growth, from the perspective of NDVI, to mean GSprec, by controlling the effect of GStemp and GSsr. Partial correlation overcomes autocorrelation among independent variables (Piao *et al*., 2017). The partial correlation was run over 15 years moving window. The time window moves by one year forward and forms a total of 15 moving windows over the periods of 1983 to 2011. Each time window was de-trended by removing the linear trend from the 15 years observations.

To calculate the effect characteristics (i.e., direction and magnitude of changes) of sensitivity, we use a robust Theil-Sen slope estimator that computes the median of the slope between observations. Both the partial correlation and Theil-Sen slope were aggregated by PFT. The PFts are defined as, a) evergreen broad-leaf trees: dominated by evergreen broad-leaf and palmate trees (>2 m) and tree cover >10 %, b) deciduous broad-leaf trees (>2 m),c) shrub (>2 m) and cover >10 %, and d) grass: herbaceous annuals (<2 m) that are not cultivated (Friedl & Sulla-Menasha, 2019).

RESULTS

Growing season vegetation productivity has shown significant changes ($p<0.05$) in large parts of Ethiopia over the study period of, 1982–2011. A significant increase in growing season NDVI is observed in about 40 %, while the statistically significant decrease accounts for only 5 % of the study area for 1982–2011 from GIMMS NDVI3g (Fig. 3). NDVI averaged per PFT also show a statistically significant ($p<0.05$) increase in growing season NDVI for all PFTs. Precipitation increased largely in the northwestern parts of the country accounting for about 18 % of Ethiopia. Growing season temperature significantly increased ($p<0.05$) in more than 85 % of the study area. The trends in solar radiation have shown predominantly non-significant changes (Fig. 3).

Fig 3: Trends of growing season NDVI and climate variables. (a) GIMMS NDVI3g for 1982-2011, (b), MODIS NDVI for 2002-2011, (c) solar radiation for 1982-2011, (d) precipitation for 1982-2011, and (d).



The correlation between the growing season NDVI and precipitation increased in deep-rooted vegetation (EBlT and DBlT) and decreased over time in shallow-rooted vegetation (shrub and grasses) (Fig. 4 and 5). However, the changes in correlation through time or between the earliest and latest 15-year period were statistically not significant ($p>0.05$) (Fig. 4 and 5b) indicating negligible changes in plant-water relationships. Except for EBIT, the correlation remains largely significant for deep and shallow-rooted vegetation for both the earliest and latest 15-year period (Fig. 5a).

Unlike the partial correlation, the sensitivity of the effect size calculated as a Theil-Sen slope of NDVI response to interannual changes in precipitation has increased for all PFTs since the 1980s (Fig. 4 and 5b). The increase of the sensitivity of the effect size is statistically significant ($p<0.05$) for forested areas while a large increase is also observed for shrub and grassland (Fig. 5b). Our results imply that a given amount of precipitation has sustained greater amounts of NDVI (i.e., photosynthetic foliage biomass) over time while the NDVI relation to temperature and solar radiation remains unchanged.

Fig.4: Sensitivity of vegetation to precipitation for evergreen broad-leaf trees (a), deciduous broad-leaf trees (b), shrub (c), and grass (d) for 1982-2011 in Ethiopia.

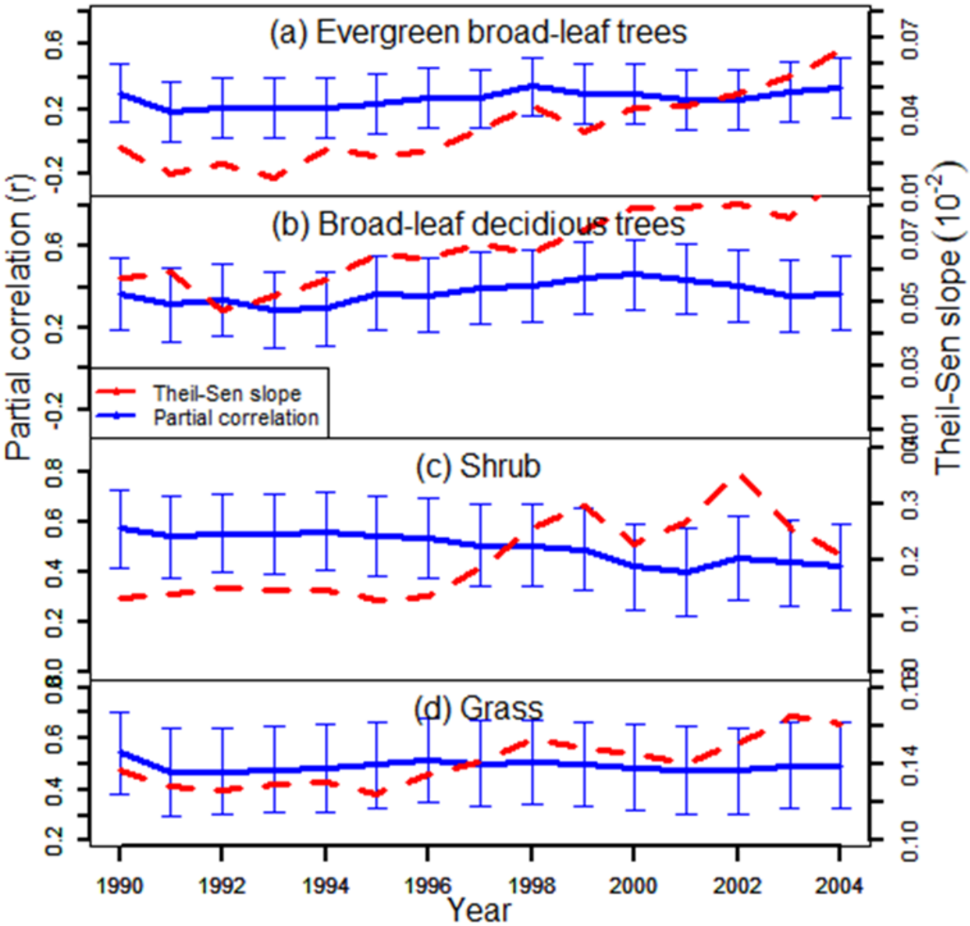
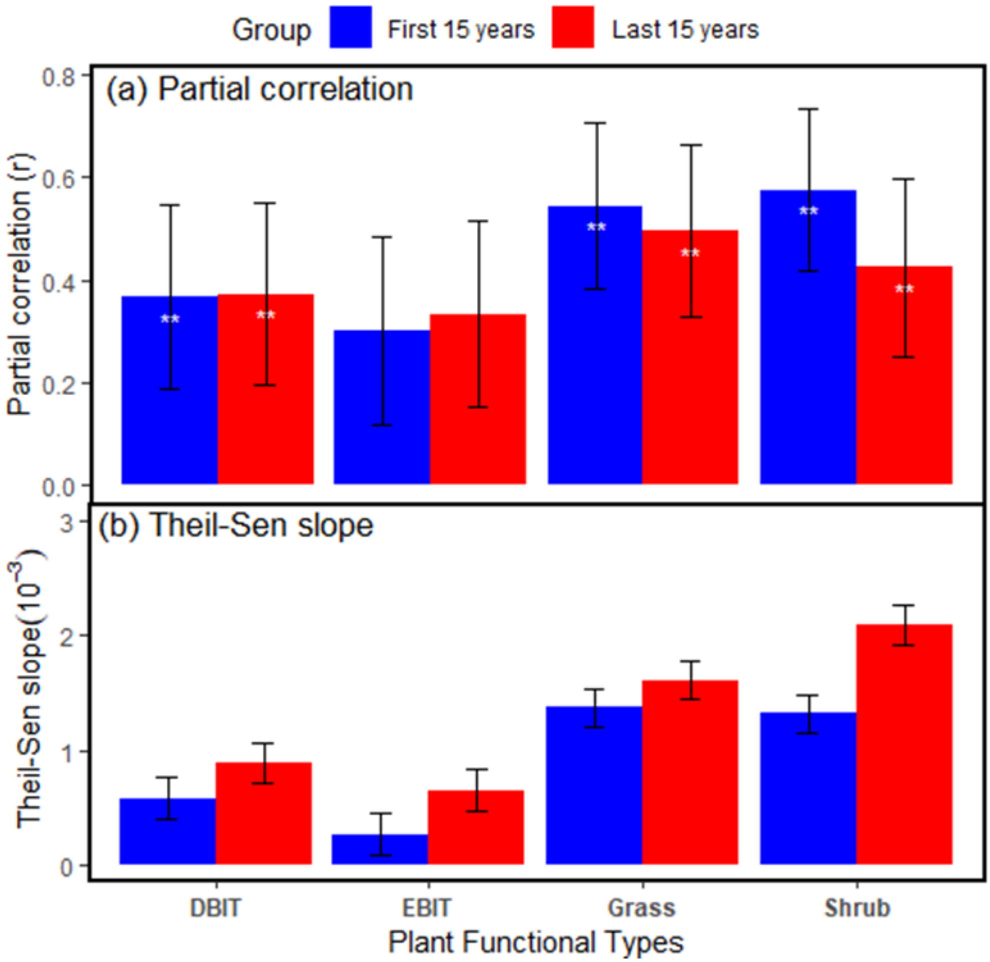


Fig. 5: Two-period comparisons of partial correlations (a) and Theil-Sen slope of the relationships between GS NDVI and GS precipitation across plant functional types, i.e Deciduous Broadleaf Trees (DBlT), Evergreen Broadleaf trees (EBlT), Grass and shrubs. The first period is the first 15 years (1983-97) and the second is the last 15 years (1997-2011). Note: ** indicates significant partial correlation (p<0.05).



Discussion

Anticipating the fates of vegetation under the global environmental change is one of the contemporary research themes (Piao *et al.*, 2017; Smith *et al.*, 2017). Precipitation is the key environmental variable that controls plant growth in the study area. Except for the EBIT; precipitation significantly explained the variability in plant growth in all PFTs (Fig. 4). Significant green up in the study area however does not coincide with increased precipitation. Under enhanced warming, both deep-rooted and shallow-rooted vegetation growth is influenced by global drivers such as the CO_2 fertilization effect. Our results that show the elevated CO_2 fertilization effect on deep-rooted vegetation are consistent with previous research findings. Tropical forests in Africa are found to be sensitive to elevated CO_2 (Traore *et al.*, 2014) and consequently increase their carbon uptake and water use efficiency (Yang *et al.*, 2016; Taub, 2015). Gonsamo *et al*. (2021) also found an increasing response of leaf area to interannual changes in soil moisture over time in tropical drylands.

Our results presented strong evidence for the increased NDVI per unit precipitation over time for all ecosystem types of Ethiopia, ranging from alpine to semi-desert eco-climatic zones. The increase is statistically significant ($p<0.05$) for forested areas while shrub and grasses also show increasing trends, but statistically not significant. Although the increased CO_2 concentration has little direct effect in shallow-rooted vegetation such as C4 grasses, which dominates the tropical grassland and savanna (Taub, 2015), it indirectly responds by decreasing stomatal conductance and thus enhance photosynthesis by avoiding water stress under drought conditions (Leakey *et al.*, 2009).

An increase in productivity of shallow-rooted vegetation over time can be attributed not only due to increased resistance to drought or water deficit but it is also confounded by evidence of increased woody encroachment in these biomes. Increasing evidence of woody encroachments into grasslands and savannas are apparent in the ecosystems of Ethiopia (Yusuf *et al.*, 2011; Belay *et al*., 2013; Liao *et al*., 2018; Abera *et al*., submitted) and other tropical countries (Buitenwerf *et al.*, 2012; Luvuno *et al.*, 2018; Sühs *et al*., 2020). It can be induced by shifts in climate and biogeochemical cycles, changes in disturbance regime e.g. fire, grazing, conservation (Amara *et al*., 2020), or modifications in ecological successions by the introduction of non-native species or predator removal (Auken, 2000; Eldridge *et al.*, 2011; Steven *et al*., 2017). In southern Brazil, avoiding the traditional fire and grazing resulted in an exponential increase in woody encroachment (Sühs *et al*., 2020). A diversity of drivers, other than CO_2 was also found to explain 78 % of the spatial variations of woody encroachment trends in Sub-Saharan Africa (Venter *et al.*, 2018). A long-term experimental study demonstrated that under a constant disturbance regime (fire and browsers), woody density increased consistently with increased CO_2 despite other global drivers such as precipitation remaining constant throughout the experiment (Buitenwerf *et al*., 2012). Therefore, the discrepancy observed between the forested areas and shrub and grasses regarding NDVI response to the precipitation over time can be explained by the reported encroachment of woody vegetation.

Under confounding climate and environmental factors, both shallow and deep-rooted vegetation alike increased their growth for the duration of the study. Growth in deep-rooted vegetation in this study is directly attributed to the CO_2 fertilization effect as an equivalent increase in precipitation is leading to a larger increase in NDVI, more so in deep-rooted vegetation. This can be explained by decreasing transpiration with increasing CO_2 concentration as expected from the CO_2 fertilization. Greenings of biomes in response to the CO_2 fertilization effect are reported in tropical and temperate forests (Traore *et al.*, 2014, Gonsamo *et al*., 2021) offsetting other climate and environmental constraints. Under enhanced warming, closed-canopy forests increase radiation use efficiency (RUE) (Yang *et al.*, 2016), WUE (Traore *et al.*, 2014), and photosynthetic rate (Avramenko *et al.*, 1998). Their deep root systems also enable them to thrive under water stress conditions. Increasing trends of growth in shallow-rooted vegetation tend to be driven by woody encroachment. Woody encroachments into savannas are one of the growing phenomena globally (Eldridge *et al.*, 2011). Different drivers are reported in different countries. Experimental studies in South Africa demonstrated an increase in woody density consistently with an increase in CO_2 concentration despite a constant disturbance regime and constant precipitation (Buitenwerf *et al.*, 2012). Other than CO_2, other factors including climate, edaphic, and disturbance regime, explained 78 % of the variance in the spatial variation of woody encroachment in

Africa (Venter *et al*., 2018). An exponential increase in woody encroachment is also reported in response to the removal of fire and grazing in Southern Brazil (Sühs *et al.*, 2020). In Taita Hills in Kenya, woody encroachment and increased above-ground carbon were identified by Pellikka *et al*., (2018), while a fenced enclosure within the conservation area increased wood cover (Amara *et al*., 2020). Encroached areas are resulting in increased carbon balance (Liao *et al.*, 2018) and contrary to globally held theories of declining carbon balance and desert expansion (Venter *et al*., 2018).

CO_2 fertilization effect is largely water-limited terrestrial ecosystems of Ethiopia results in enhanced soil water saving from the reduced stomatal conductance (Norby & Zak, 2011; Dermody *et al*., 2017; Wullschleger *et al*., 2002) and decreased transpiration per unit leaf area. As a result, plant growth may progressively increase in water-limited ecosystems. Plot and field experiments with elevated CO_2 in dry environments indicated that the CO_2 fertilization effect on water use efficiency is mediated through changes in leaf area, implying changes in NDVI (Dermody *et al*., 2017; Wullschleger *et al*., 2002). These studies showed increasing leaf area under elevated CO_2 for warmer and drier fields (Dermody *et al*., 2017), consistent with our results that show increasing NDVI for a given volume of precipitation over time.

CONCLUSION

We set out to test the sensitivity of different vegetation types in Ethiopia to climate forcing over the period from 1982-2011. In about 40 % of the territory of Ethiopia, NDVI; proxy of plant growth, has significantly increased. We found no meaningful climate variable trend to explain such increment. Our results presented strong evidence for the increased greenness per unit precipitation over time for all ecosystem types of Ethiopia, ranging from alpine to semi-desert eco-climatic zones. The increasing greenness response for changes in precipitation is more robust in deep-rooted vegetation. Deep-rooted vegetation, i.e broad-leaf evergreen trees, and deciduous broad-leaf trees thrive under elevated CO_2 concentration through enhanced water use efficiency and carbon assimilation. Shallow rooted vegetation which includes shrubs and grass also exhibited a statistically non-significant increase in growth over the duration of the study. However, the growth of shallow-rooted biomes can partly be attributed to the woody encroachment. Issues that are critical but not considered in this study that can affect the result include the effects of disturbance regimes due to land use and land cover changes, herbivory, fire, pests, etc. As Ethiopia is a densely populated country and agrarian economy, large-scale anthropogenic disturbances and fragmentation of the landscape are evident. On the contrary, the spatial resolution of the datasets used in this study is coarse (0.5^o) and the resultant mixed pixels can obscure real patterns of ecosystems sensitivities to climate forcing. In this regard, experimental studies, in limited but representative sample locations in the major plant functional types in the country can reveal the changing sensitivity of vegetation to environmental changes with better accuracy. Moreover, experimental methods are advantageous in that it can control the climate forcing as projected by climate models for the local areas. It is also critical to consider the undisturbed or relatively undisturbed vegetation in the sensitivity assessment as disturbances can affect the real responses of vegetation under different climate forces.

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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