

1 Impact of changes in climate and CO₂ on the carbon 2 storage potential of vegetation under limited water 3 availability using SEIB-DGVM version 3.02

4 Shanlin Tong^{1,2,3}, Weiguang Wang^{2,3*}, Jie Chen^{1*}, Chong-Yu Xu⁴, Hisashi Sato⁵, Guoqing Wang⁶

5 ¹State Key Laboratory of Water Resources and Hydropower Engineering Science, Wuhan University,
6 Wuhan, 430072, Peoples R China

7 ²State Key Laboratory of Hydrology-Water Resources and Hydraulic Engineering, Hohai University,
8 Nanjing, 210098, Peoples R China

9 ³Key Laboratory of Water Big Data Technology of Ministry of Water Resources, Hohai University,
10 Nanjing, 210098, Peoples R China

11 ⁴Department of Geosciences, University of Oslo, Oslo, N-0316, Norway

12 ⁵Japan Agency for Marine-Earth Science and Technology, Yokohama, 236-0001, Japan

13 ⁶Nanjing Hydraulic Research Institute, Nanjing, 210029, Peoples R China

14
15 *Correspondence to: Weiguang Wang (wangweiguang2016@126.com); Jie Chen
16 (jiechen@whu.edu.cn)

17 Abstract

18 Documenting year-to-year variations in carbon storage potential in terrestrial ecosystems is crucial for
19 the determination of carbon dioxide (CO₂) emissions. However, the magnitude, pattern and inner biomass
20 partitioning of carbon storage potential, and the effect of the changes in climate and CO₂ on inner carbon
21 stocks, remain poorly quantified. Herein, we use a spatially explicit individual based-dynamic global
22 vegetation model to investigate the influences of the changes in climate and CO₂ on the enhanced carbon
23 storage potential of vegetation. The modelling included a series of factorial simulations using the CRU
24 dataset from 1916 to 2015. The results show that CO₂ predominantly leads to a persistent and widespread
25 increase in light-gathering vegetation biomass carbon stocks (LVBC) and water-gathering vegetation
26 biomass carbon stocks (WVBC). Climate change appears to play a secondary role in carbon storage
27 potential. Importantly, with the intensification of water stress, the magnitude of the light- and water-
28 gathering responses in vegetation carbon stocks gradually decreases. Plants adjust carbon allocation to
29 decrease the ratio between LVBC and WVBC for capturing more water. Changes in the pattern of
30 vegetation carbon storage was linked to zonal limitations in water, which directly weakens and indirectly
31 regulates the response of potential vegetation carbon stocks to a changing environment. Our findings

32 differ from previous modelling evaluations of vegetation that ignored inner carbon dynamics and
33 demonstrates that the long-term trend in increased vegetation biomass carbon stocks is driven by CO₂
34 fertilization and temperature effects that are controlled by water limitations.

35 **1 Introduction**

36 As a result of the changes in climate and atmospheric carbon dioxide (CO₂), the terrestrial ecosystem
37 carbon cycle exhibits remarkable trends in interannual variations, which induce uncertainty in estimated
38 carbon budgets (Erb et al., 2018; Keenan et al., 2017). Recent studies assessing interannual fluctuations
39 in terrestrial carbon sinks have shown that the land carbon cycle is the most uncertain component of the
40 global carbon budget (Ahlstrom et al., 2015; Piao et al., 2020; Jung et al., 2017; Humphrey et al., 2018;
41 Gentine et al., 2019; Humphrey et al., 2021). These uncertainties result from an incomplete understanding
42 of vegetation biomass carbon production, allocation, storage, loss, and turnover time (Bloom et al., 2016).
43 The extent and distribution of vegetation carbon storage is central to our understanding of how to
44 maintain a balanced land carbon cycle. Changes in terrestrial vegetation carbon storage have a significant
45 effect on atmospheric CO₂ concentrations and determine whether biomes become a source or sink of
46 carbon (Erb et al., 2018; Humphrey et al., 2018; Terrer et al., 2021). Therefore, investigating the
47 processes producing changes in carbon storage is key to improving the accuracy of estimated terrestrial
48 carbon budgets, and to tap the greenhouse-gas moderation potentials of vegetation (Ipcc, 2007; Roy et
49 al., 2001).

50

51 The atmospheric CO₂ concentration is affected by the vegetation carbon stock, while the long-term trend
52 of vegetation carbon storage capacity is also affected by the changes in climate and CO₂. Since the
53 beginning of industrialization, there has been a noticeable enhancement in the plant capacity of storing
54 and sequestering carbon, which is needed for stabilizing greenhouse gas concentrations and mitigating
55 global warming (Chen et al., 2019; Pan et al., 2011; Le Noë et al., 2020; Magerl et al., 2019; Bayer et al.,
56 2015; Harper et al., 2018). Due to the interaction between terrestrial vegetation and a changing
57 environment, both photosynthesis and respiration of the vegetation also changed. To better absorb CO₂
58 and sunlight required for photosynthesis, vegetated zones are gradually covered by vegetation with
59 higher plant height and wider leaf area (Erb et al., 2008). This change has coincided with a widespread

60 change in other vegetation features, including a positive increase in annual gross primary productivity
61 and a greening of the biosphere (Madani et al., 2020; Zhu et al., 2016). The spatiotemporal distribution
62 and environmental drivers in total carbon storage potential have been well documented on the basis of
63 model estimates and satellite-based assessments (Erb et al., 2007; Erb et al., 2018; Bazilevich et al., 1971;
64 Saugier et al., 2001; Bartholome and Belward, 2005; Olson et al., 1983; Pan et al., 2013; Ajtay et al.,
65 1979; Ruesch and Gibbs, 2008; Kaplan et al., 2011; Shevliakova et al., 2009; Prentice et al., 2011; West
66 et al., 2010; Hurtt et al., 2011). In contrast, the variability of inner components of carbon storage potential
67 has not been extensively studied. Without an accurate assessment of the dynamics of each fraction,
68 attribution of carbon storage potential to environmental drivers is highly uncertain. Consequently,
69 partitioning potential vegetation carbon storage and revealing its inner processes are essential to
70 accurately comprehend the current state of carbon storage capacity and reveal the influence of various
71 drivers on the long-term trend of carbon storage potential.

72

73 The change of carbon storages in vegetation inner components is not only affected by environmental
74 factors, but also controlled by allocation scheme of assimilated carbon. Fractional dynamics of the carbon
75 stock are widely used as a key indicator to investigate the responses of vegetation to environmental
76 drivers, which also reflect the response strategies of vegetation in environments with different water
77 limitations (Yang et al., 2010). In arid regions, vegetation utilizes a tolerance strategy to allocate biomass,
78 storing more biomass carbon in roots to resist enhanced water stress (Chen et al., 2013). Conforming to
79 the optimal partitioning hypothesis, plants store more carbon in shoots and leaves in environments where
80 water is more available and shift more carbon to roots when water is more limited (Yang et al., 2010;
81 McConnaughay and Coleman, 1999). Water availability controls both carbon allocation and storage and
82 can potentially transform zones characterized by a positive response to changes in climate and CO₂ to
83 zones exhibiting a negative response. For example, global warming positively stimulates plant
84 productivity (Keenan et al. 2017), while Madani et al. (2020) found that productivity showed a negative
85 response to temperature in tropical zones due to increasing water stress. With increased warming, water
86 limitations are predicted to increasingly reduce the proportion of leaves' biomass, and decrease plant
87 photosynthesis (Ma et al., 2021). Water limitations have a strong regulating effect on the spatial pattern
88 of change in vegetation carbon storage, demonstrating the effects of the changes in climate and CO₂ on

89 the dynamics of the plant organs are affected by the terrestrial water gradient. Thus, it is important to
90 systematically investigate the distinct responses of carbon storage potential to changes in climate and
91 CO₂ under differing conditions of water stress.

92

93 As documented above, many studies have investigated the total changes in zonal and global terrestrial
94 storage of carbon, while few studies have examined trends in the components partitioning of vegetation
95 carbon storage. Large gaps in our knowledge of the effects of various drivers on the partitioning of carbon
96 stocks in vegetation biomass remain. Meanwhile, plants adjust carbon allocation scheme to adapt to
97 environmental change. With increased warming, an increase in the magnitude of water stress may
98 dramatically change or even reverse the impact of these drivers on inner components of carbon storage
99 (Ma et al., 2021). Evaluating the response pattern of carbon stocks to various drivers under conditions of
100 limited water is elemental for clearly documenting the response mechanism of vegetation carbon storage
101 potential.

102

103 Here, we use a spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM),
104 along with the components partitioning method to (1) systematically determine the long-term variability
105 of carbon storage potential and understand its response mechanisms, and (2) estimate trends in
106 partitioning of potential biomass carbon stocks of vegetation biomass. Throughout this study, the
107 potential biomass carbon stock, biomass carbon stored in vegetation without anthropogenic disturbance,
108 is recognized as an indicator of the potential of carbon storage by natural vegetation. Using a set of
109 factorial simulations to isolate responses to environmental change, we analyse the contributions of
110 multiple driving factors to the trends of two fractions of carbon stock at large scales individually. We
111 then conceptualize the role of water availability through an aridity index (AI), in which hydrological
112 zones are subdivided by their degree of aridity. By comparing the differences in the magnitude of
113 response between the fractions of light- and water-gathering carbon stocks for varying degrees of water
114 availability, we assess the effect of water limitations on the response pattern of potential carbon stocks
115 to changes in climate and CO₂.

116 **2 Model description, experimental design, observational data, and evaluation metrics**

117 In this section, we provided a list of data source (Sect. 2.1), an overview of the modelling concept (Sect.
118 2.2), the representation of biomass carbon stock partitioning in the SEIB-DGVM (Sect. 2.3), an overview
119 of the experimental scheme used in the model simulations (Sect. 2.4), and an overview about data source
120 and pre-processing of observation dataset for model evaluation (Sect. 2.5).

121 **2.1 Forcing Data**

122 Long-term daily meteorological time-series data are required to run model simulations, including
123 precipitation, daily range of air temperature, mean daily air temperature, downward shortwave radiation
124 at midday, downward longwave radiation at midday, wind velocity, and relative humidity. These data
125 were obtained from the Climatic Research Unit (CRU) time series 4.00 gridded dataset (degree 0.5°) for
126 the period 1901–2015 (Harris et al., 2020). Because the CRU dataset is a monthly based dataset, the
127 monthly meteorological data were converted into daily climatic variables by supplementing daily
128 climatic variability within each month using the National Centre for Environmental Prediction (NCEP)
129 daily climate dataset. The NCEP data, displayed using the T62 Gaussian grid with 192×94 points, was
130 interpolated into a 0.5° grid (which corresponds to the CRU dataset) using a linearly interpolation method.
131 By combining the CRU data, with the interpolated NCEP dataset, we were able to directly obtain the
132 most of driving meteorological data (details in Sato et al. (2020)). Neither the CRU nor NCEP datasets
133 included downward shortwave and longwave radiation at midday. Thus, daily cloudiness values in the
134 NCEP were used to calculate radiation values using empirical functions (Sato et al., 2007). These data
135 were all aggregated to a daily timescale with 0.5° resolution to run SEIB-DGVM.

136

137 Atmospheric CO_2 concentrations were collected from Sato et al. (2020), which contains reconstructed
138 CO_2 concentrations between 1901 and 2015. The statistical reconstruction of global atmospheric CO_2
139 was used in this analysis. These reconstructions were based on present annual CO_2 concentrations
140 recorded from the Mauna Loa monitoring station. These data assume atmospheric CO_2 concentration
141 was 284 ppm in 1750, and statistically interpolates atmospheric CO_2 concentrations to fill the gap from
142 1750 to 2015.

143

144 The physical parameters of the soil used in the model include soil moisture at the saturation point, field
145 capacity, matrix potential, wilting point and albedo. These data were obtained from the Global Soil
146 Wetness Project 2.

147 **2.2 Overview of modelling concept in SEIB-DGVM**

148 Model SEIB-DGVM version 3.02 (Sato et al., 2020) was employed in this study. This is a process-based
149 dynamic global vegetation model driven by meteorological and soil data. It is an explicit and
150 computationally efficient carbon cycle model designed to simulate transient effects of environmental
151 change on terrestrial ecosystems and land-atmosphere interactions. It describes three groups of processes:
152 land-based physical processes (e.g., hydrology, radiation, aridity), plant physiological processes (e.g.,
153 photosynthesis, respiration, litter), and plant dynamic processes (e.g., establishment, growth, mortality).
154 Twelve plant functional types (PFTs) were classified. During the simulation, a sample plot was
155 established at each grid cell, and then the growth, competition, and mortality of each the individual PFTs
156 within each plot were modelled by considering the specify conditions for that individual as it relates to
157 other individuals that surround it (Sato et al., 2007).

158

159 SEIB-DGVM treats the relationships between soil, atmosphere, and terrestrial biomes in a consistent
160 manner, including the fluxes of energy, water, and carbon. Based on specified climatic conditions and
161 soil properties, SEIB-DGVM simulates the carbon cycle, energy balance, and hydrological processes.
162 SEIB-DGVM utilizes three computational time steps: (1) During the growth phase, the metabolic
163 procedures including photosynthesis, respiration, and carbon allocation are executed for each individual
164 tree every simulation day. (2) The monthly process of tree growth including reproduction, trunk growth,
165 and expansion of a cross-sectional area of the crown are executed. (3) On the last day of each year, the
166 height of the lowest branch increases as a result of purging crown disks, or self-pruning of branches, at
167 the bottom of the crown layer. The simulated unit of the model is a 30 m × 30 m spatially explicit ‘virtual
168 forest’. A grass layer was placed under the woody layer, and provides for a comprehensive, spatially
169 explicit quantification of terrestrial carbon sinks and sources. The soil depth was set at 2 m and was
170 divided into 20 layers, each with a thickness of 0.1 m. The photosynthetic rate of a single-leaf was
171 simulated following a Michaelis-type function (Ryan, 1991). Respiration was divided into two types:
172 growth respiration and maintenance respiration. Growth respiration is defined as a construction cost for

173 plant biosynthesis, which is quantified by the chemical composition of each organ (Poorter, 1994).
174 Maintenance respiration of live plants occurs every day regardless of the phenological phase, and is
175 controlled by the temperature and nitrate content of each organ (Ryan, 1991). For a wide variety of plant
176 organs, the maintenance respiration rate is linearly related to the nitrogen content of living tissue. The
177 relative proportions of nitrogen in each organ for any PFT are linearly correlated. N-deposition isn't
178 included in SEIB-DGVM. Atmospheric CO₂ was envisioned to be absorbed by photosynthesis of woody
179 PFTs and grass PFTs. This assimilated carbon flux was then allocated into all the plant organs (leaf,
180 trunk, root, and stock), where maintenance respiration and growth respiration occur. The hydrology
181 module treats precipitation, canopy interception, transpiration, evaporation, meltwater, and penetration.

182 **2.3 Carbon stock of vegetation biomass partitioning**

183 **2.3.1 Parameterization of daily allocation**

184 Flexible allocation schemes about resources and biomass are set up in the framework of the SEIB-DGVM
185 biogeochemical model. Based on the updated observation data, the allocation schemes of Boreal Needle-
186 leaved summer-green trees and Tropical Broad-leaved evergreen trees are improved at SEIB-DGVM
187 V3.02. Allocation schemes of other PFTs are the same as the original version. Atmospheric CO₂ is
188 assimilated by the photosynthesis of both woody and grass foliage, and then is added into the non-
189 structural carbon of the plant. This non-structural carbon of photosynthetic production is allocated to all
190 the plant organs (foliage, trunk, root, and stock), supplying what is needed for the maintenance and
191 growth of each organ. When the non-structural carbon is greater than 0 during the growth phase, the
192 following dynamic carbon allocation is executed for each individual plant at the daily time scale, such
193 that:

194 (1) When the fine root biomass ($mass_{root}$) of wood or grass does not satisfy minimum requirements for
195 fulfilling functional balance ($mass_{leaf}/FR_{ratio}$), the mass of non-structural carbon is allocated to the root
196 biomass to supplement the deficit. Here, $mass_{leaf}$ is the leaf biomass, and FR_{ratio} is the ratio of $mass_{leaf}$ to
197 $mass_{root}$ satisfying the functional balance.

198 (2) The stock biomass is supplemented until it is equal to leaf biomass. This scheme is active after the
199 first thirty days of the growing phase.

200 (3) Woody leaf biomass is constrained by three limitations of the maximum leaf biomass, which are

201 calculated as follows:

$$202 \quad max_1 = (crown_{area} + \pi crown_{diameter} crown_{depth}) \frac{LA_{max}}{SLA} \quad (1)$$

$$203 \quad max_2 = ALM_1 \frac{\pi (dbh_{heartwood}/2 + dbh_{sapwood}/2)^2 - \pi (dbh_{heartwood}/2)^2}{SLA} \quad (2)$$

$$204 \quad max_3 = \frac{mass_{available}}{RG_f} \quad (3)$$

$$205 \quad mass_{leaf} = \min(max_1, max_2, max_3) \quad (4)$$

206 where max_1 , max_2 , and max_3 are, respectively, maximum leaf biomass for a given crown surface
207 area, cross-sectional area of sapwood, and non-structural carbon; SLA is a constant of PFTs leaf area
208 ($m^2 g^{-1}$); LA_{max} is the plant functional type specific maximum leaf area per unit crown surface area
209 excluding the bottom layer ($m^2 m^{-2}$); ALM_1 represents the area of transport tissue per unit biomass, and
210 is a constant (dimensionless). If the $mass_{leaf}$ is less than the minimum (max_1, max_2, max_3), the mass of
211 non-structural carbon is allocated into leaf biomass to supplement the deficit.

212 When the leaf area index of grass equals the optimal leaf area index, it stops to allocate non-structural
213 carbon to grass leaf, which is calculated as:

$$214 \quad lai_{opt} = \frac{\ln par_{grass} - \ln \left\{ \frac{p_{sat}}{lue} \left[\left(1 - \frac{cost/SLA}{0.09093 \times dlen \times p_{sat}} \right)^{-2} - 1 \right] \right\}}{eK} \quad (5)$$

215 where lai_{opt} is the optimal leaf area index ($m^2 m^{-2}$); par_{grass} is the grass photosynthetically active
216 radiation ($\mu mol \text{ photon } m^{-2} s^{-1}$); p_{sat} is the light-saturated photosynthetic rate ($\mu CO_2 m^{-2} s^{-1}$); lue is
217 the light-use efficiency of photosynthesis ($mol CO_2 mol \text{ photon}^{-1}$); $cost$ is the cost of maintaining
218 leaves per unit leaf mass per day ($g DM g DM^{-1} day^{-1}$); $dlen$ is day length (hour); and eK is light
219 attenuation coefficient at midday.

220 (4) When non-structural carbon is less than 10 g dry mass (DM) PFT^{-1} or annual NPP is less than 10 g
221 DM PFT^{-1} in the previous year, the following daily simulation processes (5-6) will be skipped.

222 (5) When total woody biomass is more than 10 kg DM, which defines the minimum tree size for
223 reproduction, 10% of non-structural carbon is used for every daily process of reproduction, including
224 having flowers, pollen, nectar, fruits, and seeds. These organs are not explicitly modelled in SEIB-
225 DGVM.

226 (6) During the simulation of trunk growth, the remaining non-structural carbon is allocated to sapwood
227 biomass. There is no direct allocation to heartwood, which is transformed slowly from sapwood biomass.
228 For grass PFTs biomass, the densities of all organs comprising the biomass never decline below 0.1 g

229 DM m⁻² even if the environment is deteriorated for grass survival. A more detailed description of SEIB-
 230 DGVM is given by Sato et al. (2007).

231

232 To control plant phenology and the rate of photosynthesis as a function of the limitation in terrestrial
 233 water, the physiological status of the limitation of terrestrial water is calculated as:

$$234 \quad p_{sat} = PMAX ce_{tmp} ce_{co_2} ce_{water} \quad (6)$$

$$235 \quad ce_{water} = \sqrt{stat_{water}} \quad (7)$$

$$236 \quad stat_{water} = \frac{\max(pool_{w(1)}/Depth_{(1)}, pool_{w(2)}/Depth_{(2)}) - W_{wilt}}{W_{fi} - W_{wilt}} \quad (8)$$

237 where p_{sat} is the single-leaf photosynthetic rate of tree PFTs and grass PFTs ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$);
 238 $PMAX$ is the potential maximum of photosynthetic rate ($\mu\text{mol mol}^{-1} \text{ CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); ce_{tmp} and ce_{co_2} are
 239 the temperature and CO₂ concentration effect coefficient (dimensionless), separately; ce_{water} is the
 240 water effect coefficient (dimensionless); $stat_{water}$ is the physiological status of the terrestrial water
 241 limitation, which ranges between 0.0–1.0, dimensionless; $pool_{w(n)}$ is the water content in soil layer n,
 242 mm; $Depth_{(n)}$ is the depth of the soil layer n, mm; W_{wilt} is soil moisture at the wilting point, m⁻¹;
 243 and W_{fi} is soil moisture at field capacity, m⁻¹. When the temperature of all soil layers is less than 0°
 244 C, $stat_{water}$ is equal to 0.

245 **2.3.2 Carbon stock partitioning method**

246 SEIB-DGVM allocates and stores the biomass carbon in four pools of woody PFT (foliage, trunk, root,
 247 and stock) and three pools of grass PFT (foliage, root, and stock). To investigate the fractional variability
 248 of carbon sequestration potential between the pools, we partitioned potential vegetation carbon stocks
 249 based on the physiological function of the plant (Figure A1). The root-shoot ratio (R/S) has been used to
 250 distinguish and investigate the ratio of below-ground biomass (root biomass) and above-ground biomass
 251 (shoot biomass) (Zhang et al., 2016). In this study, we adjusted the method of calculating the R/S ratio
 252 by distinguishing between the light-gathering vegetation biomass carbon stock (LVBC) and the water-
 253 gathering vegetation biomass carbon stock (WVBC). LVBC represents the biomass carbon invested by
 254 plant is used to gather sunlight, including biomass carbon from woody foliage, woody trunk, and grass
 255 foliage. WVBC represents biomass carbon used to gather water, including biomass carbon from woody
 256 fine roots and grass fine roots, excluding the stock pool. Stock biomass is used for foliation after dormant

257 phase and after fires, which is reserve resource in each individual tree. Fine root biomass is just a tiny
 258 fraction to the total biomass, but it has a very high turnover rate and determines the capacity of vegetation
 259 to absorb soil water. Thus,

$$260 \frac{LVBC}{WVBC} = \frac{Tmass_{leaf} + Tmass_{trunk} + Gmass_{leaf}}{Tmass_{root} + Gmass_{root}} \times 100\% \quad (9)$$

261 where *LVBC* is light-gathering vegetation biomass carbon stock (kg C m⁻²); *WVBC* is water-gathering
 262 vegetation biomass carbon stock (kg C m⁻²); *Tmass_{leaf}* is the leaf biomass carbon stock of woody
 263 vegetation (kg C m⁻²); and *Tmass_{trunk}* is the trunk biomass carbon stock of trees (kg C m⁻²), including
 264 both branch and structural roots. This biomass is simplistically attributed to light-gathering vegetation
 265 organs and is used primarily to support the plant. *Gmass_{leaf}* is the leaf biomass carbon stock of grass
 266 (kg C m⁻²); whereas *Tmass_{root}* and *Gmass_{root}* are functional root (fine roots) biomass carbon stocks
 267 of trees and grass, separately (kg C m⁻²), which absorb water and nutrition from soil.

268 2.4 Experimental design

269 2.4.1 Setup of model runs

270 SEIB-DGVM simulations begin with seeds of selected PFTs planted in bare ground. The establishment
 271 of PFTs seeds are determined by the climatic conditions in each grid cell. We inputted the transient
 272 climate data from 1901 to 1915 to spin up the model in a repetitive loop. No obvious trend in climatic
 273 factors was observed during this period (Tei et al., 2017). A spin-up period of 1050 years was necessary
 274 to bring the terrestrial vegetation carbon cycle into a dynamic equilibrium. To reach quasi-equilibrium
 275 in the vegetation biomass, about 1000 years of simulation was required as a spin-up procedure.

276 2.4.2 Factorial simulation scheme

Table 1. List of factorial simulations used in this study

| Factorial simulation | CO ₂ concentration | Precipitation | Temperature | Radiation | Other drivers |
|----------------------|-------------------------------|---------------|-------------|-----------|---------------|
| S1 | √ | √ | √ | √ | √ |
| S2 | √ | | | | |
| S3 | √ | √ | | | |
| S4 | √ | | √ | | |
| S5 | √ | | | √ | |
| S6 | √ | | | | √ |

Note: In factorial simulation S1, historical atmospheric CO₂ concentration and historical climate fields from the

CRU data set were used. In simulation S2, only historical atmospheric CO₂ concentration was used, and climate variables of the transient period (1901–1915) were repeatedly input. In simulation S3 (or S4, S5), only historical atmospheric CO₂ concentrations and precipitation (or temperature, radiation) were input, and climate variables of the transient period (1901–1915) were repeatedly input. In the last simulation S6, only historical atmospheric CO₂ concentrations and other climate variables were input, including wind velocity and relative humidity.

277 In order to further quantify the relative contributions of varying atmospheric CO₂ concentrations,
278 precipitation, temperature, radiation, and other factors (wind velocity and relative humidity), we
279 performed six factorial simulations. In simulation S1, atmospheric CO₂ concentration and all of climate
280 variables were varied. In simulation S2, only atmospheric CO₂ concentration was varied, and climate
281 variables were held constant (Climate variables of the transient period (1901-1915) were repeatedly
282 inputted). In simulation S3 (or S4, S5), atmospheric CO₂ and precipitation (or temperature, radiation)
283 were varied, and other climate variables were held constant. In simulation S6, atmospheric CO₂, wind
284 velocity, and relative humidity were varied, and other climate variables were held constant. Finally, S2
285 was used to evaluate the effects of CO₂ fertilization on carbon stock variation. The differences of S2-S3,
286 S2-S4, S2-S5, and S2-S6 were used to evaluate the response of carbon stock growth to precipitation,
287 temperature, radiation, and other drivers, respectively.

288 **2.4.3 Non-parametric test methods**

289 Each driving factor (atmosphere CO₂, precipitation, temperature, and radiation) has a different influence
290 on the carbon stock, so it is difficult to make a simple pre-assumption about the population distribution
291 pattern for factorial simulations. We used the non-parametric Mann-Kendall and Sen's slope estimator
292 statistical tests (Gocic and Trajkovic, 2013) to assess the ability of SEIB-DGVM to simulate the response
293 patterns of carbon storage potential to a change in climate and CO₂ concentrations. We regressed the
294 simulated hundred-year mean global average carbon stock time series to reveal the accumulative
295 influences of the single variables based on the factorial simulations where only one or two drivers were
296 varied. As shown in Figures A2 and A3, detection trends of LVBC and WVBC for all driving factors
297 performed statistically well (in agreement at the 95% confidence intervals), indicating this analytical
298 method was suitable for trend attribution at the global scale.

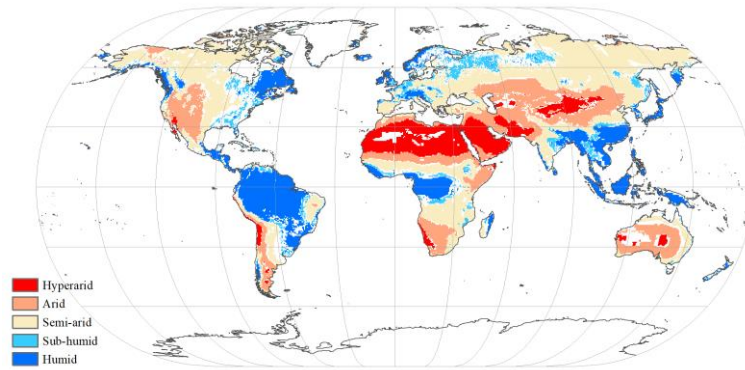


Figure 1. Global spatial patterns of water availability. Spatial variations in water availability were categorized based on the multiyear average aridity index (AI), defined as the ratio of the multiyear mean precipitation to the potential evapotranspiration. Categories include: hyper-arid ($AI \leq 0.05$), arid ($0.05 < AI \leq 0.2$), semi-arid ($0.2 < AI \leq 0.5$), sub-humid ($0.5 < AI \leq 0.65$), and humid ($AI > 0.65$). The white grid cells were not assigned hydrological category.

300 Locally available water strongly regulates and limits the response of carbon stocks to changes in climate
 301 and CO_2 . We used aridity index (AI) to distinguish between the global hydrological regions for
 302 comparing the long-term trend in carbon stocks over different hydrological environments, and for
 303 quantifying the influences of each hydrological environment on the variations in the trends. The AI was
 304 defined as:

$$305 \quad AI = \frac{\bar{P}}{\overline{ET_p}} \quad (10)$$

306 where \bar{P} is the multiyear mean precipitation ($mm \text{ year}^{-1}$); and $\overline{ET_p}$ is the multiyear mean potential
 307 evapotranspiration ($mm \text{ year}^{-1}$), which was calculated by the Penman-Monteith model (Monteith and
 308 Unsworth, 1990). As in a previous study (Chen et al., 2019), five hydrological regions were categorized
 309 based on AI value. Under the influences of climate change, the hydrological condition was changed in
 310 some grid cells (Figure A4). For example, the grid cell classified as sub-humid zone in the period of
 311 1916-1945 was redefined as semi-arid zone in the period of 1986-2015. In this study, grid cells with
 312 consistent hydrological condition between the period of 1916-1945 and the period of 1986-2015 were
 313 selected and classified (Figure 1).

314 **2.5 Observation dataset for model evaluation**

315 A global time series of potential vegetation carbon was modelled by the SEIB-DGVM between 1916-
316 2015. In terrestrial vegetation biomes, there is a high correlation between biomass carbon stock density
317 and NPP per unit (Erb et al., 2016; Kindermann et al., 2008) (Figure A1). Thus, we collected NPP
318 observation dataset and used NPP as a proxy of the carbon stock to assess model accuracy. Ecosystem
319 Model-Data Intercomparison (EMDI) builds upon the accomplishments of the original worldwide
320 synthesis of NPP measurements and associated model driver data prepared by Global Primary Production
321 Data Initiative. We obtained the monitoring station data from the EMDI working group, and then
322 compared their data with modelled multiyear average NPP in the period of 1916-1999 (Figure 2).

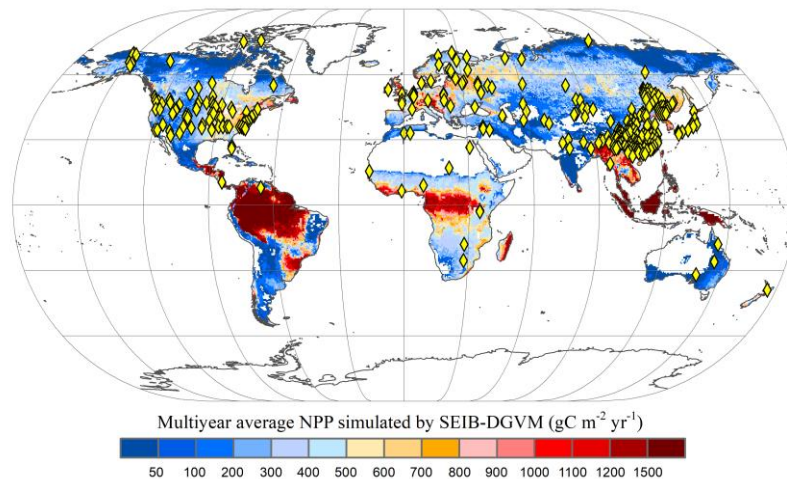


Figure 2. Multiyear average NPP simulated by SEIB-DGVM and EMDI global site distribution.

Yellow rhombuses indicate the monitoring stations of the EMDI.

323 However, *in-situ* observations are sparse for global spatial-temporal validation. Therefore, we used the
324 MOD17A3 products to further verify the simulated potential NPP in the twenty first century. These data
325 were collected by the Moderate Resolution Imaging Spectroradiometer and are some of the most widely
326 used data to assess the accuracy of global model simulations (Gulbeyaz et al., 2018). The natural
327 vegetation zones refer to the hypothetical condition that would prevail in an assumed absence of
328 anthropogenic activity, but under historical climate fields (Erb et al., 2018; Haberl et al., 2014). The
329 potential NPP is defined as that assimilated carbon stored in natural vegetation without the disturbance
330 of anthropogenic activities (Erb et al., 2018).

331

332 In order to distinguish the distribution of vegetation grid cells without anthropogenic disturbance, we

333 obtained global land cover types in the period 2001-2015 from MCD12C1 (Table A1). We included grid
334 cells whose largest vegetation component was evergreen needleleaf forest, evergreen broadleaf forest,
335 deciduous needleleaf forest, deciduous broadleaf forest, mixed forest, closed shrublands, open
336 shrublands, woody savannas, savannas or grasslands. Other grid cells were excluded from our analysis.

337

338 Part of grid cells covered by grassland were grazed by livestock, leading to the decrease of NPP of grass
339 PFTs. There is a weak anthropogenic disturbance in rangeland, while managed pasture is intensely grazed
340 by livestock. To remove pasture area with strong anthropogenic disturbance, we obtained land-use
341 forcing data from Land-Use Harmonization (LUH2) to map the distribution of managed pasture data
342 from 2001 to 2015 (Hurt et al., 2020). As shown in Figure A5, grassland in eastern Asia, western Europe,
343 south central Africa, and western South America were severely affected by grazing. For exhibit the
344 disturbance of managed pasture, we calculated the mean fraction of managed pasture within the
345 corresponding 0.5° grid unit. When the fraction of managed pasture over 10%, the grid cell was
346 considered to be affected by managed pasture. To reduce the interference effects of livestock grazing,
347 we first removed the grid cells affected by managed pasture. Then, we map the distribution of natural
348 vegetation grid cells without anthropogenic disturbance (Figure A6). This exclusion method is only used
349 for potential NPP comparison.

350 **3 Results and discussion**

351 **3.1 Evaluation of SEIB-DGVM**

352 Figure 3 illustrates the comparison between model simulated and observed multi-year mean NPP during
353 1916-1999. The determined coefficient (R^2) between EMDI observed and estimated multiyear average
354 NPP of 669 *in-situ* observations is 0.54, which is significant at the $p=0.01$ level. The slope of the
355 regressed line is 0.70 during the twentieth century.

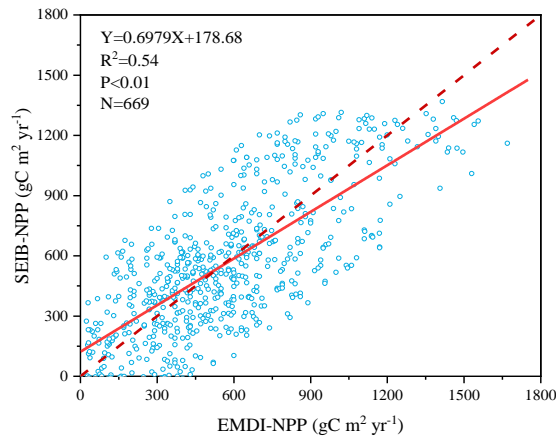


Figure 3. Comparison of multiyear average NPP calculated by SEIB-DGVM and EMDI for the twentieth century. The solid line is the best fit curve; and the dashed line represents a perfect correspondence in the results of the two.

356 Based on land cover types dataset from 2001 to 2015, we obtained NPP-MOD17A3 data in natural
 357 vegetation zones without anthropogenic disturbance at the same period. Figure 4 shows that the modelled
 358 NPP from the SEIB-DGVM exhibited a high degree of consistency with the NPP-MOD17A3 data in
 359 natural vegetation zones over the period ($R^2=0.63$, $p<0.05$). The general spatiotemporal agreement
 360 between the simulated NPP derived from SEIB-DGVM with *in-situ* observations and derived from
 361 satellites reveals that it is reasonable to use the SEIB-DGVM simulations to evaluate the same
 362 mechanisms controlling global potential biomass carbon stocks of vegetation.

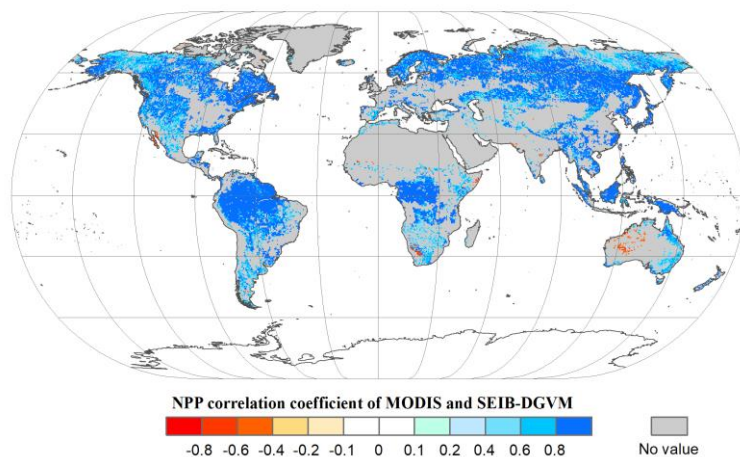


Figure 4. Spatial patterns in the potential NPP correlation coefficients ($P<0.05$) between SEIB-DGVM and MODIS between 2001–2015. These data were used to validate SEIB-DGVM.

363 Finally, the modelled result of potential vegetation biomass carbon stock was compared with current

364 existing data from the literature and state-of-the-art datasets. Figure 5 shows that the modelled results are
 365 within the range of potential carbon stocks, which indicate that the SEIB-DGVM reliably simulated the
 366 carbon stock dynamics.

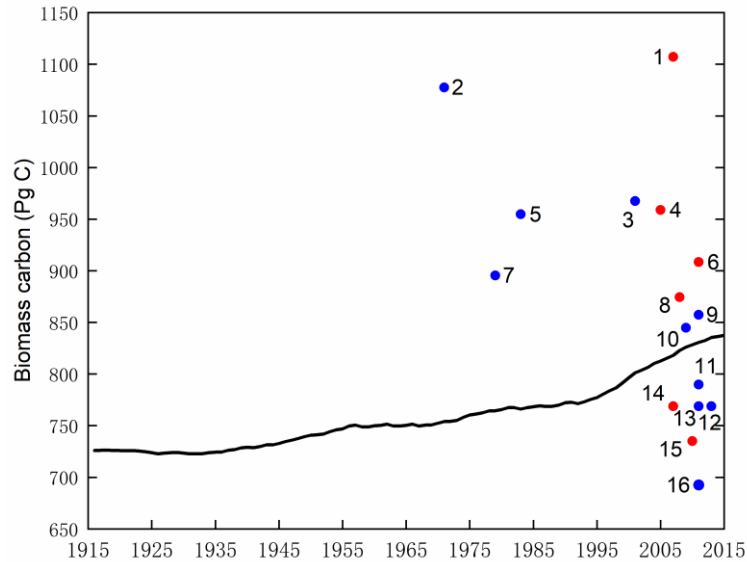


Figure 5. Estimates of the potential vegetation biomass carbon stock from the literature (blue plot), state-of-the-art datasets (red plot) and this study (black line). Datasets are from the following studies: (1)(Erb et al., 2018; Erb et al., 2007), (2)(Bazilevich et al., 1971), (3)(Saugier et al., 2001), (4)(Erb et al., 2018; Bartholome and Belward, 2005), (5)(Olson et al., 1983), (6)(Erb et al., 2018; Pan et al., 2011), (7)(Ajtay et al., 1979), (8)Erb et al., 2018; Ruesch and Gibbs, 2008), (9)(Kaplan et al., 2011), (10)(Shevliakova et al., 2009), (11)(Kaplan et al., 2011), (12)(Pan et al., 2013), (13)(Prentice et al., 2011), (14)(Erb et al., 2018; Erb et al., 2007), (15)(Erb et al., 2018; West et al., 2010), (16)(Hurtt et al., 2011).

367 3.2 Enhanced carbon stocks and its fractions

368 We distinguished the changes of LVBC and WVBC from total vegetation carbon stocks. The historical
 369 temporal trends over the period are shown in Figure 6a. The potential vegetation carbon stock exhibits a
 370 net increase of 119.26 ± 2.44 Pg C in the last century (± 2.44 represents intra-annual fluctuation in carbon
 371 stock, which is the difference between maximum value and minimum value of carbon stock within the
 372 year). Based on Pearson correlation analysis, this increasing trend of annual average carbon stock
 373 exhibits a robust agreement with the dramatic increase in atmospheric CO_2 concentration ($R^2=0.9677$,
 374 $p<0.001$), suggesting that the carbon stock is strongly affected by CO_2 fertilization. Meanwhile, the

375 positive correlation between the carbon stock and CO₂ generally extends across LVBC ($R^2=0.9669$) and
 376 WVBC ($R^2=0.9622$). After the value of the global terrestrial carbon stock and trends were partitioned
 377 among the vegetation functional classes, we see that LVBC increases 116.18 ± 2.34 Pg C (or $\sim 15.60\%$),
 378 which explains 97.42% of total carbon stock increasing trend and dominates the positive global carbon
 379 stock trend; WVBC also increases 3.08 ± 0.14 Pg C (or $\sim 18.03\%$) over the past century.

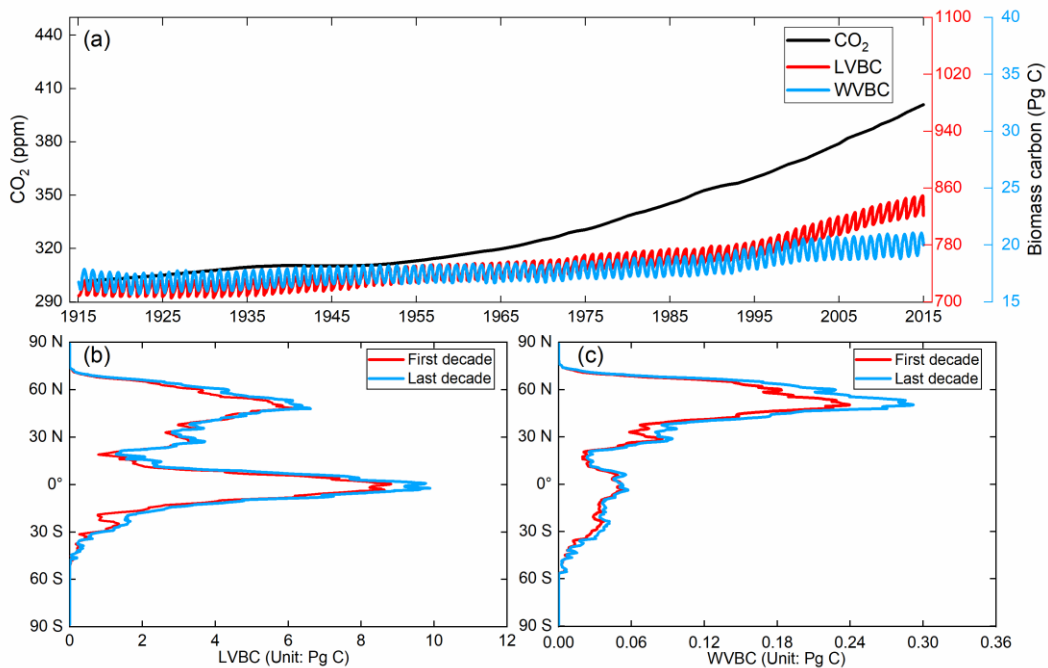


Figure 6. Global potential biomass carbon stocks of vegetation during the past 100 years. (a) The evolution of global potential biomass stocks (LVBC+WVBC), along with changes in biomass stocks that can be attributed to the variability and trend of LVBC and WVBC through the twentieth century. The red line represents the monthly value of LVBC, the blue line represents the monthly value of WVBC, and the black line represents the annual value of CO₂ concentration. (b, c) Zonal averaged sums of the annual LVBC and WVBC for latitudinal bands during the first decade (1916–1925, red line) and the last decade (2006–2015, blue line) shows the increased carbon stock capacity.

380 The global distributions of the decadal-average change in LVBC and WVBC are shown in Figures 6b
 381 and 6c, respectively. The significant historical changes in climate and CO₂ enhance the carbon stock of
 382 the terrestrial ecosystem, and their positive influences are broadly distributed across a latitudinal north–
 383 south gradient. The latitudinal bands of increasing annual LVBC are mainly distributed in the tropical
 384 and boreal latitudes, which is consistent with Figure 7b. The decadal and inter-annual variabilities of
 385 LVBC are dominated by the tropical and boreal zones where large portions of the zones are highly

386 productive (Ahlstrom et al., 2015; Poulter et al., 2014). Tropical LVBC dominates the long-term trend
387 of global LVBC in the last hundred years. Compared with LVBC, the increase of tropical WVBC is light.
388 There is a single peak in the spatial variation of annual WVBC (Figure 6c and Figure 7c). WVBC exhibits
389 robust growth at most latitudes, and increases mainly in boreal latitudes.

390 **3.3 Spatial variability in estimated LVBC and WVBC trends**

391 In Figures 7(a) and 7(b), total carbon stock and LVBC exhibited a significantly increasing trend in eastern
392 South America, southern Africa, and northern Asia, while they declined in central North America,
393 northwest South America, and central Africa. WVBC showed a more widely increasing tendency in
394 North America, southeastern South America, and Europe, while had a decreasing trend in part zones of
395 Asian. We find that the total carbon stock as well as the light- and water-gathering vegetation biomass
396 carbon stocks over the period of 1916–2015 exhibited a remarkable spatial heterogeneity. Figure 7a
397 shows that an increase in vegetation carbon stocks occurred over zones and global aggregate levels during
398 the entire study period. About 57.39% of the terrestrial grid cells exhibited an increase with a noticeable
399 trend ($p < 0.05$) in biomass carbon stock; 53.82% of global grid cells possessed increases that were
400 statistically significant at the $p = 0.01$ level. To determine the contributions of each fraction (LVBC,
401 WVBC) to the total change in the potential vegetation carbon stock, we partitioned and present the
402 historical spatial and temporal patterns for each fraction separately (Figure 7b, 7c). LVBC contributes
403 97.33% to the incremental change of total carbon stock (116.18 ± 2.34 Pg C), with about 51.32% of the
404 grid cells possessing a noticeable positive trend ($p = 0.01$). Generally, spatial patterns of LVBC and the
405 total carbon stock are consistent (Figure 7a, 7b), which further supports the argument that LVBC
406 dominates the trend in carbon stocks in most zones. Although the proportion of the total change in carbon
407 stocks is small (2.58% of total carbon stock increase), about 61.00% of the land surface shows an increase
408 in WVBC; of these terrestrial grid cells, 55.81% was characterized by a significant $p = 0.01$ increase.

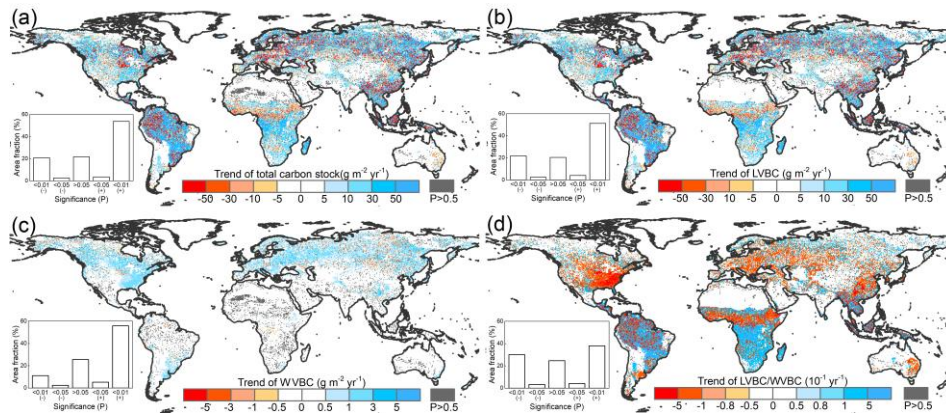


Figure 7. Spatial patterns in the trends of potential vegetation carbon stocks and their fractions from 1916 to 2015. Difference induced by changes in climate and CO₂ in terrestrial biomass carbon stock (a), LVBC (b), and WVBC (c) during the historic period 1916–2015. The blue bar indicates the significantly increasing trends and the red bar indicates the significantly decreasing trends in carbon stocks. (d) Trend in the LVBC/WVBC ratio from 1916 to 2015. The blue bar indicates significantly increasing trends in the ratio, and vice versa. The grey bar indicates the trend is statistically insignificant ($P > 0.05$). The sub-graphs show the significant test results. A ‘+’ symbol indicates a positive trend, and vice versa.

409 Under the influences of a changing climate and CO₂ concentrations, there is a slight increase in the ratio
 410 of global LVBC/WVBC; the rate of increase is 0.0171 yr^{-1} in the last hundred years, which is significant
 411 at the 0.01 level (Figure 7d). About 42.08% of the terrestrial grid cells exhibits an increase with a
 412 noticeable trend ($p < 0.05$) in the ratio of LVBC and WVBC; 37.95% of global grid cells possessed
 413 increases that are statistically significant at the $p = 0.01$ level. Meanwhile, 33.32% of the land surface
 414 shows a significant decrease in LVBC/WVBC; of these terrestrial grid cells, 30.06% is characterized by
 415 a significant $p = 0.01$ decrease. Grid cells with noticeable increases in the ratio of LVBC to WVBC are
 416 mainly located in southern Africa, central South America, and northern Eurasia. Negative trends in
 417 LVBC/WVBC ratios are found in northern America, southern Europe, and tropical Africa.

418 3.4 Responses of LVBC and WVBC to environmental drivers

419 The responses of LVBC and WVBC to changes in climate and CO₂ are both positive at the global level
 420 (Figure 8a, 8c), although zonally, they exhibit both negative and positive responses (Figure 8b, 8d).
 421 Based on the results of factorial simulations and Mann-Kendall+Sen tests, CO₂ fertilization explains the
 422 largest proportion of the change in the carbon stock; about 82.45% change in LVBC was positive (Figure

423 8a), whereas 89.28% of the change in WVBC was positive (Figure 8c). In factorial simulation S2, the
 424 long-term trend of LVBC was $15.521 \text{ g C m}^{-2} \text{ yr}^{-1}$ and that of WVBC was $0.435 \text{ g C m}^{-2} \text{ yr}^{-1}$ at the
 425 period from 1916 to 2015 (Figure A2a and Figure A3a). The separately simulated LVBC and WVBC
 426 increased by 80.98 Pg C and 2.66 Pg C with increasing atmospheric CO_2 concentrations (from 301.73
 427 ppm in 1916 to 400.83 ppm in 2015). The other climatic drivers (precipitation, temperature, radiation,
 428 humidity, and wind speed) remained at baseline values. While the increase or decrease in the carbon
 429 stock may be attributed to more than one driving factor, within any specified grid cell, the one with the
 430 highest positive or negative contribution is the dominant driver that consistently resulted in the highest
 431 increase or decrease in the carbon stock for that grid cell. The spatial pattern illustrates that CO_2
 432 dominates the variability in LVBC in 7.28% of the grid cells, including 1.21% of the grid cells that
 433 exhibited a negative change and 6.07% that exhibited a positive change (Figure 8b). CO_2 dominates the
 434 variability in WVBC in 27.60% of the grid cells, including 1.73% of the grid cells that exhibited a
 435 negative change and 25.87% of grid cells with a positive change (Figure 8d). Under the effect of CO_2
 436 fertilization, grid cells with increased trend in WVBC mainly distribute in boreal latitudes (Figure 6c).
 437 These trends are consistent with previous studies (Tharammal et al., 2019; Zhu et al., 2016; Keenan et
 438 al., 2017) in which positive trends occurred, especially for WVBC.

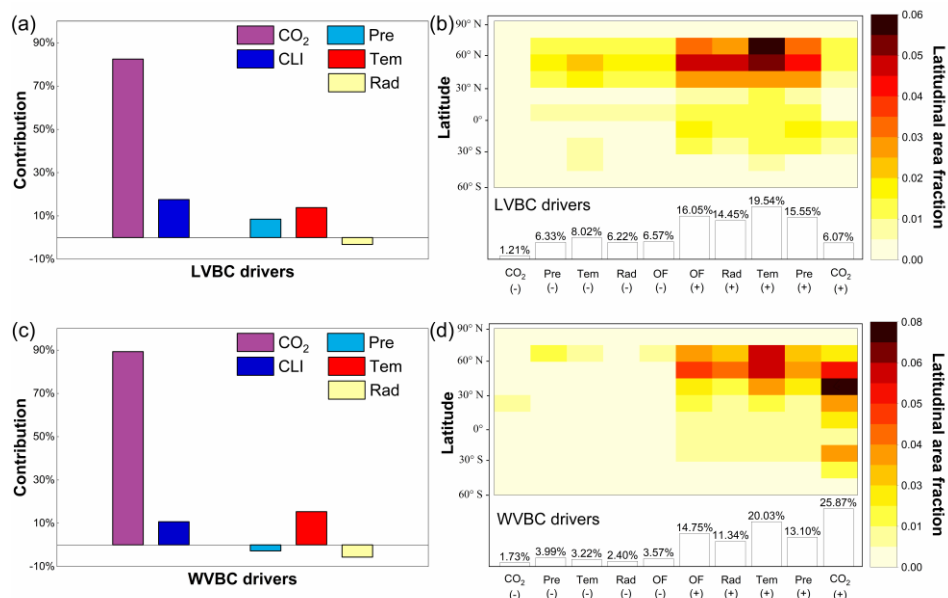


Figure 8. The proportion of changes in vegetation biomass carbon stocks attributed to driving factors. Ratios of the driving factors of CO_2 fertilization effects (CO_2), climate change effects (CLI), precipitation (Pre), temperature (Tem), radiation (Rad) for LVBC (a) and WVBC (c) are calculated

by the Mann-Kendall and Sen's slope estimator statistical tests. Attribution of LVBC (b) and WVBC (d) dynamics to driving factors calculated as averages along 15° latitude bands. At the local scale, the driving factors include CO₂, Pre, Tem, Rad, and other climate factors (OF). The fraction of global grid cells (%) that is predominantly influenced by the driving factors is showed at the bottom of the bar. The '-' symbol before fraction indicates a negative effect of the driving factor on carbon stock, and vice versa.

439 Climate change induced by the greenhouse effect explains part of the increase in carbon stocks, but unlike
440 CO₂ fertilization, climate has dramatic negative effects on some vegetated zones. Figure 8a illustrates
441 that temperature is the largest climatic contributor to the change in LVBC (13.83%, 2.572 g m⁻² yr⁻¹),
442 followed by precipitation (8.51%, 1.572 g m⁻² yr⁻¹) and radiation (-3.19%, -0.649 g m⁻² yr⁻¹). The spatial
443 distribution shows that temperature predominantly influences the change in LVBC (Figure 8b),
444 influencing over 27.56% of the global vegetated grid cells, followed by precipitation (21.88%) and
445 radiation (20.67%). Figure 8c shows there are negative effects and contributions of precipitation on the
446 change in WVBC at the global level (-2.76%, -0.013 g m⁻² yr⁻¹). Temperature is the largest climatic
447 contributor to the change in WVBC (15.36%, 0.075 g m⁻² yr⁻¹), followed by radiation (-5.63%, -0.027 g
448 m⁻² yr⁻¹). Modelled WVBC trends based on the factorial simulations have similar spatiotemporal patterns
449 to LVBC (Figures A2 and A3), and the spatial patterns of light- and water-gathering carbon stocks show
450 a significantly increasing trend in the most of boreal zones. In the Southern Hemisphere, the trends of
451 WVBC are extensively statistically insignificant in all factorial simulations, and only a small proportion
452 of grid cells show a significantly increasing trend. There is a significantly increasing trend in LVBC in
453 south-central Africa and northern South America. The effects of temperature on WVBC are stronger than
454 LVBC, because temperature has a stronger effect on the metabolism process of root growth, dominating
455 the turnover rate and the costs of maintenance respiration in root growth process (Gill and Jackson, 2000).
456 It should be noted that trends in the global carbon stock can be largely attributed to the influences of CO₂,
457 precipitation, temperature, and radiation (Figure 8). Nonetheless, at the zonal scale, the contributions of
458 other factors should be considered, such as humidity and wind speed. The effects of these other factors
459 dominate trends in LVBC in over 16.05% of the grid cells that increased and 6.57% of the grid cells that
460 decreased. In the case of changes in WVBC, other factors were dominant drivers in over 14.75% of the
461 grid cells that increased and 3.57% of grid cells that decreased. Under the effect of climate, the variability

462 of LVBC and WVBC is positive in most grid cells, promoting the noticeable increase of carbon stocks
 463 in boreal latitudes.

464 **3.5 Constraints imposed by water limitations**

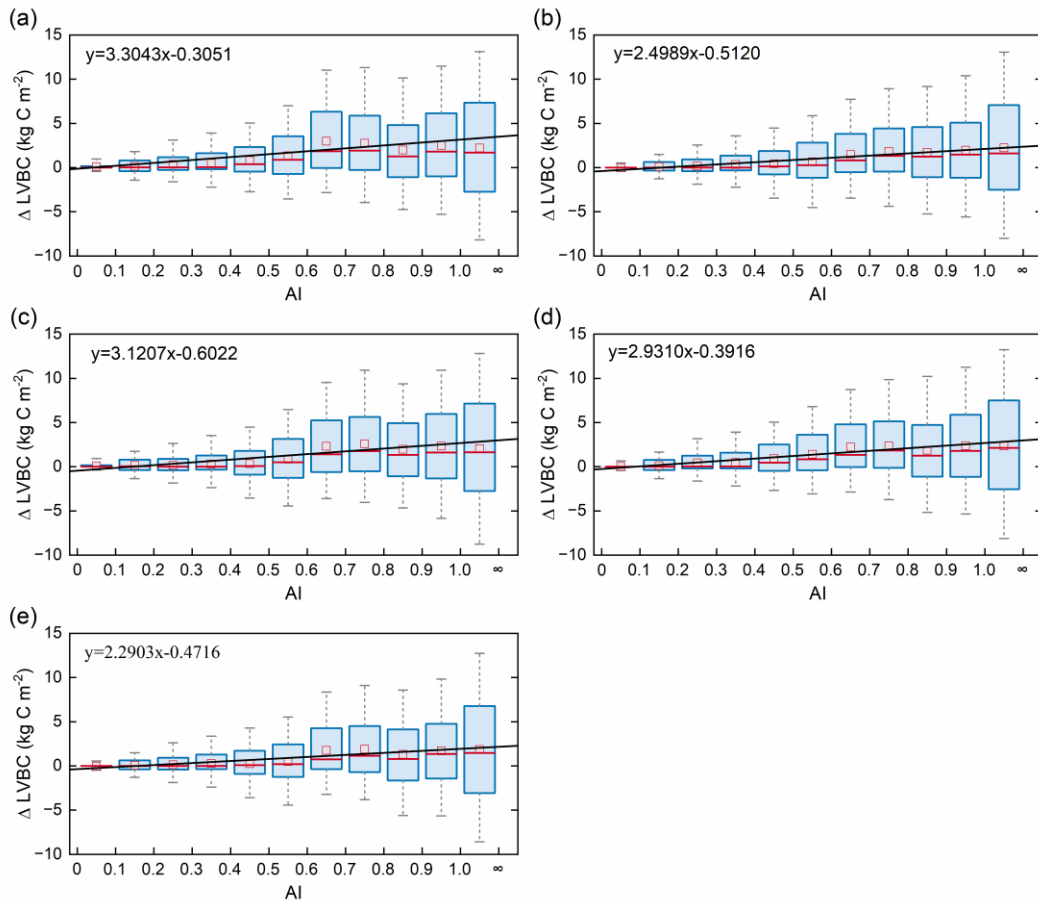


Figure 9. Relationships of the incremental change between AI and LVBC. Magnitude of change in LVBC in the historical scenario S1 (a), CO_2 in scenario S2 (b), CO_2 + precipitation in scenario S3 (c), CO_2 + temperature in scenario S4 (d), and CO_2 + radiation in scenario S5 (e). The range of the box is 25%-75% of values; the range of the whiskers is 10%-90% of values; the small red square is average value; the red line is the median line; and the black line is the fitted curve. Positive value of the Y axis represents the magnitude of increased LVBC from 1916 to 2015 under water-limitations conditions, and vice versa. AI of grid cells is calculated by multiyear average precipitation and multiyear average potential evapotranspiration in the period of 1916-2015. Categories of hydrological zones include: hyper-arid ($\text{AI} \leq 0.05$), arid ($0.05 < \text{AI} \leq 0.2$), semi-arid ($0.2 < \text{AI} \leq 0.5$), sub-humid ($0.5 < \text{AI} \leq 0.65$), and humid ($\text{AI} > 0.65$).

465 Terrestrial water availability emerged as a key regulator of terrestrial carbon storage, by affecting the
466 response mechanism of the vegetation carbon stock to changes in driving factors. As shown in Figures 9
467 and 10, with the accumulated change of LVBC and WVBC in the period of 1916 to 2015 across the
468 aridity index (i.e., an increase in available water), the magnitude and range in responses of LVBC density
469 and WVBC density gradually increase. Based on the results of the historical simulation (Figure 9), we
470 find a positive relationship between LVBC and aridity index. In extreme water stress, the increase of
471 LVBC tends to zero and plants stop increasing their carbon storage. There is no obvious difference in
472 the slopes of fitting curves between factorial simulations, which shows the robustness in the response of
473 LVBC to the change of water stress. The pattern of the enhanced magnitude and range of variation in the
474 WVBC density is unimodal with water stress gradient in all factorial simulations. With the increasing of
475 AI, the magnitude of change in WVBC increases at first and then decreases finally. The mitigation of
476 water stress promotes WVBC increase, while excess surface water limits the response of WVBC to
477 changes in climate and CO₂. These results reveal that the carbon stock increases stimulated by changes
478 in climate and CO₂ are constrained by water available. With increased warming, water limitations are
479 expected to increasingly limit the carbon stock increase, specially at arid regions. To further reveal the
480 controls of water limitation on the responses of inner carbon storages to each driver, we analyse the long-
481 term variability of potential vegetation carbon stocks by means of factorial simulations for each
482 hydrological region (Figure 1). Figure A7b shows that the fluctuation range (the difference between
483 maximum value and minimum value in each factorial simulation) of LVBC density across all factorial
484 simulation is 1.202 kg C m⁻² in the hyper-arid regions for the 1916-2015 period. As shown in Figure A7f,
485 the fluctuation range of LVBC density in humid regions is 6.068 kg C m⁻² during the same period. In
486 Figure A8b, the maximum change magnitude of WVBC density across all factorial simulation is 0.011
487 kg C m⁻² in the hyper-arid regions during the time of 1916-2015. In Figure A8f, the maximum change
488 magnitude of WVBC density is 0.046 kg C m⁻² in humid regions during the same period. Compared with
489 plants in arid regions, plants in humid regions show more dramatic responses to the stimulation from
490 drivers' change. With a lessening of water stress (from hyper-arid to humid region), the response
491 magnitudes of the carbon stock to the changes of climate and CO₂ gradually become more noticeable.
492 The robust pattern in the zonal average density of the carbon stock shows that terrestrial water limitations
493 strongly regulate the enhanced magnitude of the carbon stock.

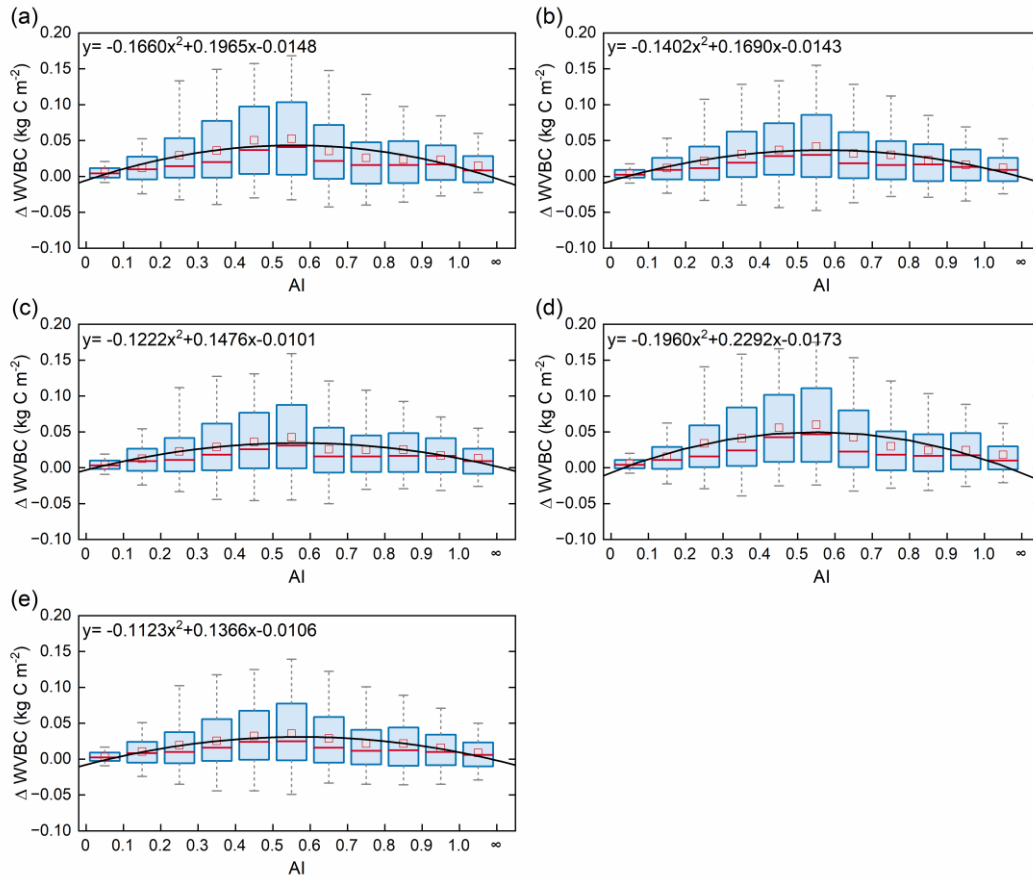


Figure 10. Relationships of the incremental change in AI and WVBC. Magnitude of change in WVBC in the historical scenario S1 (a), CO₂ in scenario S2 (b), CO₂ + precipitation in scenario S3 (c), CO₂ + temperature in scenario S4 (d), and CO₂ + radiation in scenario S5 (e). The range of the box is 25%-75% of values; the range of the whiskers is 10% -90% of values; the small red square is average value; the red line is the median line, and the black line is the fitted curve. Positive value of the Y axis represents the magnitude of increased WVBC from 1916 to 2015 under water-limitations conditions, and vice versa. AI of grid cells is calculated by multiyear average precipitation and multiyear average potential evapotranspiration in the period of 1916-2015. Categories of hydrological zones include: hyper-arid (AI ≤ 0.05), arid (0.05 < AI ≤ 0.2), semi-arid (0.2 < AI ≤ 0.5), sub-humid (0.5 < AI ≤ 0.65), and humid (AI > 0.65).

494 Water limitations not only directly reduced the magnitude of the response in the two fractions' carbon
 495 stock (LVBC and WVBC) to changes in climate and CO₂, but also indirectly confined the response
 496 direction of each fractions' carbon stock by transforming vegetation structure and function. Figure 11
 497 illustrates temporal variations in the carbon stock ratio within and between hydrological regions. From
 498 hyper-arid regions to humid regions, the fluctuation range of LVBC/WVBC ratio significantly changes.

499 The fluctuation magnitudes of LVBC/WVBC in humid and hyper-arid regions are greater than that in
500 other hydrological regions. Compared with plants in hyper-arid regions, plants in humid regions exhibit
501 more significant responses to changes in climate and CO₂. Meanwhile, the long-term effects of driver
502 changes have a remarkable influence on this carbon allocation pattern at global level (Figure 7d). Under
503 the synergistic effect of drivers and water stress, the trends of light- and water-gathering vegetation
504 carbon stock are upward in the past hundred years (Figure 6). However, there is a difference in the
505 increasing rate between LVBC and WVBC, resulting in a dramatic and complicated fluctuation in global
506 LVBC/WVBC ratio (Figure 11a). Whereas LVBC decreases and WVBC increases in hyper-arid and arid
507 regions (Fig. A7 and A8), causing a downward trend in LVBC:WVBC ratio, semiarid regions see an
508 increase in LVBC. So, the ratio of LVBC and WVBC shows a downward trend in these regions. LVBC
509 in semi-arid regions shows upward tendency in the past years (Figure A7d) because of the aridity
510 mitigation. There is an upward trend in WVBC in semi-arid regions (Figure A8d). Plants in semi-arid
511 regions still utilize a tolerance strategy and allocates more non-structural carbon to water-gathering
512 vegetation organ to resist water stress, resulting in the decline of LVBC/WVBC ratio. In humid regions,
513 light- and water-gathering biomass carbon stocks both increased (Figures A7 and A8). The proportion of
514 LVBC increases more than that of WVBC for capturing more resources like CO₂ and radiation energy,
515 leading to an increase in the LVBC/WVBC ratio. The value of LVBC/WVBC in S3 is higher than that
516 in S4 and S5, which represents that precipitation makes more contributions to the change of
517 LVBC/WVBC ratio among meteorological factors.

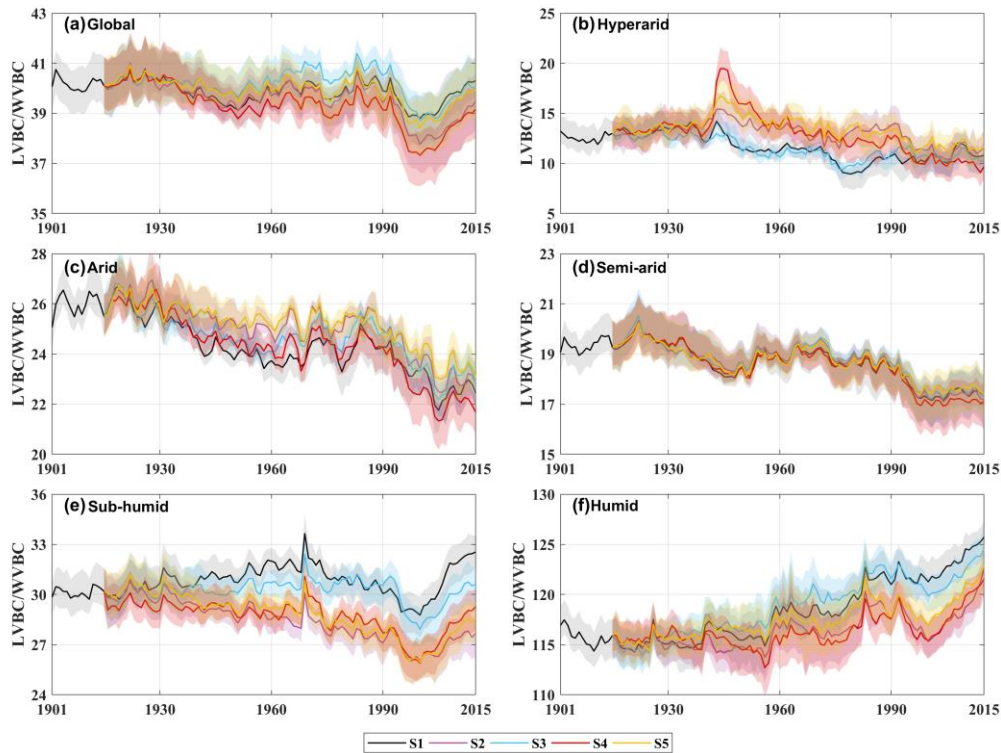


Figure 11. Temporal fluctuations in carbon stock dynamics in vegetation biomass in different factorial simulations. Black indicates historical factorial simulation from 1901-2015, green indicates the CO₂-driven factorial simulation, blue indicates the precipitation-driven factorial simulation, red indicates the temperature-driving factorial simulation and yellow indicates radiation driven factorial simulation. Uncertainty bounds are provided as shaded areas reflect the intra-annual fluctuation (± 1 s.d.) (a) Modelled trend of LVBC/WVBC ratio in Global area. (b-f) Modelled trend of the LVBC/WVBC ratio in different hydrological regions (Figure 1).

518 **4 Discussions and conclusion**

519 To understand the response of carbon storage potential and its inner biomass carbon stocks to
 520 environmental change, we conducted a series of factorial simulations using SEIB-DGVM V3.02. More
 521 importantly, we investigated the extent of the responses of carbon stocks to water limitations.

522

523 Over the past 100 years, there has been an ongoing increase in the carbon storage capacity of the
 524 terrestrial ecosystem from 735 Pg C in 1916 to 855 Pg C in 2015 (Figure 6), which has slowed the rate
 525 at which atmospheric CO₂ has increased and may have mitigated global warming. These findings are

526 consistent with the conclusions of research conducted at the local scale. For example, based on carbon
527 flux data, Erb et al. (2008) suggested that the vegetation carbon stock in Austria increased from 1043 Mt
528 C to 1249 Mt C (aboveground carbon stocks growth was $1.059 \text{ Mt C yr}^{-1}$ and belowground carbon stocks
529 growth was 0.2 Mt C yr^{-1}) since industrialization. Le Noë et al. (2020) showed that increases in the
530 carbon stocks and carbon density were the predominant drivers in the forest terrestrial carbon
531 sequestration capacity in France from 1850 to 2015. Tong et al. (2020) also found a substantial increase
532 of aboveground carbon stocks in southern China ($0.11 \text{ Pg C yr}^{-1}$) during the period 2002–2017. However,
533 these studies focused on zonal trends in total vegetation carbon stocks and did not investigate the extent
534 of the response in vegetation carbon stocks partitioned between light- and water-gathering biomass. Our
535 results show that the increase in carbon stock in light-gathering vegetation organs was much larger than
536 that in water-gathering vegetation organs, and light-gathering biomass carbon stock dominates the
537 historical trend of the terrestrial carbon stock. During the past decades, the global land surface has been
538 greening because of the flux and storage of more carbon into plant trunks and foliage (Zhu et al., 2016).
539 LVBC increases $116.18 \pm 2.34 \text{ Pg C}$ from 1916 to 2015, accounting for 97.42% of the total carbon stock
540 increase ($119.26 \pm 2.44 \text{ Pg C}$). The long-term trends and spatial pattern of vegetation carbon stock
541 predominated the variability characteristic of LVBC. The latitudinal bands of increasing annual change
542 in LVBC are mainly distributed in tropical latitudes, a conclusion consistent with prior knowledge that
543 tropical zones dominate carbon uptake and storage (Erb et al., 2018; Schimel et al., 2015). Biomass
544 carbon allocation between light- and water-gathering vegetation organs reflect the changes in individual
545 growth, community structure and ecosystem function, which are important attributes in the investigation
546 of carbon stocks and carbon cycling within the terrestrial biosphere (Hovenden et al., 2014; Fang et al.,
547 2010; Ma et al., 2021). During the past hundred years, the ratio of LVBC/WVBC showed a slight upward
548 trend since LVBC increased relatively more than WVBC. The rate of increase is 0.0171 yr^{-1} , which is
549 significant at the 0.01 level. To better absorb CO_2 and sunlight required for photosynthesis, vegetated
550 regions are gradually covered by vegetation with higher plant height and wider leaf area, thereby
551 adjusting their characteristic ecosystem functions (Erb et al., 2008).

552

553 Based on our factorial simulations (Figure 8), the influences of CO_2 fertilization induce the most
554 significant variation of the vegetation carbon stock. In addition, the responses of carbon stocks to the

555 changes of climatic factors are obvious, particularly at the grid cell scale. Previous studies have pointed
556 out that the variation of the terrestrial carbon stock caused by releasing or sequestering carbon is sensitive
557 to anomalous changes in water availability and light use efficiency (Madani et al., 2020; Humphrey et
558 al., 2018). At the grid cell scale, as shown in Figures 8b and 8d, temperature, radiation, precipitation, and
559 other climate factors (humidity and wind speed) dominate the long-term trend of carbon stocks over two
560 thirds of global grid cells. At the global scale, climate factors explain 17.55% and 10.72% of long-term
561 trend in LVBC and WVBC, respectively (Figures 8a and 8c). LVBC and WVBC variations driven by
562 climate factors are ultimately offset by spatially compensatory effects, which dampens the response of
563 the carbon stock to these factors at the global scale (Jung et al., 2017). Thus, contributions of precipitation
564 and radiation to the variability of LVBC and WVBC are relatively low at the global scale, and the effects
565 of humidity and wind speed on global carbon stock are minor. This spatially compensatory effect of
566 climate changes is consistent with a previous analysis (Zhu et al. 2016) which found that climate changes
567 explain only 8% of the increasing trend in foliage carbon storage at the global level but that they dominate
568 the trend over 28.4% of global land area. Results show that trends in temperature drive historical long-
569 term trends in the potential carbon stocks, with faster increases and considerable variation occurring by
570 grid cell. Thus, our results reveal that temperature dominates the long-term trends of carbon stock among
571 climatic drivers, while a relatively strong compensatory effect exists in the global change in the carbon
572 stock induced by precipitation, radiation, humidity, and wind speed.

573

574 By partitioning the trends of LVBC and WVBC into five hydrological regions (Figure 1), we found that
575 the long-term change in carbon stocks is tightly coupled to terrestrial water availability. These results
576 indicate that vegetation in humid regions is responsible for most of the trend in global LVBC, while
577 plants in semi-arid regions play a dominate global role in controlling the long-term trend in WVBC
578 (Figures 9 and 10). As water stress decreases, the magnitude and range in variation of LVBC gradually
579 increase (Figure 9), which suggests that limited water availability constrains the response magnitude of
580 the changes in LVBC to changes in CO₂ and climate. The response pattern of WVBC growth to the
581 increasing water availability is different from that of LVBC. Drought mitigation promotes the growth of
582 WVBC. In sub-humid and humid regions, plants face low water limitations and intensified light-
583 competition and have to invest as much non-structural carbon as possible into leaf and trunk. This

584 allocation scheme leads to the decreased investment of Δ WVBC in wet regions. The result is consistent
585 with previous finding that plants reduce investment to roots in dense forests where aboveground
586 competition for light is high (Ma et al. 2021). Moreover, we found that indirect effects of water limitation
587 regulate increasing rate of each carbon pool. Although vegetation carbon stocks dramatically increase
588 under the effects of climate and CO₂ changes, the increasing rate of LVBC faster than WVBC in humid
589 regions. Vegetation stores more biomass in aboveground plant organs (trunk and foliage) to gather light.
590 Dryland plants decrease the LVBC/WVBC ratios and store more biomass below ground to enhance the
591 capture of water resources. Based on these results, we demonstrate that water limitations controlled the
592 variable response of terrestrial vegetation carbon stocks.

593

594 Our findings are consistent with other reports about the impact of increasing water limitations on
595 terrestrial ecosystem. Based on observation from satellite remote sensing, Madani et al. (2020) found
596 that the constraining impact of water limitation determines whether global ecosystem productivity
597 responds positively or negatively to the changes in climate factors. Humphrey et al. (2021) found that
598 increasing water stress limits the response magnitude of carbon uptake rates through a down-regulation
599 of stomatal conductance and suggested that land carbon uptake is driven by temperature and vapour
600 pressure deficit effects that are controlled by terrestrial water availability. Ma et al. (2021) found that
601 plants increase investment into building roots in arid region because the extent of water limitation there
602 is exacerbated by global warming. Terrestrial hydrological conditions significantly affect the carbon
603 cycle of terrestrial ecosystems, including carbon uptake, allocation, and stock. Terrestrial ecosystems
604 utilize sensitive strategies to allocate and store biomass to adjust to local hydrological conditions. A
605 significant conclusion is that water constraints not only confine the responses of vegetation carbon stocks
606 to drivers, but also constrain the proportion of biomass carbon stocks in gather- and water-gathering
607 fractions.

608

609 Distinguishing the response of carbon stock fractions estimated by SEIB-DGVM improves the
610 understanding of the interactive impacts of terrestrial carbon and water dynamics. However, uncertainty
611 still exists because of the limitations in the processes of modelling vegetation metabolism with SEIB-
612 DGVM. Trunk biomass contains tree branches and structural roots (coarse roots and tap roots) (Sato et

613 al., 2007), so the R/S ratio of potential vegetation in factorial simulations is smaller than the R/S of actual
614 vegetation in observation stations. Root biomass only contains the fine root biomass, leading to an
615 apparent underestimate in belowground organ biomass of trees and grasses compare with previous
616 conclusion (Ma et al., 2021; Yang et al., 2009). Availability of nitrogen is a key limiting factor for
617 vegetation growth, especially when higher CO₂ fertilization effects exist (Tharammal et al., 2019). The
618 limitation could be alleviated by nitrogen deposition in most temperate and boreal ecosystems. The
619 SEIB-DGVM experiments were conducted with a focus on documenting CO₂ fertilization and climate
620 change interactions; these experiments did not consider the influences of nitrogen deposition, which
621 should cause an underestimate of the contributions of CO₂ fertilization on biomass production.

622

623 In summary, we evaluated SEIB-DGVM V3.02 and used this model to offer new perspectives on the
624 response of vegetation carbon storage potential to changes in climate and CO₂. Our simulation results
625 show that changes in CO₂, rather than climate, dominate the light- and water-gathering partitioning of
626 the carbon storage potential. More importantly, we suggest that the impact of CO₂ fertilization and
627 temperature effects on vegetation carbon-sequestration potential depends on water availability and its
628 impacts on plant stress. With increased global warming, water limitations are expected to increasingly
629 confine global carbon sequestration and storage. Our findings highlight the need to account for terrestrial
630 water limitation effects when estimating the response of the terrestrial carbon storage capacity to global
631 climate change, and the need for stronger interactions between those involved in vegetation model
632 development and those in between the hydrological and ecological research communities.

634 **Table A1. MCD12C1 legend and class descriptions**

| Name | Value | Description |
|-------------------------------------|-------|--|
| Evergreen Needleleaf Forests | 1 | Dominated by evergreen conifer trees (canopy >2m). Tree cover >60%. |
| Evergreen Broadleaf Forests | 2 | Dominated by evergreen broadleaf and palmate trees (canopy >2m). Tree cover >60%. |
| Deciduous Needleleaf Forests | 3 | Dominated by deciduous needleleaf (larch) trees (canopy >2m). Tree cover >60%. |
| Deciduous Broadleaf Forests | 4 | Dominated by deciduous broadleaf trees (canopy >2m). Tree cover >60%. |
| Mixed Forests | 5 | Dominated by neither deciduous nor evergreen (40-60% of each) tree type (canopy >2m). Tree cover >60%. |
| Closed Shrublands | 6 | Dominated by woody perennials (1-2m height) >60% cover. |
| Open Shrublands | 7 | Dominated by woody perennials (1-2m height) 10-60% cover. |
| Woody Savannas | 8 | Tree cover 30-60% (canopy >2m). |
| Savannas | 9 | Tree cover 10-30% (canopy >2m). |
| Grasslands | 10 | Dominated by herbaceous annuals (<2m). |
| Permanent Wetlands | 11 | Permanently inundated lands with 30-60% water cover and >10% vegetated cover. |
| Croplands | 12 | At least 60% of area is cultivated cropland. |
| Urban and Built-up Lands | 13 | At least 30% impervious surface area including building materials, asphalt, and vehicles. |
| Cropland/Natural Vegetation Mosaics | 14 | Mosaics of small-scale cultivation 40-60% with natural tree, shrub, or herbaceous vegetation. |
| Permanent Snow and Ice | 15 | At least 60% of area is covered by snow and ice for at least 10 months of the year. |
| Barren | 16 | At least 60% of area is non-vegetated barren (sand, rock, soil) areas with less than 10% vegetation. |
| Water Bodies | 17 | At least 60% of area is covered by permanent water bodies. |
| Unclassified | 255 | Has not received a map label because of missing inputs |

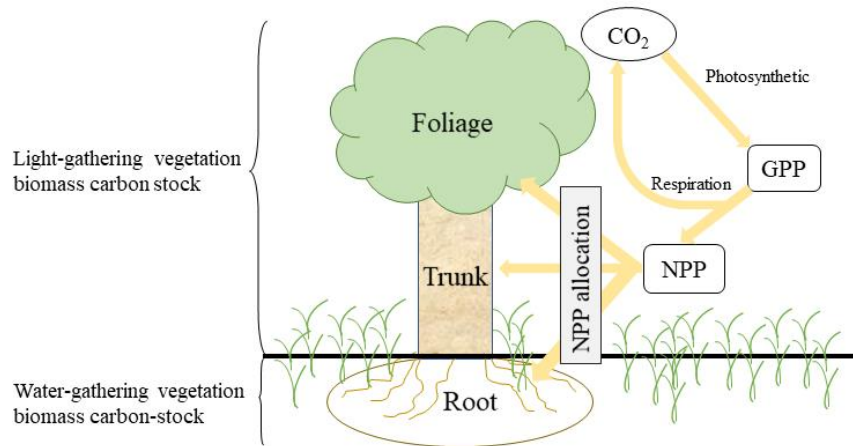


Figure A1. Schematic of ecosystem carbon cycle. Yellow arrow indicates carbon flux. Atmospheric CO₂ transitions into gross primary production (GPP) by photosynthesis. GPP is partitioned into respiration and net primary production (NPP). NPP is partitioned into three biomass carbon pools (foliage, trunk, and root).

636

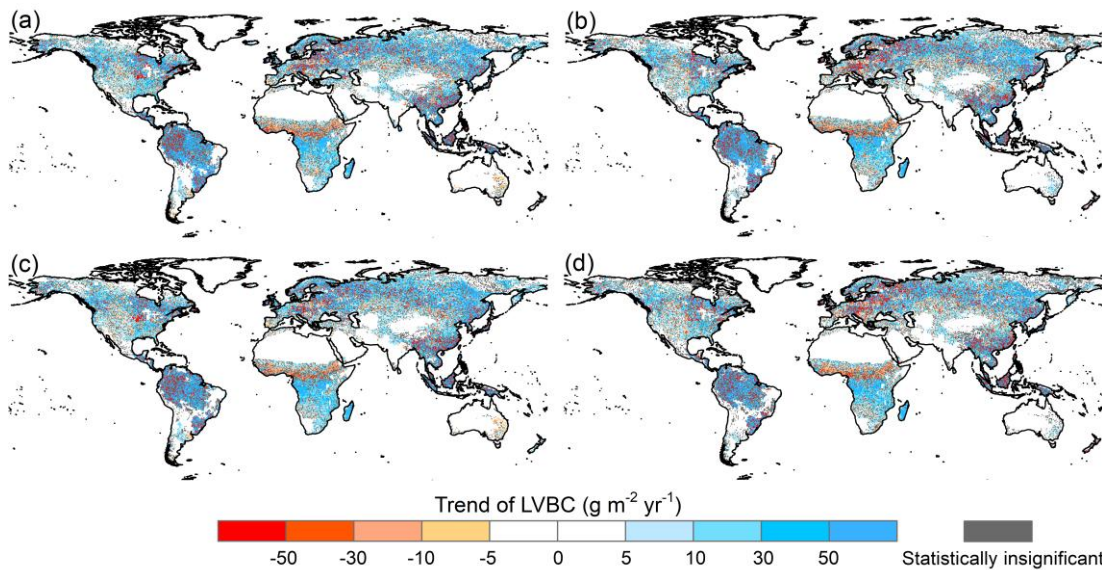


Figure A2. Potential LVBC trend maps during the period of 1916 to 2015 under different factorial simulations. (a) CO₂ driving factorial simulation (S2); (b) CO₂+precipitation driving factorial simulation (S3); (c) CO₂+temperature driving factorial simulation (S4); and (d) CO₂+radiation driving factorial simulation (S5). Positive values indicate increasing trends in the ratio, and vice versa. All results from Mann-Kendall and Sen's slope statistical tests correspond to the 95% confidence interval.

637

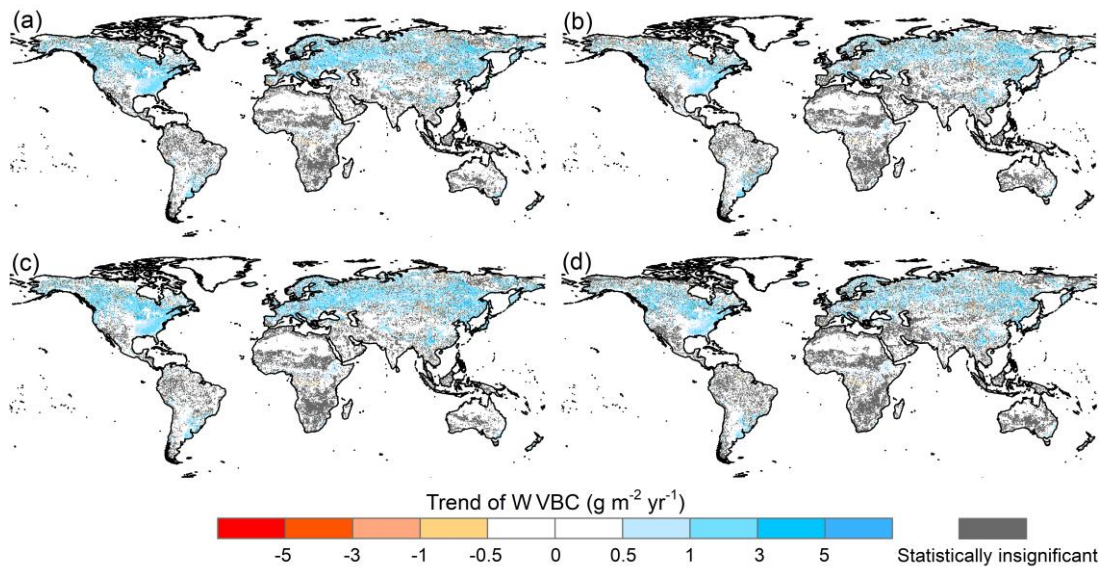


Figure A3. Potential WVC variation trend maps during the period of 1916 to 2015 under different factorial simulations. (a) CO_2 driving factorial simulation (S2); (b) CO_2 +precipitation driving factorial simulation (S3); (c) CO_2 +temperature driving factorial simulation (S4); and (d) CO_2 +radiation driving factorial simulation (S5). Positive values indicate increasing trends in the ratio, and vice versa. All results from Mann-Kendall and Sen's slope statistical tests correspond to the 95% confidence interval.

638

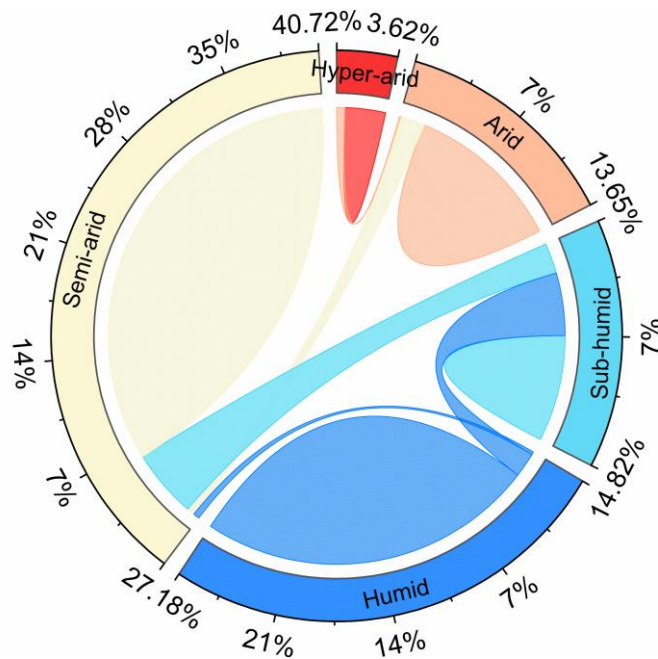


Figure A4. The shift of hydrological regions defined by the multiyear average AI index from the period of 1916-1945 to the period of 1986-2015. The outermost number represent the percentage of hydrological regions in 1916-1945.

639

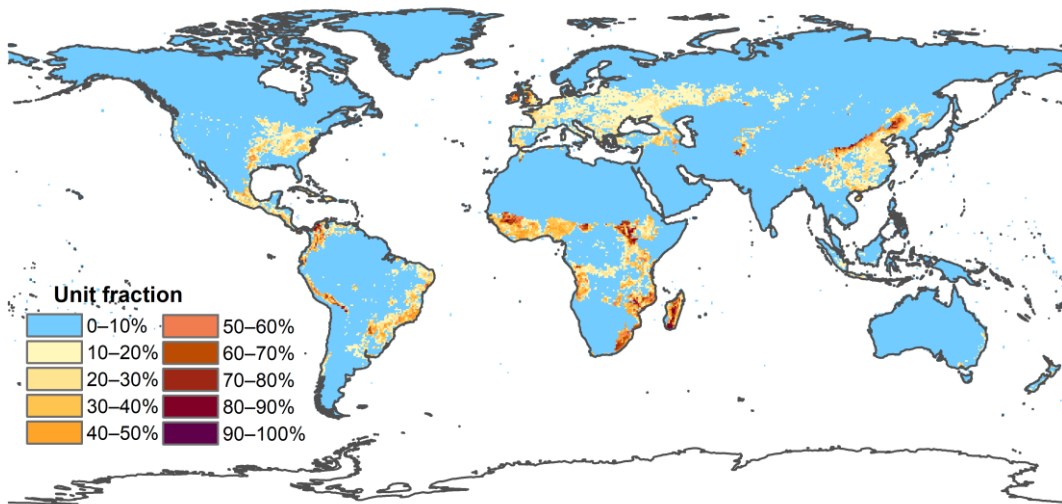


Figure A5. Spatial distribution of multi-year average fraction of managed pasture from 2001-2015 at 0.5×0.5 arc-degree resolution.

640

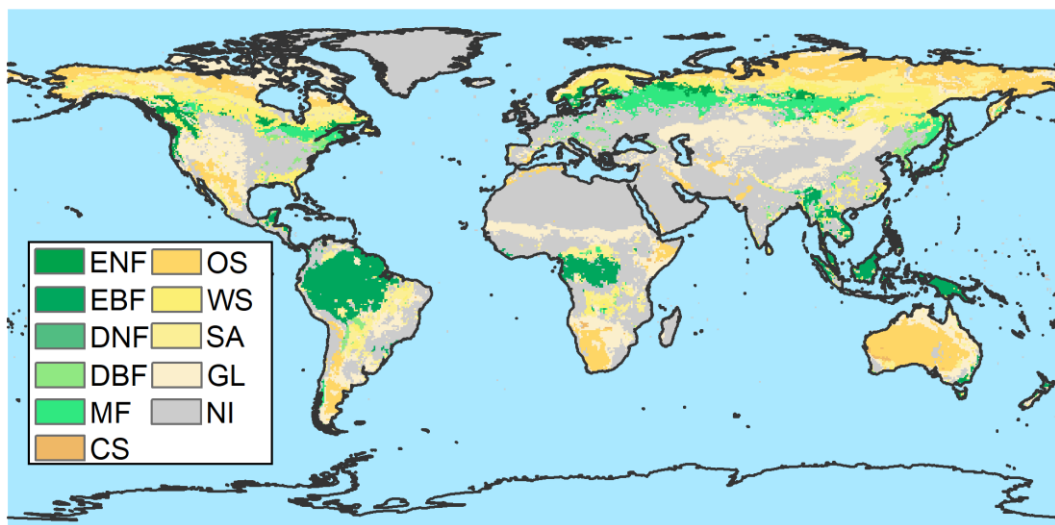


Figure A6. Map showing the largest vegetation component of each grid cell without anthropogenic disturbance from MCD12C1 and LUH2. ENF: Evergreen needleleaf forest, EBF: Evergreen broadleaf forest, DNF: Deciduous needleleaf forest, DBF: Deciduous broadleaf forest, MF: Mixed forest, CS: Closed shrublands, OS: Open shrublands, WS: Woody savannas, SA: Savannas, GL: Grasslands, NI: Not included, which means the zone is not covered by vegetation without anthropogenic disturbance.

641

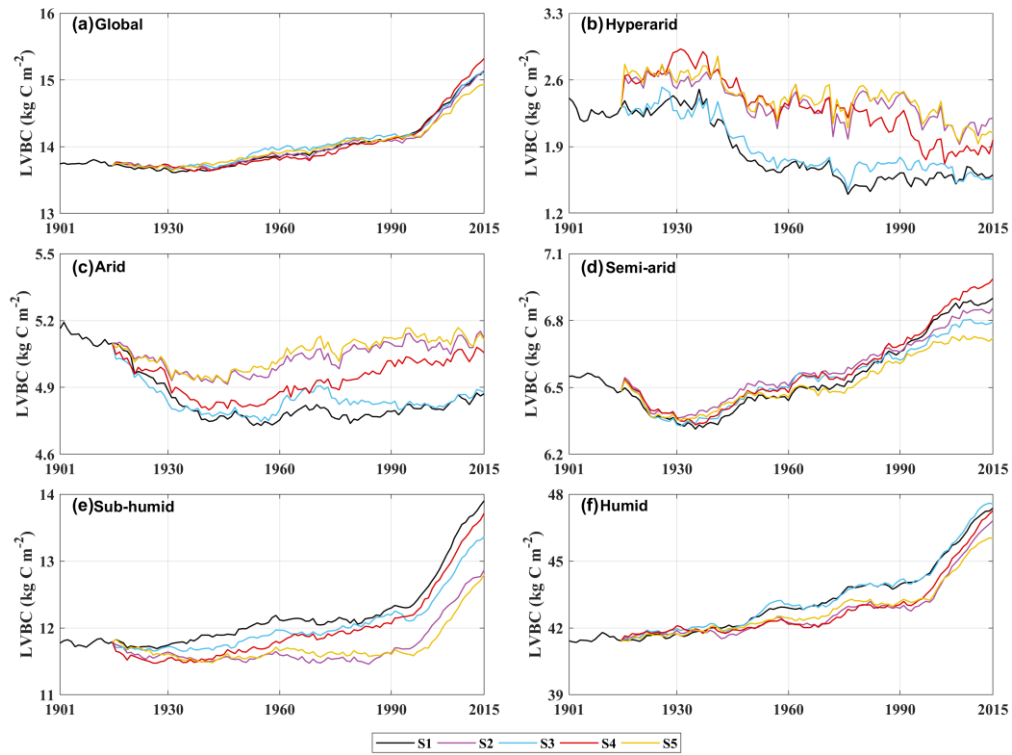


Figure A7. Trends in average density of potential LVBC. (a) Modelled trend of annual averaged LVBC globally. Modelled trends in annual averaged LVBC in hyper-arid region (b), arid region (c), semi-arid region (d), sub-humid region (e), and humid region (f).

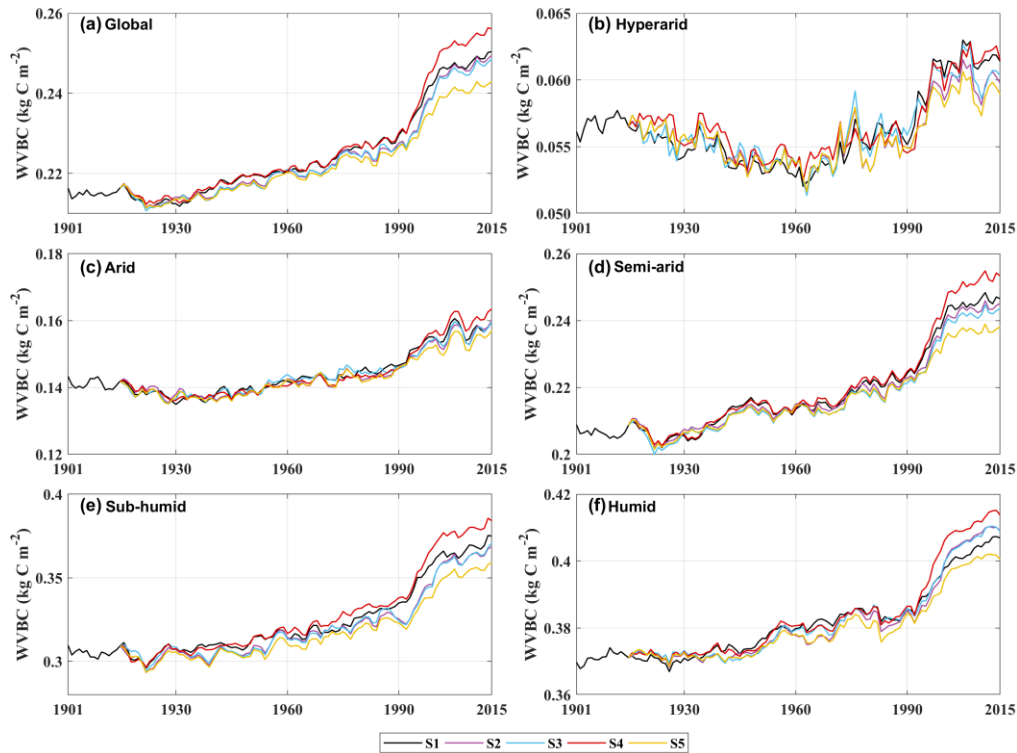


Figure A8. Trends in average density of potential WVBC. (a) Modelled trend of annual averaged WVBC globally. Modelled trends in annual averaged WVBC in hyper-arid region (b), arid region (c), semi-arid region (d), sub-humid region (e), and humid region (f).

643 **Code and data availability statement**

644 The code of SEIB-DGVM version 3.02 can be download from <http://seib-dgvm.com/>. Climatic Research
 645 Unit data can be downloaded from <https://crudata.uea.ac.uk/cru/data/hrg/>. The soil physical parameters
 646 can be downloaded from www.iges.org/gswp. The reconstructed CO₂ concentration dataset and SEIB
 647 code can be downloaded from <http://seib-dgvm.com/>. In model validation, Ecosystem Model-Data
 648 Intercomparison (multiyear average NPP product) data were collected from
 649 https://daac.ornl.gov/NPP/guides/NPP_EMDI.html. Remote sensing product MOD17A3 data were
 650 obtained from <https://lpdaac.usgs.gov/products/mod17a3hgf006/>, MCD12C1 data were obtained from
 651 <https://ladsweb.modaps.eosdis.nasa.gov/search/order>, and LUH2 data were obtained from
 652 <https://luh.umd.edu/>.

653 **Authors contributions**

654 T.S. designed research. T.S., and S.H. performed research and developed the methodology. T.S. analyzed
655 data and produced the outputs. T.S., S.H., C.J., and X.C. wrote the first manuscript draft. W.W. and W.G.
656 supervised the study. All the authors discussed the methodology and commented on various versions of
657 the manuscript.

658 **Competing interests**

659 The authors declare that they have no conflict of interest.

660 **Acknowledgments**

661 This work was jointly supported by the National Natural Science Foundation of China (Grant Nos.
662 51979071, 51779073, 91547205, U2240218), the National Key Research and Development Program of
663 China (2018YFA0605402, 2021YFC3201100), the Distinguished Young Fund Project of Natural
664 Science Foundation of Jiangsu Province (BK20180021), the QingLan Project of Jiangsu Province, the
665 National “Ten Thousand Program” Youth Talent, and the “333 project” of Jiangsu Province. We thank
666 Zefeng Chen for technical support. We gratefully thank the following data providers and model
667 developers for their continuous efforts and for sharing their data: the University of East Anglia, the
668 National Centers for Environmental Prediction (NCEP), the National Oceanic and Atmospheric
669 Administration (NOAA), University of Maryland, and the Center for Ocean-Land-Atmosphere Studies
670 (COLA). Cordial thanks are extended to the editor, Dr. Hans Verbeeck, and two anonymous referees for
671 the valuable comments which greatly improve the quality of the paper.

672 **References**

- 673 Ahlstrom, A., Raupach, M. R., Schurgers, G., Smith, B., Arneeth, A., Jung, M., Reichstein, M., Canadell,
674 J. G., Friedlingstein, P., Jain, A. K., Kato, E., Poulter, B., Sitch, S., Stocker, B. D., Viovy, N., Wang,
675 Y. P., Wiltshire, A., Zaehle, S., and Zeng, N.: The dominant role of semi-arid ecosystems in the
676 trend and variability of the land CO₂ sink, *Science*, 348, 895-899, 10.1126/science.aaa1668, 2015.
- 677 Ajtay, G. L., Ketner, P., and Duvigneaud, P.: Terrestrial primary production and phytomass In: *The*
678 *Global Cycle.*, Glob. Carbon Cycle, SCOPE, 129-181 pp.1979.
- 679 Bartholome, E. and Belward, A. S.: GLC2000: a new approach to global land cover mapping from Earth
680 observation data, *Int J Remote Sens*, 26, 1959-1977, 10.1080/01431160412331291297, 2005.
- 681 Bayer, A. D., Pugh, T. A. M., Krause, A., and Arneeth, A.: Historical and future quantification of
682 terrestrial carbon sequestration from a Greenhouse-Gas-Value perspective, *Global Environmental*
683 *Change*, 32, 153-164, 10.1016/j.gloenvcha.2015.03.004, 2015.
- 684 Bazilevich, N. I., Rodin, L. Y., and Rozov, N. N.: Geographical Aspects of Biological Productivity,
685 *Soviet Geograpy Review and Translation*, 5, 293-317 pp.1971.
- 686 Bloom, A. A., Exbrayat, J. F., van der Velde, I. R., Feng, L., and Williams, M.: The decadal state of the
687 terrestrial carbon cycle: Global retrievals of terrestrial carbon allocation, pools, and residence times,
688 *Proceedings of the National Academy of Sciences of the United States of America*, 113, 1285-1290,
689 10.1073/pnas.1515160113, 2016.
- 690 Chen, J., Ju, W., Ciais, P., Viovy, N., Liu, R. G., Liu, Y., and Lu, X. H.: Vegetation structural change
691 since 1981 significantly enhanced the terrestrial carbon sink, *Nat Commun*, 10, 4259,
692 10.1038/S41467-019-12257-8, 2019.
- 693 Chen, L.-P., Zhao, N.-X., Zhang, L.-H., and Gao, Y.-B.: Responses of two dominant plant species to
694 drought stress and defoliation in the Inner Mongolia Steppe of China, *Plant Ecology*, 214, 221-229,
695 10.1007/s11258-012-0161-y, 2013.
- 696 Cheng, L., Zhang, L., Wang, Y. P., Canadell, J. G., Chiew, F. H. S., Beringer, J., Li, L. H., Miralles, D.
697 G., Piao, S. L., and Zhang, Y. Q.: Recent increases in terrestrial carbon uptake at little cost to the
698 water cycle, *Nat Commun*, 8, 10.1038/s41467-017-00114-5, 2017.
- 699 Erb, K.-H., Gingrich, S., Krausmann, F., and Haberl, H.: Industrialization, Fossil Fuels, and the
700 Transformation of Land Use, *Journal of Industrial Ecology*, 12, 686-703, 10.1111/j.1530-
701 9290.2008.00076.x, 2008.
- 702 Erb, K.-H., Gaube, V., Krausmann, F., Plutzar, C., Bondeau, A., and Haberl, H.: A comprehensive global
703 5min resolution land-use data set for the year 2000 consistent with national census data, *Journal of*
704 *Land Use Science*, 2, 191-224, 10.1080/17474230701622981, 2007.
- 705 Erb, K.-H., Fetzel, T., Plutzar, C., Kastner, T., Lauk, C., Mayer, A., Niedertscheider, M., Körner, C., and
706 Haberl, H.: Biomass turnover time in terrestrial ecosystems halved by land use, *Nat Geosci*, 9, 674-
707 678, 10.1038/ngeo2782, 2016.
- 708 Erb, K.-H., Kastner, T., Plutzar, C., Bais, A. L. S., Carvalhais, N., Fetzel, T., Gingrich, S., Haberl, H.,
709 Lauk, C., Niedertscheider, M., Pongratz, J., Thurner, M., and Luyssaert, S.: Unexpectedly large
710 impact of forest management and grazing on global vegetation biomass, *Nature*, 553, 73-76,
711 10.1038/nature25138, 2018.
- 712 Fan, L., Wigneron, J. P., Ciais, P., Chave, J., Brandt, M., Fensholt, R., Saatchi, S. S., Bastos, A., Al-
713 Yaari, A., Hufkens, K., Qin, Y. W., Xiao, X. M., Chen, C., Myneni, R. B., Fernandez-Moran, R.,
714 Mialon, A., Rodriguez-Fernandez, N. J., Kerr, Y., Tian, F., and Penuelas, J.: Satellite-observed

715 pantropical carbon dynamics, *Nat Plants*, 5, 944-951, 10.1038/s41477-019-0478-9, 2019.

716 Fang, J., Yang, Y., Ma, W., Mohammat, A., and Shen, H.: Ecosystem carbon stocks and their changes
717 in China's grasslands, *Science China. Life sciences*, 53, 757-765, 10.1007/s11427-010-4029-x, 2010.

718 Friedlingstein, P., Joel, G., Field, C. B., and Fung, I. Y.: Toward an allocation scheme for global
719 terrestrial carbon models, *Global Change Biol*, 5, 755-770, DOI 10.1046/j.1365-2486.1999.00269.x,
720 1999.

721 Gentine, P., Green, J. K., Guérin, M., Humphrey, V., Seneviratne, S. I., Zhang, Y., and Zhou, S.:
722 Coupling between the terrestrial carbon and water cycles—a review, *Environ Res Lett*, 14, 083003,
723 10.1088/1748-9326/ab22d6, 2019.

724 Gill, R. and Jackson, R.: Global patterns of root turnover for terrestrial ecosystems, *New Phytol*, 147,
725 13-31, 10.1046/j.1469-8137.2000.00681.x, 2000.

726 Gocic, M. and Trajkovic, S.: Analysis of changes in meteorological variables using Mann-Kendall and
727 Sen's slope estimator statistical tests in Serbia, *Global and Planetary Change*, 100, 172-182,
728 10.1016/j.gloplacha.2012.10.014, 2013.

729 Gulbeyaz, O., Bond-Lamberty, B., Akyurek, Z., and West, T. O.: A new approach to evaluate the MODIS
730 annual NPP product (MOD17A3) using forest field data from Turkey, *Int J Remote Sens*, 39, 2560-
731 2578, 10.1080/01431161.2018.1430913, 2018.

732 Haberl, H., Erb, K. H., and Krausmann, F.: Human Appropriation of Net Primary Production: Patterns,
733 Trends, and Planetary Boundaries, *Annu Rev Env Resour*, 39, 363-391, 10.1146/annurev-environ-
734 121912-094620, 2014.

735 Harper, A. B., Wiltshire, A. J., Cox, P. M., Friedlingstein, P., Jones, C. D., Mercado, L. M., Sitch, S.,
736 Williams, K., and Duran-Rojas, C.: Vegetation distribution and terrestrial carbon cycle in a carbon
737 cycle configuration of JULES4.6 with new plant functional types, *Geosci Model Dev*, 11, 2857-
738 2873, 10.5194/gmd-11-2857-2018, 2018.

739 Harris, I., Osborn, T. J., Jones, P., and Lister, D.: Version 4 of the CRU TS monthly high-resolution
740 gridded multivariate climate dataset, *Scientific Data*, 7, 109, 10.1038/s41597-020-0453-3, 2020.

741 Hovenden, M. J., Newton, P. C., and Wills, K. E.: Seasonal not annual rainfall determines grassland
742 biomass response to carbon dioxide, *Nature*, 511, 583-586, 10.1038/nature13281, 2014.

743 Humphrey, V., Zscheischler, J., Ciais, P., Gudmundsson, L., Sitch, S., and Seneviratne, S. I.: Sensitivity
744 of atmospheric CO₂ growth rate to observed changes in terrestrial water storage, *Nature*, 560, 628-
745 631, 10.1038/s41586-018-0424-4, 2018.

746 Humphrey, V., Berg, A., Ciais, P., Gentine, P., Jung, M., Reichstein, M., Seneviratne, S. I., and
747 Frankenberg, C.: Soil moisture–atmosphere feedback dominates land carbon uptake variability,
748 *Nature*, 592, 65-69, 10.1038/s41586-021-03325-5, 2021.

749 Hurtt, G. C., Chini, L. P., Frolking, S., Betts, R. A., Feddema, J., Fischer, G., Fisk, J. P., Hibbard, K.,
750 Houghton, R. A., Janetos, A., Jones, C. D., Kindermann, G., Kinoshita, T., Goldewijk, K. K., Riahi,
751 K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., van Vuuren, D. P., and
752 Wang, Y. P.: Harmonization of land-use scenarios for the period 1500-2100: 600 years of global
753 gridded annual land-use transitions, wood harvest, and resulting secondary lands, *Climate Change*,
754 109, 117-161, 10.1007/s10584-011-0153-2, 2011.

755 Hurtt, G. C., Chini, L., Sahajpal, R., Frolking, S., Bodirsky, B. L., Calvin, K., Doelman, J. C., Fisk, J.,
756 Fujimori, S., Goldewijk, K. K., Hasegawa, T., Havlik, P., Heinemann, A., Humpenöder, F.,
757 Jungclaus, J., Jed Kaplan, Kennedy, J., Kristzin, T., Lawrence, D., Lawrence, P., Ma, L., Mertz, O.,
758 Pongratz, J., Popp, A., Poulter, B., Riahi, K., Shevliakova, E., Stehfest, E., Thornton, P., Tubiello,

759 F. N., van Vuuren, D. P., Zhang, X.: Harmonization of Global Land-Use Change and Management
760 for the Period 850-2100 (LUH2) for CMIP6, Geoscientific Model Development, 13, 5425-5464,
761 10.5194/gmd-13-5425-2020, 2021.

762 IPCC: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth
763 Assessment Report of the Intergovernmental Panel on Climate Change, 2007.

764 Jung, M., Reichstein, M., Schwalm, C. R., Huntingford, C., Sitch, S., Ahlstrom, A., Arneth, A., Camps-
765 Valls, G., Ciais, P., Friedlingstein, P., Gans, F., Ichii, K., Jain, A. K., Kato, E., Papale, D., Poulter,
766 B., Raduly, B., Rodenbeck, C., Tramontana, G., Viovy, N., Wang, Y. P., Weber, U., Zaehle, S., and
767 Zeng, N.: Compensatory water effects link yearly global land CO₂ sink changes to temperature,
768 *Nature*, 541, 516-520, 10.1038/nature20780, 2017.

769 Kaplan, J. O., Krumhardt, K. M., Ellis, E. C., Ruddiman, W. F., Lemmen, C., and Goldewijk, K. K.:
770 Holocene carbon emissions as a result of anthropogenic land cover change, *Holocene*, 21, 775-791,
771 10.1177/0959683610386983, 2011.

772 Keenan, T. F., Prentice, I. C., Canadell, J. G., Williams, C. A., Wang, H., Raupach, M., and Collatz, G.
773 J.: Recent pause in the growth rate of atmospheric CO₂ due to enhanced terrestrial carbon uptake
774 *Nat Commun*, 7, 10.1038/Ncomms16137, 2017.

775 Kindermann, G. E., Mcallum, I., Fritz, S., and Obersteiner, M.: A global forest growing stock, biomass
776 and carbon map based on FAO statistics, *Silva Fenn*, 42, 387-396, 10.14214/Sf.244, 2008.

777 Le Noë, J., Matej, S., Magerl, A., Bhan, M., Erb, K. H., and Gingrich, S.: Modeling and empirical
778 validation of long-term carbon sequestration in forests (France, 1850-2015), *Glob Chang Biol*, 26,
779 2421-2434, 10.1111/gcb.15004, 2020.

780 Liu, J., Bowman, K. W., Schimel, D. S., Parazoo, N. C., Jiang, Z., Lee, M., Bloom, A. A., Wunch, D.,
781 Frankenberg, C., Sun, Y., O'Dell, C. W., Gurney, K. R., Menemenlis, D., Gierach, M., Crisp, D.,
782 and Eldering, A.: Contrasting carbon cycle responses of the tropical continents to the 2015-2016 El
783 Nino, *Science*, 358, eaam5690, 10.1126/science.aam5690, 2017.

784 Ma, H. Z., Mo, L. D., Crowther, T. W., Maynard, D. S., van den Hoogen, J., Stocker, B. D., Terrer, C.,
785 and Zohner, C. M.: The global distribution and environmental drivers of aboveground versus
786 belowground plant biomass, *Nat Ecol Evol*, 5, 1110+, 10.1038/s41559-021-01485-1, 2021.

787 Madani, N., Parazoo, N. C., Kimball, J. S., Ballantyne, A. P., Reichle, R. H., Maneta, M., Saatchi, S.,
788 Palmer, P. I., Liu, Z., and Tagesson, T.: Recent Amplified Global Gross Primary Productivity Due
789 to Temperature Increase Is Offset by Reduced Productivity Due to Water Constraints, *AGU*
790 *Advances*, 2, e2020AV000180, 10.1029/2020AV000180, 2020.

791 Magerl, A., Le Noë, J., Erb, K.-H., Bhan, M., and Gingrich, S.: A comprehensive data-based assessment
792 of forest ecosystem carbon stocks in the U.S. 1907–2012, *Environ Res Lett*, 14, 125015,
793 10.1088/1748-9326/ab5cb6, 2019.

794 McConnaughay, K. D. M. and Coleman, J. S.: Biomass allocation in plants: ontogeny or optimality? A
795 test along three resource gradients, *Ecology*, 80, 2581-2593, 10.1890/0012-
796 9658(1999)080[2581:BAIPOO]2.0.CO;2, 1999.

797 Monteith, J. L. and Unsworth, M. H.: *Principles of Environmental Physics*, 2nd ed., London 1990.

798 Olson, J., Watts, J., and Allison, L.: *Carbon in Live Vegetation of Major World Ecosystems*, Oak Ridge
799 National Laboratory 1983.

800 Pan, Y. D., Birdsey, R. A., Phillips, O. L., and Jackson, R. B.: The Structure, Distribution, and Biomass
801 of the World's Forests, *Annu Rev Ecol Evol S*, 44, 593-622, 10.1146/annurev-ecolsys-110512-
802 135914, 2013.

803 Pan, Y. D., Birdsey, R. A., Fang, J. Y., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L.,
804 Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A.
805 D., Piao, S. L., Rautiainen, A., Sitch, S., and Hayes, D.: A Large and Persistent Carbon Sink in the
806 World's Forests, *Science*, 333, 988-993, 10.1126/science.1201609, 2011.

807 Piao, S. L., Friedlingstein, P., Ciais, P., Zhou, L. M., and Chen, A. P.: Effect of climate and CO₂ changes
808 on the greening of the Northern Hemisphere over the past two decades, *Geophys Res Lett*, 33,
809 L23402, 10.1029/2006GL028205, 2006.

810 Piao, S. L., Wang, X., Wang, K., Li, X., Bastos, A., Canadell, J. G., Ciais, P., Friedlingstein, P., and
811 Sitch, S.: Interannual variation of terrestrial carbon cycle: Issues and perspectives, *Glob Chang Biol*,
812 26, 300-318, 10.1111/gcb.14884, 2020.

813 Poorter, H.: Construction costs and payback time of biomass: a whole plant perspective, *A Whole-Plant*
814 *Perspective on Carbon-Nitrogen Interactions*, SPB Academic Publishing, The Hague 1994.

815 Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., Chevallier,
816 F., Liu, Y. Y., Running, S. W., Sitch, S., and van der Werf, G. R.: Contribution of semi-arid
817 ecosystems to interannual variability of the global carbon cycle, *Nature*, 509, 600-603,
818 10.1038/nature13376, 2014.

819 Prentice, I. C., Harrison, S. P., and Bartlein, P. J.: Global vegetation and terrestrial carbon cycle changes
820 after the last ice age, *New Phytol*, 189, 988-998, 10.1111/j.1469-8137.2010.03620.x, 2011.

821 Roy, J., Saugier, B., and Mooney, H. A.: Estimations of global terrestrial productivity: converging toward
822 a single number? In: *Terrestrial Global Productivity*, Academic Press, San Diego 2001.

823 Ruesch, A. and Gibbs, H. K.: New IPCC Tier-1 global biomass carbon map for the year 2000, 2008.

824 Ryan, M. G.: Effects of Climate Change on Plant Respiration, *Ecological Applications*, 1, 157-167,
825 10.2307/1941808, 1991.

826 Sato, H., Itoh, A., and Kohyama, T.: SEIB-DGVM: A new Dynamic Global Vegetation Model using a
827 spatially explicit individual-based approach, *Ecological Modelling*, 200, 279-307,
828 10.1016/j.ecolmodel.2006.09.006, 2007.

829 Sato, H., Kobayashi, H., Beer, C., and Fedorov, A.: Simulating interactions between topography,
830 permafrost, and vegetation in Siberian larch forest, *Environ Res Lett*, 15, 095006, 10.1088/1748-
831 9326/Ab9be4, 2020.

832 Saugier, B., Roy, J., and Mooney, H.: Estimations of Global Terrestrial Productivity, *Terrestrial Global*
833 *Productivity*, Academic Press, San Diego, Calif 2001.

834 Schimel, D., Stephens, B. B., and Fisher, J. B.: Effect of increasing CO₂ on the terrestrial carbon cycle,
835 *Proceedings of the National Academy of Sciences of the United States of America*, 112, 436-441,
836 10.1073/pnas.1407302112, 2015.

837 Seo, H. and Kim, Y.: Interactive impacts of fire and vegetation dynamics on global carbon and water
838 budget using Community Land Model version 4.5, *Geosci Model Dev*, 12, 457-472, 10.5194/gmd-
839 12-457-2019, 2019.

840 Shevliakova, E., Pacala, S. W., Malyshev, S., Hurtt, G. C., Milly, P. C. D., Caspersen, J. P., Sentman, L.
841 T., Fisk, J. P., Wirth, C., and Crevoisier, C.: Carbon cycling under 300 years of land use change:
842 Importance of the secondary vegetation sink, *Global Biogeochem Cy*, 23, 10.1029/2007gb003176,
843 2009.

844 Sun, F., Roderick, M. L., and Farquhar, G. D.: Changes in the variability of global land precipitation,
845 *Geophys Res Lett*, 39, L19402, 10.1029/2012gl053369, 2012.

846 Tei, S., Sugimoto, A., Liang, M. C., Yonenobu, H., Matsuura, Y., Osawa, A., Sato, H., Fujinuma, J., and

847 Maximov, T.: Radial Growth and Physiological Response of Coniferous Trees to Arctic
848 Amplification, *J Geophys Res-Bioge*, 122, 2786-2803, 10.1002/2016JG003745, 2017.

849 Terrer, C., Phillips, R. P., Hungate, B. A., Rosende, J., Pett-Ridge, J., Craig, M. E., van Groenigen, K. J.,
850 Keenan, T. F., Sulman, B. N., Stocker, B. D., Reich, P. B., Pellegrini, A. F. A., Pendall, E., Zhang,
851 H., Evans, R. D., Carrillo, Y., Fisher, J. B., Van Sundert, K., Vicca, S., and Jackson, R. B.: A trade-
852 off between plant and soil carbon storage under elevated CO₂, *Nature*, 591, 599-603,
853 10.1038/s41586-021-03306-8, 2021.

854 Tharammal, T., Bala, G., Devaraju, N., and Nemani, R.: A review of the major drivers of the terrestrial
855 carbon uptake: model-based assessments, consensus, and uncertainties, *Environ Res Lett*, 14,
856 093005, 10.1088/1748-9326/Ab3012, 2019.

857 Tong, X. W., Brandt, M., Yue, Y. M., Ciais, P., Jepsen, M. R., Penuelas, J., Wigner, J. P., Xiao, X.
858 M., Song, X. P., Horion, S., Rasmussen, K., Saatchi, S., Fan, L., Wang, K. L., Zhang, B., Chen, Z.
859 C., Wang, Y. H., Li, X. J., and Fensholt, R.: Forest management in southern China generates short
860 term extensive carbon sequestration, *Nat Commun*, 11, 10.1038/s41467-019-13798-8, 2020.

861 West, P. C., Gibbs, H. K., Monfreda, C., Wagner, J., Barford, C. C., Carpenter, S. R., and Foley, J. A.:
862 Trading carbon for food: Global comparison of carbon stocks vs. crop yields on agricultural land,
863 *Proceedings of the National Academy of Sciences of the United States of America*, 107, 19645-
864 19648, 10.1073/pnas.1011078107, 2010.

865 Wild, M., Gilgen, H., Roesch, A., Ohmura, A., Long, C. N., Dutton, E. G., Forgan, B., Kallis, A., Russak,
866 V., and Tsvetkov, A.: From dimming to brightening: Decadal changes in solar radiation at Earth's
867 surface, *Science*, 308, 847-850, 10.1126/science.1103215, 2005.

868 Yang, Y., Fang, J., Ma, W., Guo, D., and Mohammat, A.: Large-scale pattern of biomass partitioning
869 across China's grasslands, *Global Ecology and Biogeography*, 19, 268-277, 10.1111/j.1466-
870 8238.2009.00502.x, 2010.

871 Zhang, H., Song, T. Q., Wang, K. L., Yang, H., Yue, Y. M., Zeng, Z. X., Peng, W. X., and Zeng, F. P.:
872 Influences of stand characteristics and environmental factors on forest biomass and root-shoot
873 allocation in southwest China, *Ecol Eng*, 91, 7-15, 10.1016/j.ecoleng.2016.01.040, 2016.

874 Zhu, Z. C., Piao, S. L., Myneni, R. B., Huang, M. T., Zeng, Z. Z., Canadell, J. G., Ciais, P., Sitch, S.,
875 Friedlingstein, P., Arneeth, A., Cao, C. X., Cheng, L., Kato, E., Koven, C., Li, Y., Lian, X., Liu, Y.
876 W., Liu, R. G., Mao, J. F., Pan, Y. Z., Peng, S. S., Penuelas, J., Poulter, B., Pugh, T. A. M., Stocker,
877 B. D., Viogy, N., Wang, X. H., Wang, Y. P., Xiao, Z. Q., Yang, H., Zaehle, S., and Zeng, N.:
878 Greening of the Earth and its drivers, *Nat Clim Change*, 6, 791-+, 10.1038/Nclimate3004, 2016.