



**Intercomparison of Terrestrial Carbon Fluxes and Carbon Use Efficiency Simulated by
CMIP5 Earth System Models**

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50 **Abstract**

51 This study compares historical simulations of the terrestrial carbon cycle produced by 10
52 Earth System Models (ESMs) that participated in the fifth phase of the Coupled Model
53 Intercomparison Project (CMIP5). Using MODIS satellite estimates, this study validates the
54 simulation of gross primary production (GPP), net primary production (NPP), and carbon use
55 efficiency (CUE), which depend on plant function types (PFTs). The models show noticeable
56 deficiencies compared to the MODIS data in the simulation of the spatial patterns of GPP and
57 NPP and large differences among the simulations, although the multi-model ensemble (MME)
58 mean provides a realistic global mean value and spatial distributions. The larger model spreads
59 in GPP and NPP compared to those of surface temperature and precipitation suggest that the
60 differences among simulations in terms of the terrestrial carbon cycle are largely due to
61 uncertainties in the parameterization of terrestrial carbon fluxes by vegetation. The models also
62 exhibit large spatial differences in their simulated CUE values and at locations where the
63 dominant PFT changes, primarily due to differences in the parameterizations. While the MME-
64 simulated CUE values show a strong dependence on surface temperatures, the observed CUE
65 values from MODIS show greater complexity, as well as non-linear sensitivity. This leads to
66 the overall underestimation of CUE using most of the PFTs incorporated into current ESMs.
67 The results of this comparison suggest that more careful and extensive validation is needed to
68 improve the terrestrial carbon cycle in terms of ecosystem-level processes.

69

70 Keywords: earth system models, carbon use efficiency, CMIP5, MODIS, GPP, NPP

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73 1. Introduction

74 Earth system models (ESMs) have been developed in the past several decades to simulate
75 vegetation changes in space and time through carbon cycle-related interactions between the
76 biosphere and the atmosphere. The temporal variations in atmospheric CO₂ in the models are
77 driven by CO₂ emissions from natural and anthropogenic sources, as well as uptake by
78 vegetated land surfaces and the ocean. Net imbalances in carbon fluxes drive the secular trend
79 in CO₂. The magnitude of the imbalance is model-dependent and results in differences in the
80 future warming projected by various ESMs. Previous studies showed that the observed trend
81 of atmospheric CO₂ was not reproduced correctly during the past century, given the historical
82 record. There was also substantial spread among models, even though they were forced by
83 identical anthropogenic emissions (Friedlingstein et al., 2006, 2014; Hoffman et al., 2013; Zhao
84 and Zeng, 2014). The model bias persists into their future projections. Hoffman et al. (2013)
85 pointed out that the spread of projected CO₂ concentrations among fifteen Coupled Model
86 Intercomparison Project (CMIP5; Taylor et al., 2012) ESMs in 2100 was approximately 20 %
87 of their multi-model average. Friedlingstein et al. (2014) showed that the degree of surface
88 temperature warming by 2100 was different by more than a factor of two, depending on the
89 models and representative concentration pathway (RCP) 8.5 scenarios used.

90 Previous studies (Friedlingstein et al., 2006; Booth et al., 2012; Hoffman et al., 2013; Anav
91 et al., 2013; Aroa et al., 2013; Friedlingstein et al., 2014) have suggested that the uncertainty
92 in CO₂ concentrations simulated by ESMs should be largely attributed to the terrestrial carbon
93 uptake, rather than to the uptake by ocean. Hoffman et al. (2013) and Friedlingstein et al. (2014)
94 compared the carbon uptake by land and ocean, simulated by ESMs and found that the amount
95 of carbon accumulated by the ocean is positive in all models by 2100, whereas the models
96 exhibited a large spread in the amount of carbon taken up by the land; the results even had



97 different signs. Aroa et al. (2013) indicated that the simulated sensitivity of terrestrial carbon
98 storage to the atmospheric CO₂ concentration was 3-4 times larger than that of ocean. This
99 suggests that the terrestrial carbon cycle is one of the important factors that need improvement
100 for minimizing uncertainty in future climate predictions.

101 It is generally recognized that changes in the carbon pools in the biosphere should play a key
102 role in determining atmospheric CO₂ concentration levels in the future. Shao et al. (2013)
103 showed that the net biome production (NBP) simulated by CMIP5 ESMs is enhanced in the
104 21st century and that the biomass particularly increases over tropical rainforests and vegetated
105 surfaces in the mid-latitudes through the CO₂ fertilization effect. Not only long-term increases
106 in biomass but also future changes in its seasonal cycle would significantly affect CO₂
107 concentrations. Zhao and Zeng (2014) indicated that the amplitude of the seasonal cycle of
108 atmospheric CO₂ tends to increase in the future, due to an increase of 68 % in the seasonal
109 cycle of NBP during the growing season in their future simulations. Comprehensive model
110 intercomparisons on the simulation of biome production at various ecosystem levels are needed
111 to explain the differences among simulations and minimize projection uncertainties.

112 The exchange of carbon between the atmosphere and terrestrial ecosystems consists of
113 complicated biogeochemical processes operating over a heterogeneous surface, and the quality
114 and the performance of the global model simulations is often diagnosed using carbon cycle
115 variables such as gross primary production (GPP) and autotrophic respiration (Ra) by plants.
116 Net primary production (NPP) is defined as GPP minus Ra. Heterotrophic respiration (Rh),
117 involving the decomposition of soil litter, is also an important process involved in the carbon
118 cycle. By validation using ground and satellite observational data, previous studies identified
119 the systematic biases of ESMs and discussed the possible reasons for these biases. Anav et al.
120 (2013) indicated that current ESMs tend to overestimate terrestrial biomass and global GPP



121 (Anav et al., 2013). Shao et al. (2013) showed that ESMs exhibit large disagreements in the
122 relationship between carbon cycle variables and hydrological variables, such as precipitation
123 and soil moisture, emphasizing the importance of the hydrological cycle in terms of its effects
124 on the terrestrial carbon cycle. The simulated soil carbon amount in the subsurface root zone,
125 which is the major source of plant growth, showed systematic biases and large model spread,
126 from 40 to 240 %, compared with observational data (Todd-Brown et al., 2013). That study
127 suggested that it might be responsible for the large spread of atmospheric CO₂ concentrations
128 simulated by the models.

129 While most previous intercomparison studies involving ESMs have focused on the
130 validation of the global mean budget of terrestrial carbon pools and fluxes (Anav et al., 2013;
131 Shao et al., 2013; Todd-Brown et al., 2013), which is useful for evaluating the overall
132 performance of ESMs and quantifying simulation uncertainties, more detailed analyses
133 addressing regional scales and different vegetation types are needed to identify the key sources
134 of systematic biases in the models. Anav et al. (2013) evaluated regional changes in
135 biogeochemical variables for two hemispheres and the tropical region separately. In particular,
136 an investigation of systematic biases in different types of ecosystems is required to improve
137 the existing parameterizations of terrestrial carbon fluxes by vegetation. In contrast to the many
138 observational studies in biology that address various plant function type (PFT) levels (De Lucia
139 et al., 2007; Zhang et al., 2009; Zhang et al., 2014), studies that benchmark model simulations
140 of PFT levels have obtained less attention, and this is one of the primary motivations of this
141 study.

142 For a better elucidation of systematic biases in the models, this study focuses particularly on
143 the comparison of carbon use efficiency (CUE), which is sensitive to the various PFTs. For the
144 short-term carbon cycle, Ra is a primary measure of the release of carbon to the atmosphere,



145 and its magnitude is known to be about half of GPP for most vegetated surfaces (King et al.,
146 2006; Piao et al., 2010). CUE is defined as the ratio of NPP to GPP, which is a useful diagnostic
147 measure for the comparison of parameterizations for the terrestrial carbon fluxes driven by
148 vegetation that are implemented differently in current ESMs. The absolute magnitudes of the
149 production terms are the results of feedbacks between climate and vegetation. Normalized flux
150 terms can highlight the differences among simulations driven by parameterization differences
151 in terrestrial carbon fluxes. Previous studies based on in situ (De Lucia et al., 2007) and satellite
152 (Zhang et al., 2009) data analyses have indicated that CUE is not a constant with a value of
153 approximately 0.47 (Gifford, 1994; Dewar et al., 1999) but varies depending on climatic
154 conditions and PFTs. In this regard, the Moderate Resolution Imaging Spectroradiometer
155 (MODIS) satellite data provide the global coverage of GPP and NPP as a useful reference for
156 the model validation for CUE at the PFT level. Zhang et al. (2014) suggested observed CUE
157 by MODIS tends to slightly increase in the recent years.

158 The purpose of this study is the intercomparison of CMIP5 ESMs in terms of their
159 simulations of the terrestrial carbon cycle, based on a quantitative evaluation of the
160 performance of terrestrial carbon flux parameterizations in their land surface models (LSM).
161 This analysis specifically focuses on the assessment of CUE at the PFT level and makes an
162 effort to provide useful suggestions to the modeling community for reducing systematic biases
163 in the terrestrial carbon cycle in current ESMs. This study consists of following sections:
164 Section 2 describes the observational data and model output used in this study. Section 3
165 compares the model simulations in terms of their climate and terrestrial carbon cycle variables,
166 comparing first the multi-model ensemble (MME) average to diagnose common and systematic
167 biases in the current models and then identifies differences among simulations across the ESMs
168 in their simulated climates and carbon fluxes. The comparison of CUE at various PFT levels is



169 followed by more comprehensive comparisons for identifying differences among simulations
170 driven by model parameterizations. Finally, Section 4 provides a summary and conclusions.

171

172 **2. Data and Analysis Methods**

173 **2.1 Observational data**

174 This study used GPP and NPP as primary variables to validate the global carbon cycle as
175 simulated by various ESMs. Reference observational data were obtained from the NASA
176 MODIS MOD17 data product, which includes the first satellite-driven estimates of carbon
177 fluxes on vegetated surfaces on a global scale (Running and Gower, 1991; Zhao et al., 2005).

178 The MODIS algorithm uses a data model based on the radiation use efficiency logic of
179 Monteith (1972) to estimate GPP, which is basically a linear function of the amount of
180 Photosynthetically Active Radiation (PAR) absorbed. The fraction of PAR and the leaf area
181 index (LAI) are provided to the model by the MODIS MOD15 products. A conversion
182 efficiency parameter relating absorbed radiation to the actual productivity depends on
183 vegetation type and climate condition. The upper limit of conversion efficiency uses the Biome
184 Parameter Lookup Table (BPLUT) for different vegetation types. The vegetation types include
185 evergreen needleleaf forest (ENF), evergreen broadleaf forest (EBF), deciduous needleleaf
186 forest (DNF), deciduous broadleaf forest (DBF), mixed forests (MF), open and closed
187 shrublands (SHR), grasslands (GRA), and croplands (CROP), which are based on the land
188 cover classification from the MODIS MCD12Q1
189 (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd12q1). Figure 1
190 shows the horizontal distribution of vegetation types from MODIS. The conversion efficiency
191 is modified by climate conditions such as incoming solar radiation, temperature, and vapor
192 pressure deficit, which are obtained from atmospheric reanalyses developed by NASA's Global



193 Modeling and Assimilation Office and the NCEP/NCAR Reanalysis II. The NPP estimation
194 by MODIS calculates daily leaf and fine root maintenance respiration, annual growth
195 respiration, and annual maintenance respiration of live cells in woody tissue, which are
196 subtracted from the GPP. Biome-specific physiological parameters are also specified by
197 BPLUT for respiration calculations.

198 The MOD17 dataset provides 8-day, monthly, and annual mean GPP and NPP for 2000-2012.
199 This study used the gridded GPP and NPP products, which have a spatial resolution of 30
200 arcsec (0.0083 degree), provided by the Numerical Terradynamic Simulation Group (NTSG)
201 of the University of Montana (NTSG MOD17 v55).

202 Although MODIS is affected by uncertainties in biomass types and meteorological data sets
203 (Zhao et al. 2005), the derived GPP and NPP values are able to capture realistic spatial and
204 temporal variations over different biomes and climate regimes. Zhao et al. (2005) and Heinsch
205 et al. (2006) demonstrated that the data are consistent with ground-based flux tower
206 measurements of GPP and field-observed NPP estimates with high correlation ($r=0.859$).

207 For comparison with MODIS, this study also used GPP estimates from FLUXNET-MTE
208 (Multi-Tree Ensemble; Jung et al., 2011), which is an upscaled data set providing global
209 coverage that is derived from 178 surface flux tower observations using a machine learning
210 technique. FLUXNET-MTE provides an explicit estimate of carbon fluxes over vegetated
211 surfaces. The dataset provides monthly data at a $0.5^\circ \times 0.5^\circ$ (latitude \times longitude) spatial
212 resolution and covers the period 1982 – 2007. Although this gridded global dataset is useful
213 for validation of ESMs, its key limitations are also discussed in the literature (Jung et al., 2011).
214 Wide geographical regions are not represented by measurement stations; for example, there is
215 a lack of samples over Siberia, Africa, South America and tropical Asia compared with North
216 America and Europe. Estimates of annual-mean upscaled ecosystem respiration have higher



217 certainty than the anomalies and show approximately 5-10 % underestimation. Additionally,
218 the data have limitations in accounting for disturbances due to land use changes, given that
219 unchanged land cover data from the International Geosphere-Biosphere Program (IGBP)
220 satellite are used for all periods. This may introduce spurious trends into the GPP estimates
221 from the FLUXNET-MTE project. The dataset does not provide estimates of R_a , but instead
222 provides the summation of R_a and R_h . The geographical distribution of satellite-derived GPP
223 from MODIS shows a high degree of consistency with that from in situ FLUXNET
224 observations. Figure 2 compares the annual GPP distributions from MODIS and FLUXNET
225 for the same period, 2000-2005. A notable difference between the two appears in the Amazon,
226 where MODIS tends to underestimate the productivity significantly. In the remaining regions,
227 MODIS tends to produce slight underestimates in the tropics and overestimates in the high
228 latitudes when compared with FLUXNET. The annual GPP values from MODIS and
229 FLUXNET are 108.76 GtC and 107.41 GtC, respectively, for the averaging period of 2000-
230 2005, with a small difference that is no more than 1 % of the total value. The pattern of
231 differences did not change significantly even if the FLUXNET data were averaged over a
232 longer period (1983-2005). In fact, the interannual variation did not modify the global-mean
233 annual GPP value significantly when the reference period was extended to 1983-2005, which
234 yielded a small reduction to 106.55 GtC using the FLUXNET data.

235 This study also used the observed surface air temperature and precipitation data from the
236 Institute for Climate Impact Research based on the CRU (Climate Research Unit)
237 meteorological dataset (Harris et al., 2014). In this data product, temperature and precipitation
238 at stations worldwide were interpolated to a horizontal resolution of $0.5^\circ \times 0.5^\circ$ (latitude
239 \times longitude) covering the global land surface.



240

241 **2.2 Model Data**

242 Historical simulations performed using 10 ESMs were used in this study. Brief descriptions
243 of these models is provided in Table 1. The historical simulations (that is, experiment 5.2 or
244 the ESM historical 1850–2005 simulation; Taylor et al., 2012) were forced by gridded CO₂
245 emissions data for fossil fuel consumption from Andres et al. (2011). While conventional CO₂
246 concentration-driven runs have no vegetation feedback on atmospheric CO₂, these emissions-
247 driven runs enables climate-carbon cycle feedbacks via changes in vegetation. Note that three
248 models – GFDL-ESM2M, GFDL-ESM2G, and MPI-ESM LR – of them enabled the dynamic
249 vegetation model in their historical simulations for 1850 – 2005, which model was able to
250 consider dynamic change of PFT boundaries by climate conditions (Table 1). Atmospheric CO₂
251 concentrations are simulated prognostically from the net budget of natural and anthropogenic
252 carbon fluxes to and from the atmosphere. The simulation of GPP is directly controlled by the
253 formulae representing photosynthesis in the models. As shown in Table 1, the parameterization
254 of photosynthesis by vegetation is formulated similarly in the 10 ESMs. This parameterization
255 is mostly based on Farquhar et al. (1980) for C3 plants in cold climates, with revisions for C4
256 plants in warm climates by Collatz et al. (1992). Leaf photosynthesis in CLM4 is proportional
257 to the concentration of carbon dioxide in the atmosphere, as well as the temperature and
258 moisture surrounding leaves. It adjusted the minimum rate among the light-use, water-use and
259 carbon assimilation approaches in CLM4.

260 NPP is diagnosed in ESMs by subtracting Ra from GPP. Parameterizations for Ra are more
261 diverse in formulation across the models compared to that of photosynthesis. Note that
262 CESM1-BGC and NorESM-ME1 incorporate identical land surface models, in which the
263 nitrogen cycle is allowed to limit plant assimilation for the parameterization of carbon fluxes



264 by terrestrial vegetation, so called the interactive carbon-nitrogen (CN) cycle. Respiration is
265 proportional to temperature and nitrogen concentration. The models without interactive
266 nitrogen cycles diagnose nitrogen concentrations from the carbon concentration in each carbon
267 pool, whereas the models with interactive nitrogen cycles predict the nitrogen concentrations.
268 The only exception is MRI-ESM, which uses an empirical formula for estimating NPP based
269 on Obata (2007). In the model, the monthly NPP is empirically derived from physical variables
270 such as temperature and precipitation from the Miami model (Lieth, 1975; Friedlingstein et al.,
271 1995).

272 The model data were obtained from the Earth System Grid Federation (ESGF), an
273 international network of distributed climate data servers (Williams et al., 2011). For the
274 purposes of comparison, the model outputs, as well as the MODIS data, were interpolated onto
275 the same $1^{\circ} \times 1^{\circ}$ grid (latitude \times longitude).

276

277 **2.3 Analysis Methods**

278 In Section 3.3, CUE is diagnosed at the ecosystem level for the MODIS observations and
279 the various ESM simulations. For simplicity, an identical distribution of vegetated surfaces
280 based on to the MODIS classification (Figure 1) was applied to both the observed and the
281 simulated fluxes. This is because each model has their own vegetation classifications, which
282 are not available from the CMIP5 data archive.

283 It is noted that the deficiency in the simulation of CUE by individual models is not only
284 caused by deficiencies in the parameterization of carbon fluxes due to vegetation but also by
285 differences in the classifications of PFTs, which are specified differently in each model. For
286 example, LM3.0 in GFDL ESM2 M and ESM2G simulate 5 PFTs (i.e., 3 types of trees and 2
287 types of grasses), while NCAR and NorESM's CLM4.0 specifies the PFTs in much greater



288 detail by including 17 different types (i.e., 8 types of trees, 3 types of shrubs, 3 types of grasses
289 and 3 types of crops). Although referencing PFTs from the observations instead of using own
290 PFTs in each model might not be a perfect comparison, it is still meaningful to identify the first
291 order differences driven by parameterization method and the classification difference as well
292 where the latter is regarded as the model bias too.

293

294

295 **3. Results**

296 **3.1. Systematic Biases in the Multi-Model Ensemble**

297 Systematic biases in the ESM simulations are examined first by taking multi-model
298 ensemble averages (MME) for simulated surface air temperature and precipitation, respectively
299 (Figure 3). Despite the realistic representation of annual-mean surface temperatures, MME
300 exhibits systematic biases with significant hemispheric differences. Warm biases are seen in
301 the Northern Hemisphere, particularly in northeastern Asia and North America, whereas there
302 exists a cold bias in most of the Southern Hemisphere. MME generally shows wet biases in
303 precipitation, except over South America. Wet biases seem to be consistent with cold biases in
304 the tropical regions, where the deep convective rainfall tends to produce deep clouds that
305 attenuate incoming solar radiation at the surface.

306 The annual GPP, NPP and Ra values from the MODIS observations and the MME are
307 compared in Figure 4. The observed GPP values from MODIS are generally high in areas of
308 EBF in tropical regions, such as Amazon, South Asia, and Central Africa, and in areas of DBF,
309 such as those in Indochina, China, India, Europe and the southeastern part of North America.
310 GPP is observed to be small in areas of SHR in Australia and in boreal regions of MF and GRA
311 in northern Eurasia. GPP is close to zero over dry and non-vegetated surfaces, such as the



312 Sahara Desert and central Australia. The MME of the ESMs tends to reproduce these
313 geographical differences realistically, although the estimated magnitudes are too large over
314 most of the globe. Although Ra tends to be overestimated as well, MME shows a net positive
315 bias in NPP in most terrestrial regions, suggesting that the MME should underestimate the
316 observed trend of atmospheric CO₂ increase.

317 The global-mean values of GPP, NPP, and Ra are compared in Figure 5. Note that spread of
318 the simulations is large, particularly due to the outlier value produced by MRI-ESM1. The
319 median value of GPP simulated by ESMs is centered slightly above the value from MODIS
320 and is approximately 20 % higher (+18 GtC). The median value of NPP is also overestimated
321 by 10.2 GtC compared with the 52.1 GtC NPP from MODIS. The median value of Ra is
322 underestimated.

323 The formulations of GPP and Ra are closely related to temperature and precipitation
324 (Rahman et al., 2005; Yang et al., 2006), and, the model biases in those carbon fluxes might be
325 driven both by systematic biases in climate conditions such as temperature and precipitation
326 and the uncertainty in the parameterization formulations themselves. The Taylor diagram is a
327 common and useful measure for simulated spatial distributions that calculates spatial
328 correlation coefficients between observed and simulated values and the normalized standard
329 deviation of simulated values from the global mean over the whole domain of comparison.
330 Figures 6a and 6b show Taylor diagrams for the annual mean surface air temperature and
331 precipitation, respectively. The MME simulation of temperature by the CMIP5 ESMs is quite
332 close to the CRU observations. The spatial correlations are greater than 0.95 in all models. The
333 normalized standard deviations are within the range of 0.8 to 1.5, which is relatively small
334 compared with other simulated variables. The Taylor diagram of precipitation shows less
335 accuracy and more model spread than that of SATs. The spatial correlation of the MME is



336 approximately 0.76; the MME also shows higher normalized standard deviations compared
337 with temperature, suggesting that current ESMs exhibit relatively larger discrepancies in
338 precipitation and the terrestrial water cycle. Spatial patterns of GPP simulated by the ESMs
339 (Figure 6c) show even larger systematic biases with lower spatial correlations and larger spatial
340 changes (i.e., higher normalized standard deviations) than the observed values. Model spread
341 becomes much larger than that of temperature and precipitation. The simulated pattern
342 correlations from the ESMs are lowest for NPP (Figure 6d). The correlation for the MME is
343 slightly higher than 0.5. The models also exhibit much higher spatial variation than the
344 observed values for both GPP and NPP.

345 The Taylor diagram analysis suggests that the systematic biases in the ESMs may be
346 successively amplified by deficiencies in the simulation of climate and the terrestrial carbon
347 cycle. Regarding the climate conditions that affect the terrestrial carbon cycle, particularly the
348 distribution of precipitation and the water cycle seem to contribute more to the bias than does
349 temperature. In addition, the much larger spread in GPP and NPP simulated by the ESMs
350 compared to that in temperature and precipitation suggests that there should be much larger
351 uncertainty in the parameterization of terrestrial carbon cycle in the current ESMs. Biases and
352 model spread are even larger in NPP compared with GPP, implying that the simulation
353 uncertainty is much larger when the photosynthesis and the respiration are combined. The
354 performance of the MME in terms of GPP and NPP is not necessarily higher than that of the
355 individual models in this case, due to the presence of persistent and large deficiencies in the
356 individual models.

357

358 **3.2. Model Dependences**

359 The simulation of annual GPP values shows significant model dependence as shown in



360 Figure 5. MRI-ESM1 shows the largest value among the models. The three models, ESM2G,
361 ESM2 M, and MPI-ESM-LR, simulate relatively larger values of GPP than the rest of the
362 models. As the simulation of Ra shows relatively small model dependence, models that
363 simulate larger GPP values tend to produce larger NPP in general. MRI-ESM1 is an exception,
364 and the simulated GPP of this model is significantly reduced by its large Ra, leading to an NPP
365 value close to the median value. The two models, CESM1-BGC and NorESM1-ME, that share
366 the same land surface model simulate the smallest NPP values, which is a significant
367 underestimation relative to the MODIS estimate.

368 To examine further what causes the global bias in carbon fluxes, the spatial distribution of
369 the GPP bias pattern in carbon fluxes simulated using each model is compared in Figure 7.
370 Each model exhibits its own systematic biases. MRI-ESM1 shows a significant positive bias
371 in most vegetated regions, which is particularly pronounced in tropical rainforests. The group
372 of models with higher global-mean GPP values in Figure 5 (i.e., MPI-ESM1-LR, ESM2 M,
373 and ESM2G) shows GPP bias patterns that are remarkably similar to each other. GPP is
374 overestimated in most regions in these models except for the upper inland region of the Amazon.
375 The rest of the models show mixed spatial patterns of positive and negative biases. The large
376 negative GPP bias in part of the Amazon is primarily responsible for the lowest global-mean
377 GPP values, which are simulated by CanESM2 and BCC_CSM1 M. The negative bias is clear
378 in the boreal high-latitude regions above 40 N in the CESM1-BGC and NorESM1-ME models.
379 The systematic biases in the models reflect the uncertainties in the parameterized carbon cycles,
380 as well as in the simulated climates. Most models simulate larger production in the tropics, due
381 to abundant rainfall and high temperatures, and smaller production in high latitudes due to less
382 precipitation and low temperatures. As GPP is much larger in magnitude than Ra, the NPP bias
383 pattern in each model is mostly dominated by that of GPP rather than Ra, leading to consistent



384 patterns (cf. Figure 7 and Figure 8). The two GFDL models implemented with the same LM3
385 land surface model (i.e., ESM2M and ESM2G) and the other two models that use CLM4
386 (CESM1-BGC and NorESM1-ME) show NPP biases with opposite signs in the boreal regions
387 above 40 N, highlighting significant model differences in parameterizations of carbon fluxes
388 due to vegetation.

389

390 **3.3. Carbon Use Efficiency**

391 The bias patterns of GPP and NPP simulated by the various ESMs presented in Figure 7 and
392 8 are the result of complicated feedbacks between the carbon cycle (mostly by terrestrial
393 vegetation) and climate. As the magnitude of the bias is also a function of biomass, this study
394 further compared carbon use efficiency by dividing NPP by GPP. This normalized carbon flux
395 ratio can highlight the difference among simulations driven by parameterization differences in
396 terrestrial carbon fluxes by vegetation. The spatial pattern of CUE obtained by MODIS shows
397 significant variations (Figure 9). In MODIS, most tropical areas with high GPP values
398 generally show low CUE values below 0.4, particularly over the Amazon, central Africa and
399 Southeast Asia. In contrast, CUE is in general greater than 0.5 over wide areas in high latitudes
400 and a few low-latitude, high-elevation regions. The spatial distribution of CUE apparently
401 depends on climate conditions such as precipitation and temperature in that regions with large
402 amounts precipitation and warm climates show low CUE values, while regions experiencing
403 dry and cold climates show high CUE values. Overall, the MME of 10 ESMs tends to reproduce
404 the observed distribution from MODIS reasonably well. However, the MME values are lower
405 than the observed values in most regions, which can largely be attributed to the underestimation
406 of CUE values by MRI-ESM1. The bias pattern of CUE differs strongly among the models.
407 Note that the bias pattern of CUE tends to characterize the parameterization differences in the



408 terrestrial carbon fluxes used in the ESMs. The bias patterns of CUE are almost identical to
409 each other for models that share the same land surface model, such as BCC_CSM1 and
410 BCC_CMS1 M, and ESM2 M and ESM2G, and CESM1-BGC and NorESM1-ME,
411 respectively. The two BCC models tend to overestimate CUE in Eurasia, North America, and
412 Africa, while they produce underestimates in Australia and South America. CanESM2 shows
413 a similar pattern as the two BCC models. MPI-ESM1-LR shows a similar bias structure except
414 in that it produces overestimates in South America. CESM1-BGC, NorESM1-ME, and MRI-
415 ESM1 exhibit an underestimation of CUE over most terrestrial regions.

416 The model dependence is depicted better by the zonal mean CUE distribution (Figure 10).
417 The observed CUE values show a clear latitudinal dependence and generally increases with
418 latitude. The zonal mean of CUE from MODIS ranges from 0.3 to 0.7, with a global average
419 of 0.49. It indicates that the biomass in high latitudes tends to take up atmospheric carbon more
420 efficiently compared with that in tropics. Even though the model spread is larger, the zonal
421 mean MME is able to reproduce the observed relationship between CUE and latitude. Some
422 models, such as CESM1-BGC, NorESM1-ME and MRI-ESM1, are notably different from the
423 other models, as well as from MODIS, and simulate low values, particularly at middle to high
424 latitudes. These results are consistent with those in Shao et al. (2013). They suggested that
425 respiration decreases more rapidly than production in response to latitudinal decreases in mean
426 temperature in all models except NorESM1-ME and CESM1-BGC. The reason for the
427 underestimation of CUE in the two models are caused by their low estimates of NPP. Using the
428 same data from MODIS, Zhang et al. (2009) suggested that there exists a clear relationship
429 between CUE and climate conditions, such as surface air temperature and precipitation, that
430 are critical for biomass growth.

431 Figure 11 compares the relationship from MODIS with the model simulations. The observed



CUE from MODIS is more influenced by temperature than precipitation, as is particularly clear in dry regions with precipitation below 50 mm yr⁻¹. In general, the observed CUE decreases with increasing temperature. Moreover, observed CUE values show the sensitivity of CUE to precipitation in the tropics, where plant growth is more sensitive to precipitation compared with high latitudes. The MME basically follows this temperature sensitivity, although it tends to underestimate CUE. It is caused by the overestimation of Ra in most models compared with the MODIS estimates (Figure S3). Individual models show their own deficiencies. For example, the GFDL models (ESM2 M and ESM2G) tend to overestimate the sensitivity of CUE to precipitation in tropical regions compared with MODIS. It indicates that the gradients in CUE with temperature in the GFDL models are weaker than those in MODIS. In contrast, the models based on CLM4.0, such as CESM1-BGC, NorESM1-ME and MRI-ESM1, show a weaker sensitivity of CUE to both temperature and precipitation than the other models. This result might be caused by other limiting and trigger processes, such as nitrogen limitation, which are larger than the sensitivity to temperature and precipitation. This large divergence in the model sensitivity of CUE to temperature and precipitation induces differences in the atmospheric CO₂ concentrations in the future among the full coupled ESMs.

Figure 12 compares the observed values and differences among simulations in terms of CUE depending on the dominant PFTs according to the classification in Figure 1. In the MODIS observations, the CUE values over broadleaf forests (DBF and EBF) are generally lower than over needleleaf forests (DNF and ENF), implying that dense forests tend to not only take up large amounts of atmospheric carbon for photosynthesis but also release large amounts of carbon to the atmosphere through respiration. In this regard, the efficiency of carbon uptake by the broadleaf forests is smaller than that of needleleaf forests.

The observed variations in CUE depending on the PFTs are reproduced realistically by the



456 MME. The differences between MODIS and the MME is large in areas of DNF and DBF, but
457 those vegetation types occupy relatively small fractions of the vegetated surface. The model
458 spread is large, regardless of plant function types. This is primarily due to the low CUE values
459 produced by three of the models, CESM1-BGC, MRI-ESM1 and NorESM1-ME, for all of the
460 plant function types. These three ESMs have their own unique formulations in parameterizing
461 terrestrial carbon fluxes. In the case of MRI-ESM1, it determines the monthly R_a empirically
462 based on a function of the surface air temperature and precipitation (Obata, 2007). The
463 simulated NPP in MRI-ESM1 is the residual term between GPP and R_a that is evidently
464 different from that of the other ESMs. The two CLM 4.0-based models, CESM1-BGC and
465 NorESM1-ME, include coupled carbon and nitrogen (CN) cycles, which seems to lead to
466 dramatic differences in CUE compared with the other models that do not represent interactions
467 between the carbon and nitrogen cycles. Inclusion of the nitrogen cycle in the models tends to
468 constrain the amount of carbon uptake in vegetated land surface (Zaehle et al., 2010;
469 Friedlingstein et al., 2014) and produces higher simulated growth respiration than in other
470 models (Shao et al., 2013).

471 To examine the impact of the CN cycle in the model further, this study conducted two
472 additional sensitivity experiments using CESM1-BGC, one with interactive carbon-nitrogen
473 cycle (CN) and the other with no nitrogen cycle (Only C). Figure 13 shows that CN tends to
474 decrease GPP in most of areas compared with Only C, which suggests that the implementation
475 of nitrogen cycle in this model reduces the amount of carbon uptake by vegetation drastically
476 as a limiting factor. Accordingly NPP also tends to decrease in most of the regions at the
477 decrease of GPP. It is interesting to see that CUE decrease is particularly significant in mid- to
478 high-latitudes rather than in the tropics. This result is quite consistent with the simulation
479 difference between the CN models (CESM1-BGC and NorESM1-ME) and the rest of ESMs



480 (e.g., the zonal mean CUE shown in Figure 10).

481 This study further compares the observed and the MME-simulated CUE sensitivity to the
482 surface temperature for each plant function type (Figure 14). The MODIS observations show
483 more scatter in CUE values for a given temperature, suggesting that the natural carbon cycle is
484 not simply determined by temperature, but is also controlled by other factors. In most PFTs,
485 the observed CUE is maintained close to or even higher than 0.6, particularly in low canopy
486 plants such as SHR, CROP and GRA, for surface temperatures lower than 10 °C. CUE tends
487 to decrease significantly at temperatures higher than 10 °C. This observed feature may be
488 interpreted based on the ecological significance of the resistance to low temperatures by plants
489 (Allen et al., 2010). Low temperatures tend to reduce biosynthetic production by plants and
490 can even disturb vital functions to cause permanent injuries and death. The survival capacity
491 of plants tries to make its metabolic processes continue to function under low temperature
492 stresses and using its cold resistance (Larcher, 1968). It suggests that the CUE values of
493 vegetation may be lowered in favorable environmental conditions, such as warm temperatures
494 and abundant precipitation, as there is plenty of production and plant growth. Vegetation
495 experiencing cold temperatures and insufficient precipitation adapts to survive by increasing
496 CUE.

497 In contrast, even though the multi-model ensemble average is taken for the various ESMs,
498 the simulated CUE variation shows a clearer change with temperature, suggesting that the
499 parameterization of the terrestrial carbon cycle in current ESMs depends too much on
500 temperature conditions. A decreasing trend is clear in the MME regardless of PFTs in response
501 to an increase in temperature. From the MME simulation results, CUE values in all PFTs shows
502 a clear linear change in response to temperature variation. This implies that the current models



do not adequately consider the observed ecological resistance to temperature, and the balance between respiration and production in the models is more simplified than the observations. In fact, the parameterizations of most land surface models are based on conceptual leaf-level formulations, such as those used in the calculation of biochemical photosynthesis processes and the dependence of CO₂ exchange on stomatal conductance, which use temperature and soil moisture explicitly in their formulations. The comparison results in this study suggest that the models might need to consider ecosystem-level parameterizations which simulate carbon and nitrogen fluxes and vegetation and soil pools and are estimated at a long (e.g., monthly) time step based on spatially explicit information on climate, ecosystem type, soil type, and elevation (Zhu and Zhuang, 2015) to reflect the nonlinear relationship for the interaction between climate condition and vegetation.

514

4. Summary and Concluding Remarks

The simulations of climate and the terrestrial carbon cycle have been examined by comparing surface temperatures and precipitation, as well as GPP, Ra, and NPP values, simulated by 10 different CMIP5 ESMs with the CRU surface observational data for climate-related variables and the MODIS satellite estimates for the carbon cycle over 6 years (2000-2005).

Despite the systematic biases with significant hemispheric differences, the spatial distributions of temperature and precipitation, which are closely related to biogeochemical variables (Rahman et al., 2005; Yang et al., 2006), are relatively similar when compared with observations. More model discrepancies appeared in the simulation of the carbon cycle, which reflects overestimation of GPP over most of the globe. The terrestrial carbon fluxes simulated by the ESMs are diverse, and the models exhibit large spread, even though the multi-model ensemble mean (MME) shows strong resemblance in terms of its spatial distribution to the



527 observed pattern by cancelling out the systematic biases in each model. The results show that
528 the biases of terrestrial carbon fluxes are due less to the bias in the spatial distribution of climate
529 conditions but more to the larger uncertainty in their parameterizations.

530 We also analyzed carbon use efficiency (CUE) by dividing NPP by GPP, which is a
531 physiological parameter defined as the proportion of carbon acquisition (e.g., GPP) to
532 vegetation growth (NPP). Analyzing CUE help us to understand the carbon storage in
533 simulated terrestrial ecosystem in ESMs. At first, the spatial distribution of observed CUE from
534 space (e.g., MODIS) depends on climate condition such as precipitation and temperature. For
535 example, the regions of large precipitation and warm climate show low CUE, while the regions
536 of dry and cold climate show high CUE. It indicates that CUE at the regions with warm
537 temperature and abundant precipitation could be lowered as there is a plenty of production and
538 plant growth. The vegetation in cold temperature and insufficient precipitation adapts to the
539 environmental condition for survival by increasing CUE.

540 In different with MODIS, we found clear difference of CUE between ESMs. The bias pattern
541 of two ESMs from BCC showed the hemispheric contrast to positive in NH and negative in
542 SH. The strong negative bias of CUE over southern hemisphere is shown in GFDL's models.
543 The CUE in ESMs based on CLM4 (e.g., CESM-BGC and NorESM-ME) are significantly
544 underestimated globally. This large uncertainty of CUE in individual models is influenced by
545 biogeochemical parameterization of land surface model. In the MME, the spatial distribution
546 of CUE is reasonably simulated. However, Strong negative bias is found over Amazon. It is
547 caused that unbalanced ratio of GPP and Ra in the terrestrial carbon fluxes over tropical forest
548 such as evergreen broadleaf forest the most models. The inverse relationship between
549 temperature and CUE is reasonably simulated in the MME over dry regions. Generally, Ra is
550 more sensitive to temperature than GPP in the real world over a certain range of temperatures



551 (Woodwell et al., 1990; Ryan, 1991; Piao et al., 2010). It means that the sensitivity of
552 temperature to photosynthesis is weaker than that of respiration (Arnone and Korner, 1997;
553 Enquist et al., 2007).

554 The CUE variation depending to the PFTs, MME is realistically reproduced in every PFTs.
555 The model spread is large. It indicates a wide spread due to the different PFTs in each land
556 models and systematic bias such as failure of PFT description in land models. The observed
557 CUE values show a reasonable degree of non-linearity in terms of its response to temperature.
558 In contrast, the stronger sensitivity of CUE to temperature increases in the MME is reflected
559 by the systematic biases of simulated biogeochemical processes which depends on temperature
560 conditions strongly in every PFTs.

561 However, most of the advanced ESMs have adopted leaf-scale biogeochemistry which
562 involves parameterizations of photosynthesis and respiration based on small spatio-temporal
563 scales that depend on laboratory experiments and limited in situ studies. It makes up one of the
564 major uncertainties of carbon cycle processes in future climate change simulations from recent
565 advanced ESMs. Atkin et al. (2008) suggested that most biogeochemical models are adjusted
566 and incomplete parameterizations of biogeochemical processes. Due to the lack of
567 observational data, many biogeochemical studies have focused on the total amount of primary
568 production and respiration. Therefore, understanding and evaluating the global-scale
569 ecosystem is challenging, based on the leaf scale biogeochemical parameterization used in the
570 models. This leaf-level parameterization for biogeochemical processes is insufficient for long-
571 term simulations (Zaehle et al., 2014). For realistic long-term simulations, such as climate
572 change experiments including the carbon cycle and feedback processes, parameterizations
573 representing idealized and generalized ecosystem-level processes are needed, rather than site-
574 specific and leaf-level processes.



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576

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Table 1. List of ESMs used in this study and their features

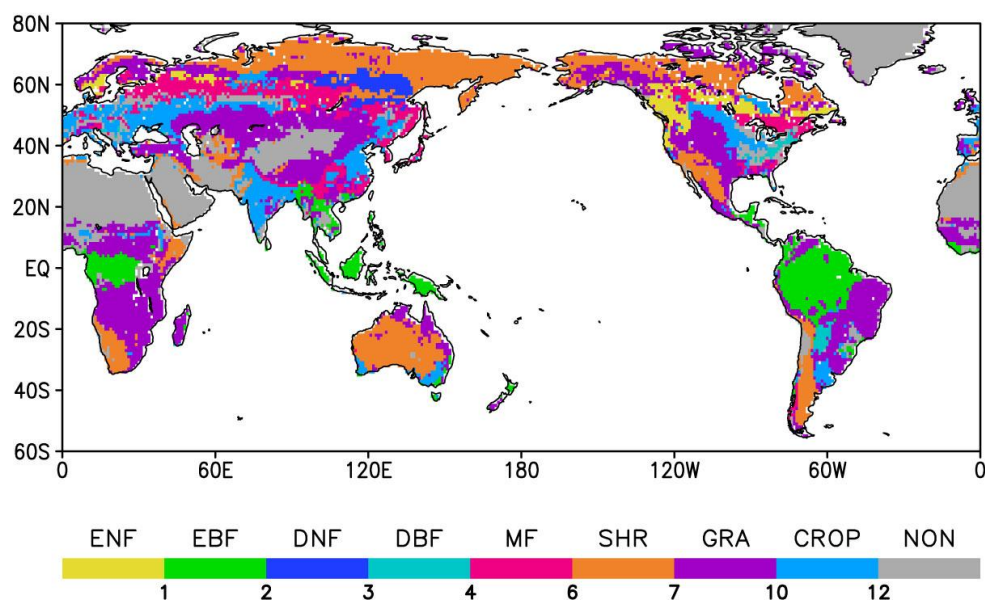
Number	Models	Modeling center	Horizontal resolution	ESM Reference	Land model	Photosynthesis	Autotrophic Respiration	Nitrogen Cycle	Dynamic Vegetation
1	BCC-CSM 1	Beijing Climate Center, China	2.812° × 2.812°	Wu et al. (2013)	BCC-AVIM1	Farquhar et al., (1980)	Foley et al. (1996)	No	No
2	BCC-CSM 1M	Beijing Climate Center, China	1.125° × 1.125°	Wu et al. (2013)	BCC-AVIM1	Farquhar et al., (1980) Collatz et al. (1992)	Foley et al. (1996)	No	No
3	CanESM2	Canadian Centre for Climate Modeling and Analysis, Canada	2.812° × 2.812°	Arora et al. (2011)	CTEM	Farquhar et al., (1980) Collatz et al. (1992)	Ryan (1991)	No	No
4	CESM1 - BGC	Community Earth System Model Contributors, NSF-DOE-NCAR, USA	1.25° × 0.9°	Long et al. (2013)	CLM4	Farquhar et al., (1980) Collatz et al. (1992)	Foley et al. (1996)	Yes	No
5	GFDL-ESM2M	NOAA Geophysical Fluid Dynamics Laboratory, USA	2.5° × 2°	Dunne et al. (2013)	LM3	Farquhar et al., (1980) Collatz et al. (1992)	Foley et al. (1996)	No	Yes
6	GFDL-ESM2G	NOAA Geophysical Fluid Dynamics Laboratory, USA	2.5° × 2°	Dunne et al. (2013)	LM3	Farquhar et al., (1980) Collatz et al. (1992)	Ryan (1991)	No	Yes



7	MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, and Atmosphere and Ocean Research Institute, and National Institute for Environmental Studies, Japan	$2.812^{\circ} \times 2.812^{\circ}$	Watanabe et al. (2011)	MATSIR O+ SEIB- DGVM	Farquhar et al., (1980)	Ryan (1991)	No	No
8	MPI-ESM LR	Max Planck Institute for Meteorology, Germany	$2.812^{\circ} \times 2.812^{\circ}$	Ilyina et al. (2013)	JSBACH	Farquhar et al., (1980)	Obata (2007)	No	Yes
9	MRI-ESM1	Meteorological Research Institute, Japan	$1.125^{\circ} \times 1.125^{\circ}$	Yukimoto et al. (2011)	HAL	Farquhar et al., (1980) Collatz et al. (1992)	Ryan (1997)	No	No
10	NorES-MI-ME	Norwegian Climate Centre, Norway	$2.5^{\circ} \times 1.875^{\circ}$	Tjiputra et al. (2013)	CLM4	Farquhar et al., (1980) Collatz et al. (1992)	Foley et al. (1996)	Yes	No



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734 **Figure 1.** Horizontal distribution of dominant plant function types (PFTs) using the MODIS
 735 land cover data that include evergreen needleleaf forest (ENF), evergreen broadleaf forest
 736 (EBF), deciduous needleleaf forest (DNF), deciduous broadleaf (DBF), mixed forest (MF),
 737 shrub land (SHR), grass (GRA), cropland (CROP) and non-vegetated area (NON).

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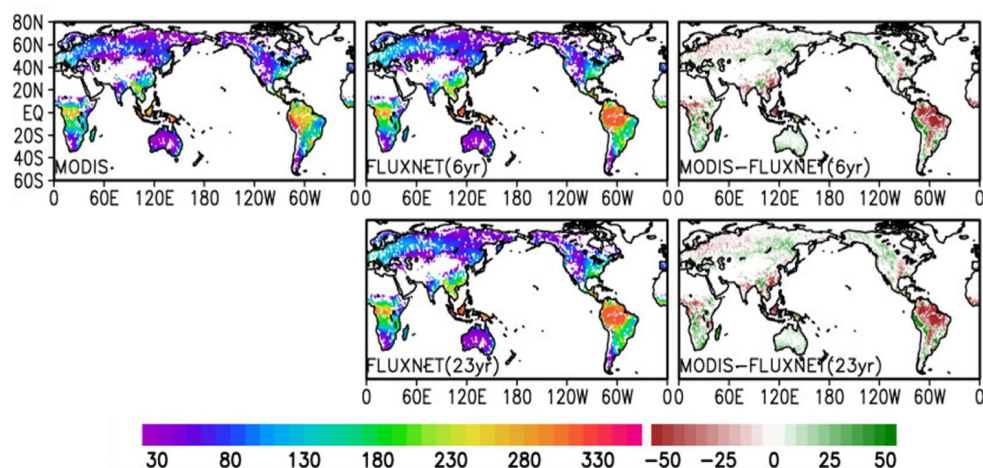
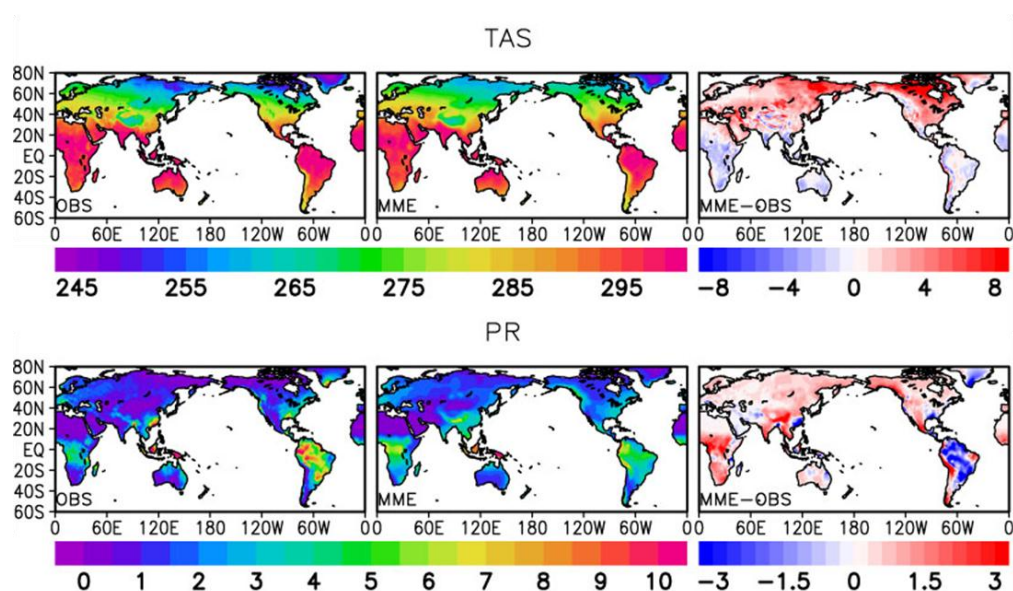


Figure 2. Spatial distributions of annual-mean GPP from MODIS (upper left), FLUXNET (upper middle), and MODIS minus FLUXNET (upper right) averaged for 6 years (2000-2005). Bottom panels show the GPP from FLUXNET averaged for 23 years (1983-2005, bottom left), and its difference from MODIS averaged for 6 years (bottom right). The unit is $\text{gC m}^2 \text{mon}^{-1}$.



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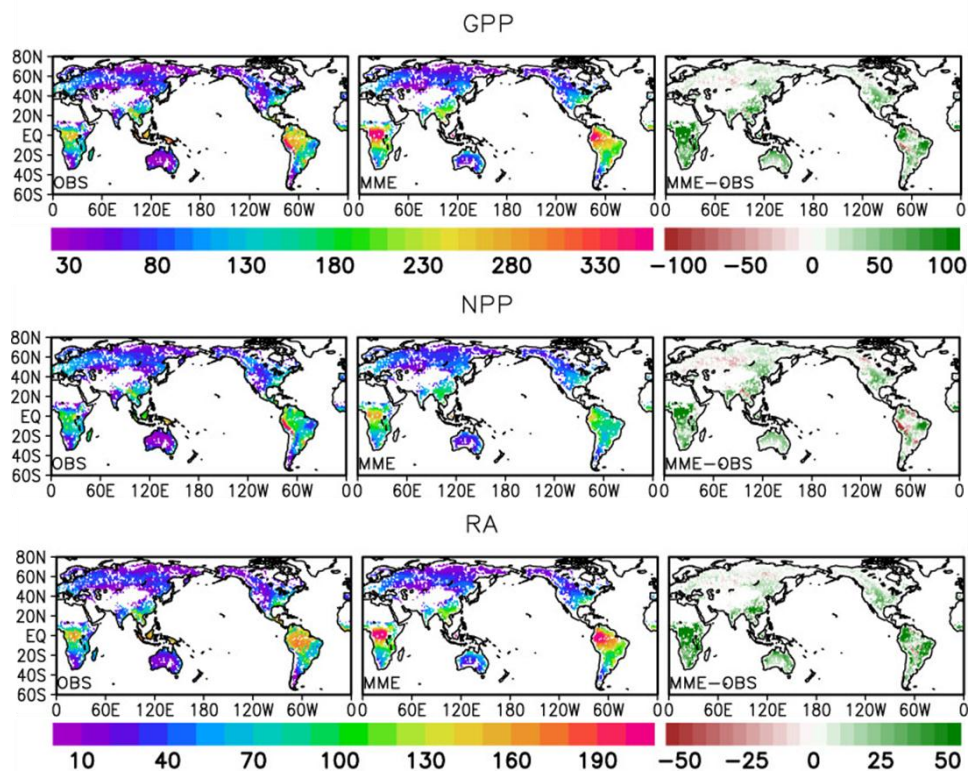
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767 **Figure 3.** Annual-mean surface air temperature (top panels, unit: K) and precipitation (bottom
 768 panels, mm d^{-1}) averaged for 2000-2005 from the CRU observations (left), and the multi-model
 769 ensemble (MME) mean (middle), and the model biases (MME minus CRU, right).

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773 **Figure 4.** Same as in Figure. 3 except GPP (top), NPP (middle), and Ra (bottom) from the
 774 MODIS observations and MME. The unit is $\text{gC m}^2 \text{mon}^{-1}$.

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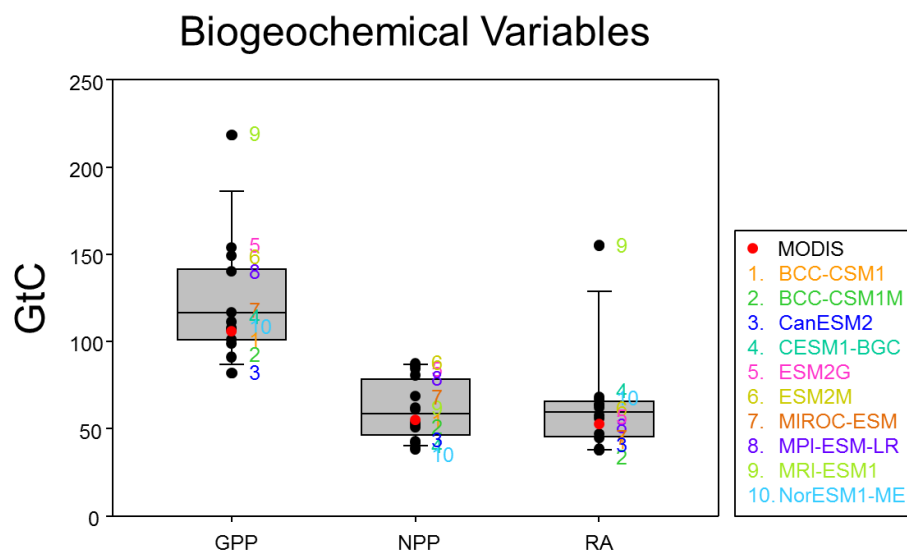
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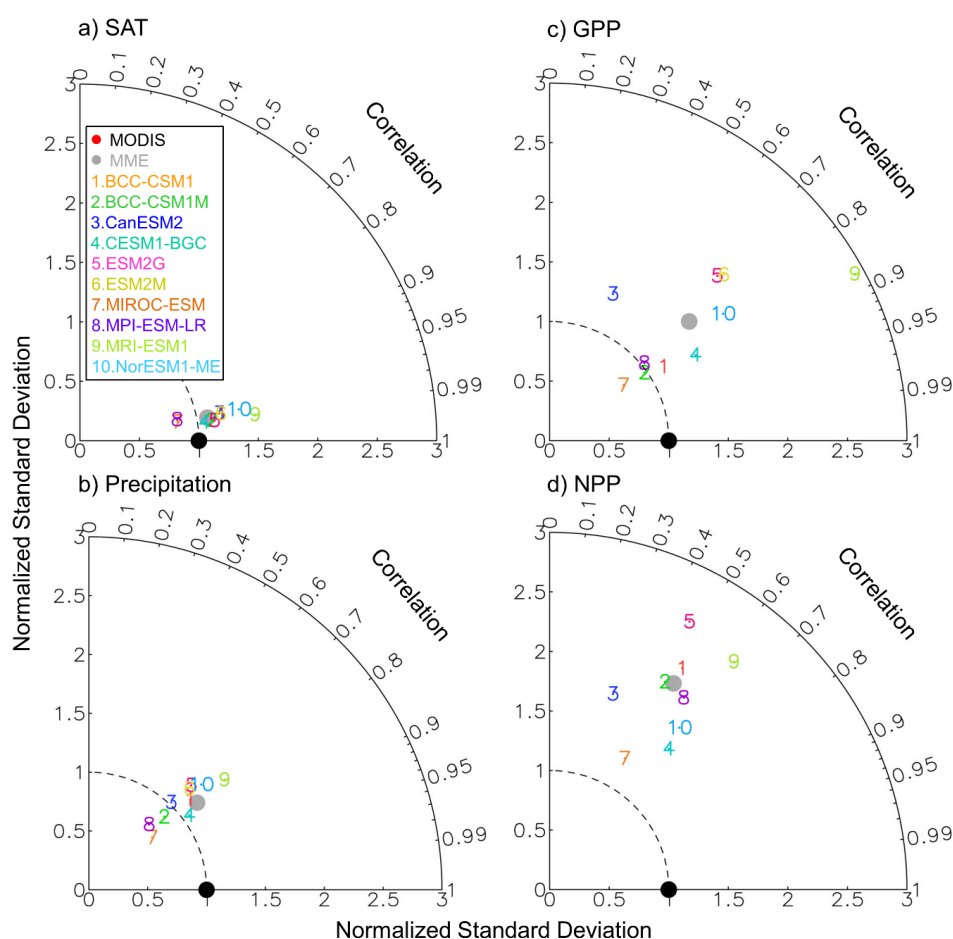


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Figure 5. Global-mean values of GPP, NPP and Ra from MODIS and CMIP5 ESMs. The values are the average over the land grids only with latitude weighting for the period of 2000 – 2005.



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793 **Figure 6.** Taylor diagram of CMIP5 ESMs for annual-mean distribution of (a) surface air
 794 temperature, (b) precipitation, (c) gross primary production (GPP) and (d) net primary
 795 production (NPP) with respect to the corresponding observations for 6 years (2000-2005). Only
 796 the vegetated grid points were included. The observed values are from CRU for temperature
 797 and precipitation are MODIS for GPP and NPP.

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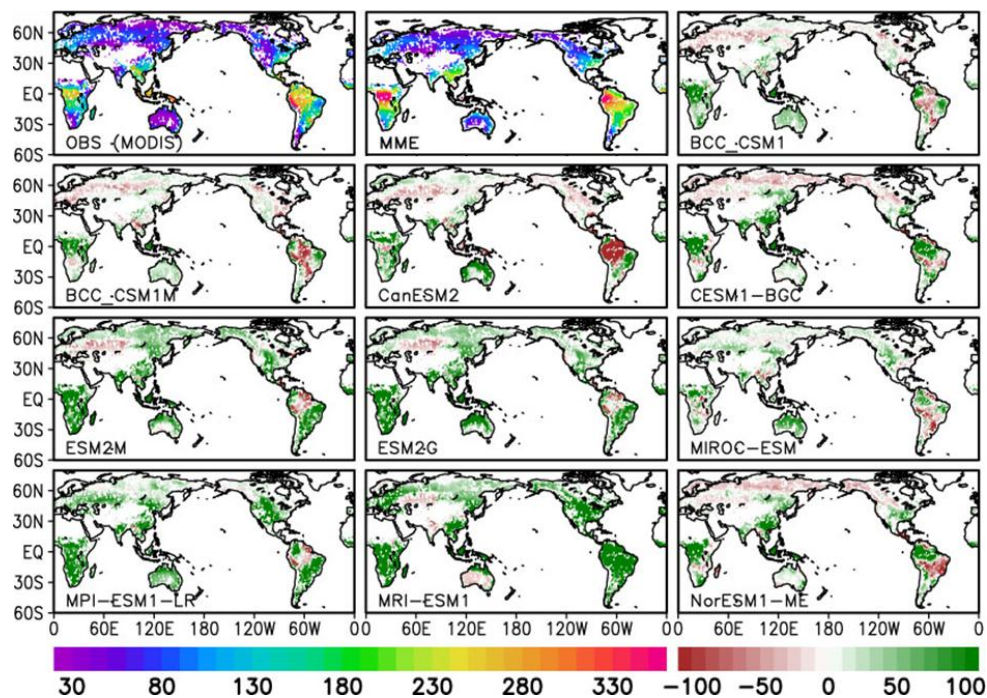
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804 **Figure 7.** Spatial distribution of annual GPP from the MODIS observation (top left), MME

805 (top middle) and the simulation bias in each model (model minus MODIS). The unit is gC m^2

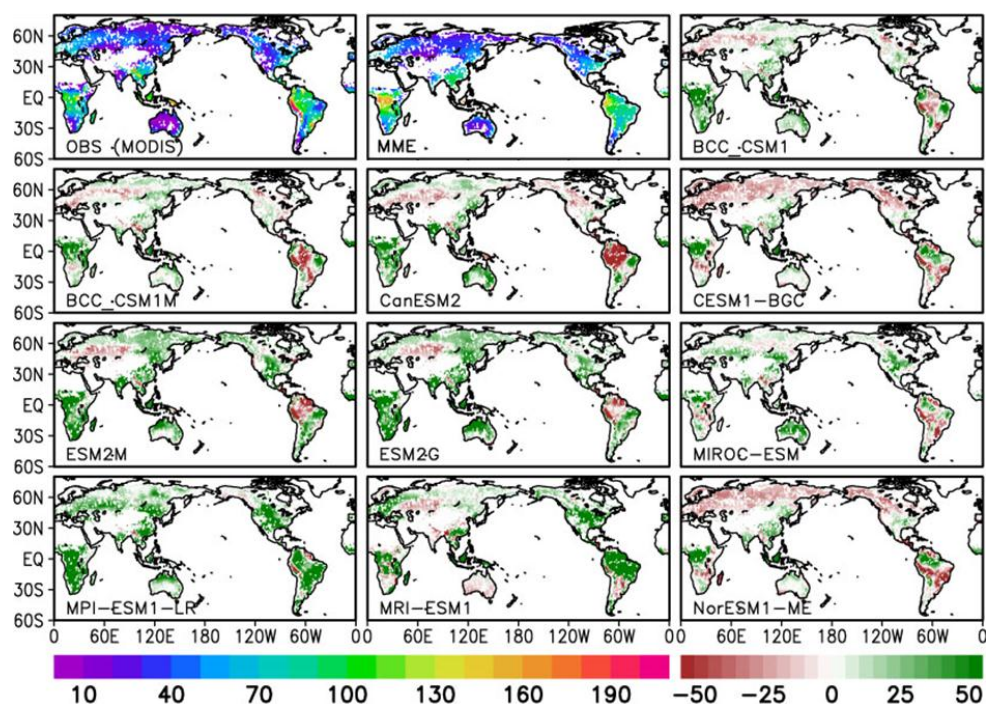
806 mon^{-1} .

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811 **Figure 8.** Spatial distribution of annual NPP from the MODIS observation (top left), MME

812 (top middle) and the simulation bias in each model (model minus MODIS). The unit is gC m^2

813 mon^{-1} .

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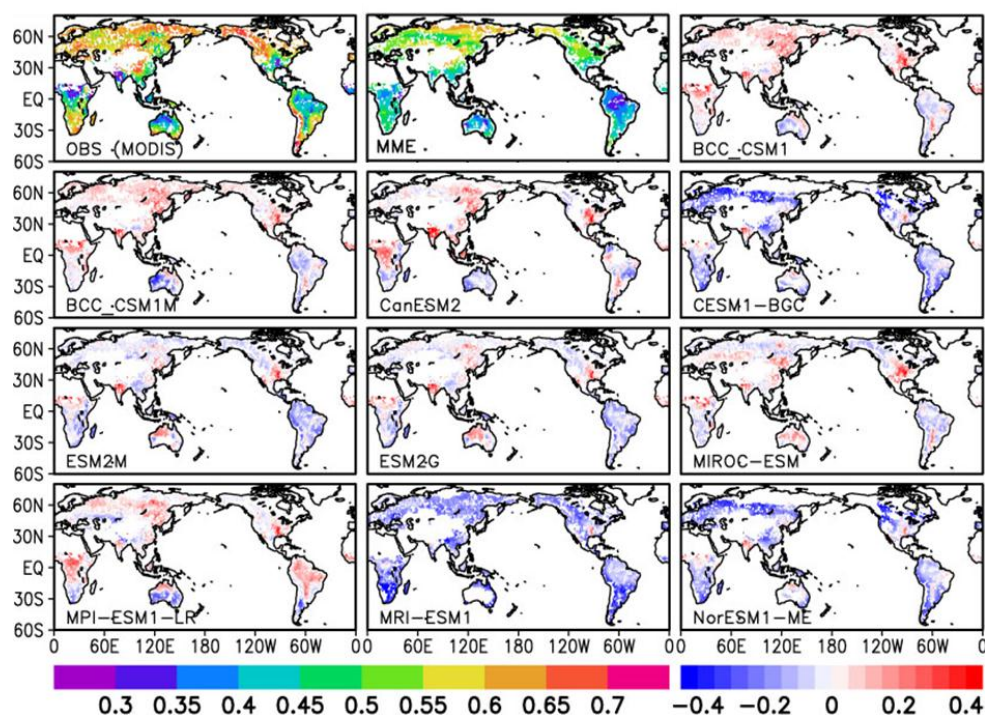


Figure 9. Spatial distribution of annual CUE from the MODIS observation (top left), MME (top middle) and the simulation bias in each model (model minus MODIS). CUE is a positively-defined ratio as NPP divided by GPP and less than or equal to 1.

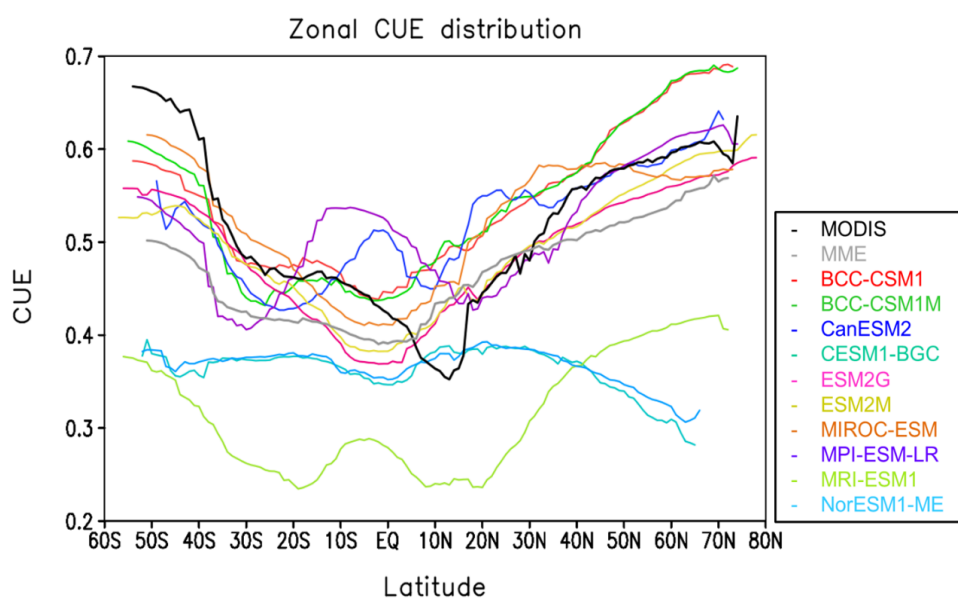


Figure 10. The zonal mean CUE from MODIS (black), MME (grey), and 10 ESMs (grey circles with number).

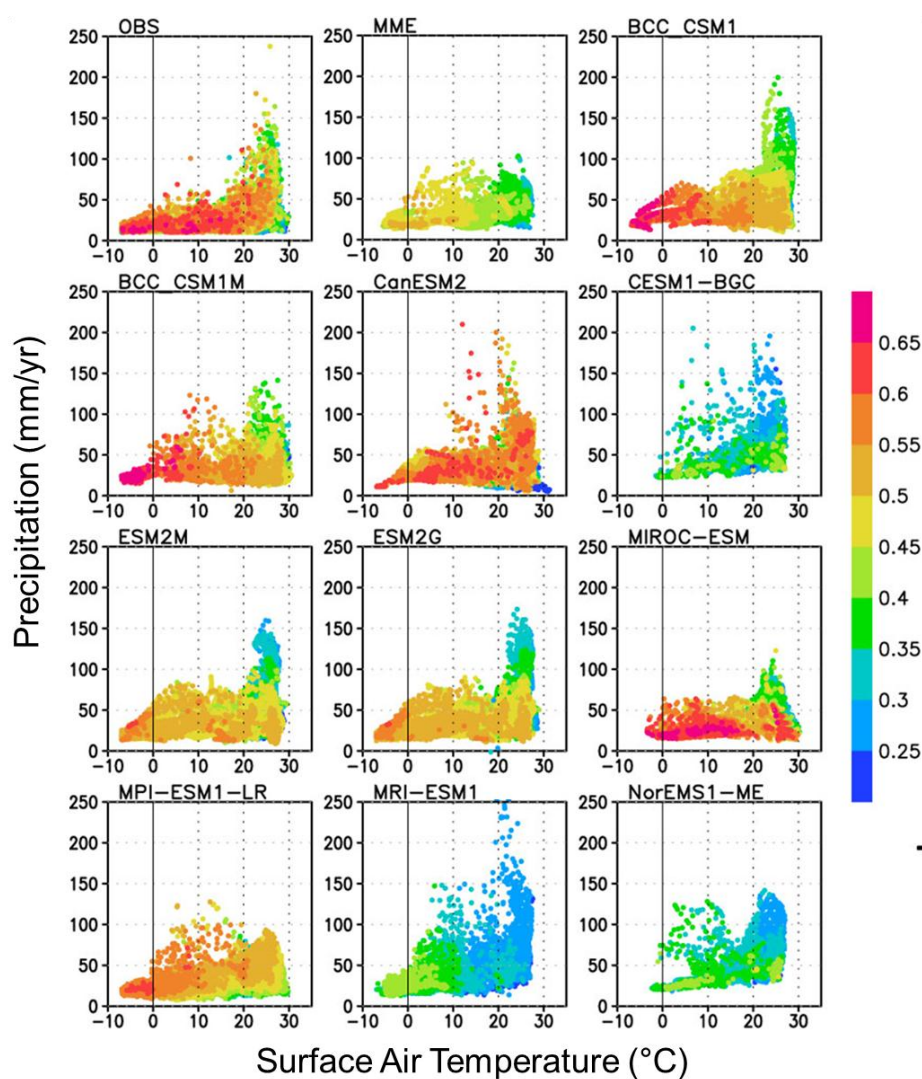


Figure 11. Scatter plot of CUE with the variation of surface air temperature (x-axis) and precipitation (y-axis). Color indicates CUE.

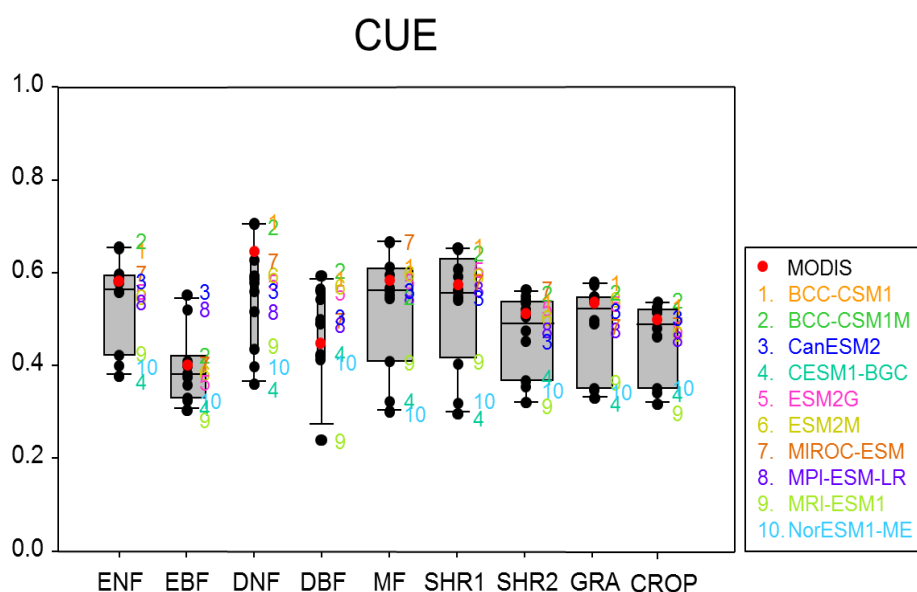


Figure 12. CUE averaged for each PFT. The box widths are proportional to the root mean square of number of grids. The coefficients of proportionality box widths in each PFTs are: ENF (0.80), EBF (0.48), DNF (0.12), DBF (0.11), MF (1.25), SHR1 (0.91), SHR2 (1.78), GRA (0.70) and CROP (0.73).

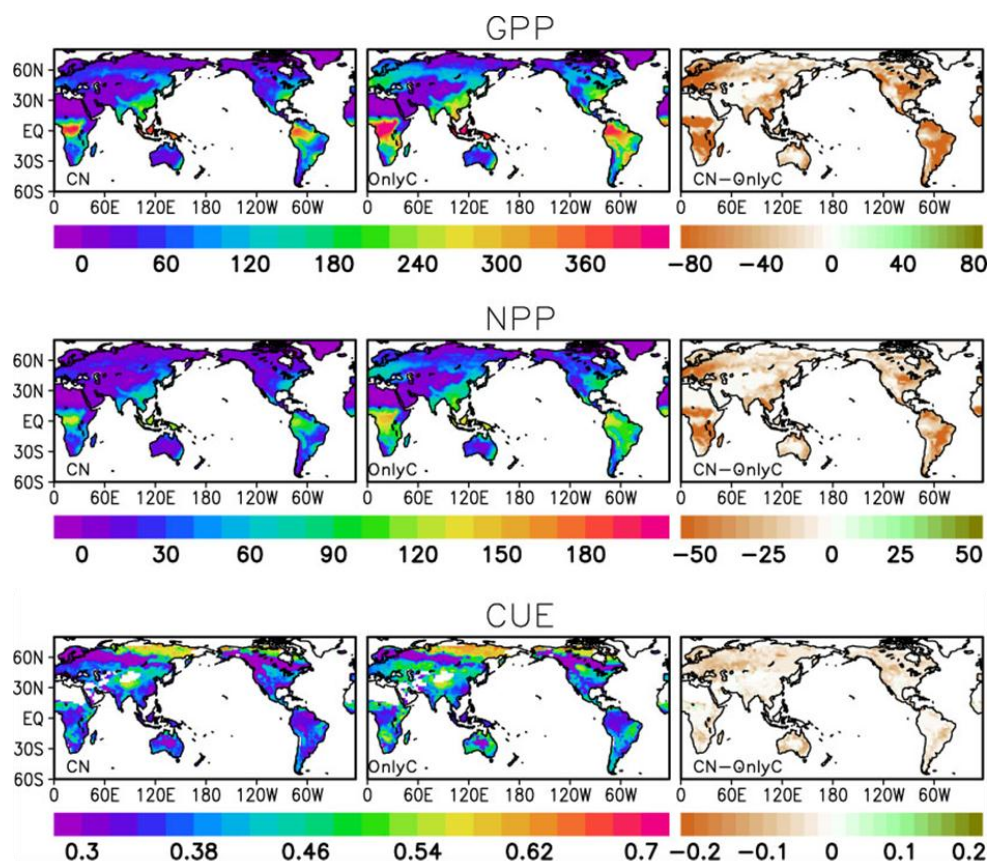
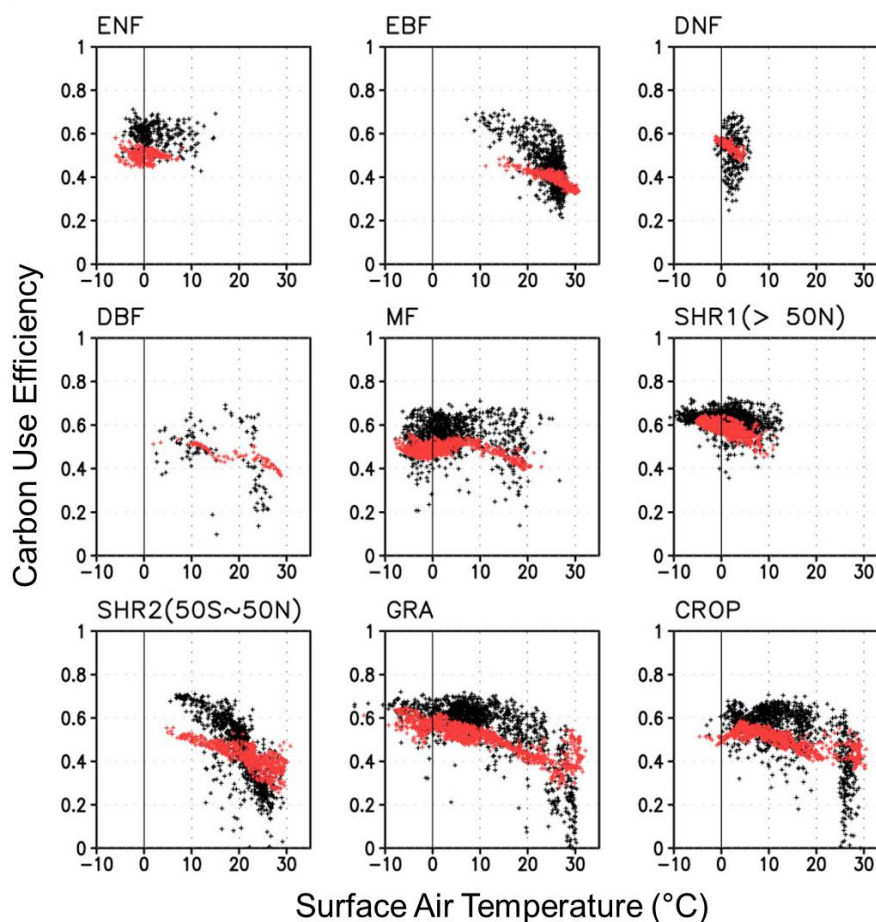


Figure 13. Spatial distributions of annual GPP, NPP and CUE and their differences from the interactive carbon-nitrogen cycle simulation (CN) and the run with no nitrogen cycle (Only C) by CESM-BGC. The units of GPP and NPP are $\text{gC m}^{-2} \text{mon}^{-1}$. CUE is a positively-defined ratio as NPP divided by GPP and less than or equal to 1.



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883 **Figure 14.** Scatter plots of CUE (y-axis) as a function of temperature (x-axis). Each panel
 884 shows the plot for different PFT. Satellite-derived values from MODIS are presented with black
 885 dots and the multi-model ensemble (MME) means by 10 ESMs are with red dots.

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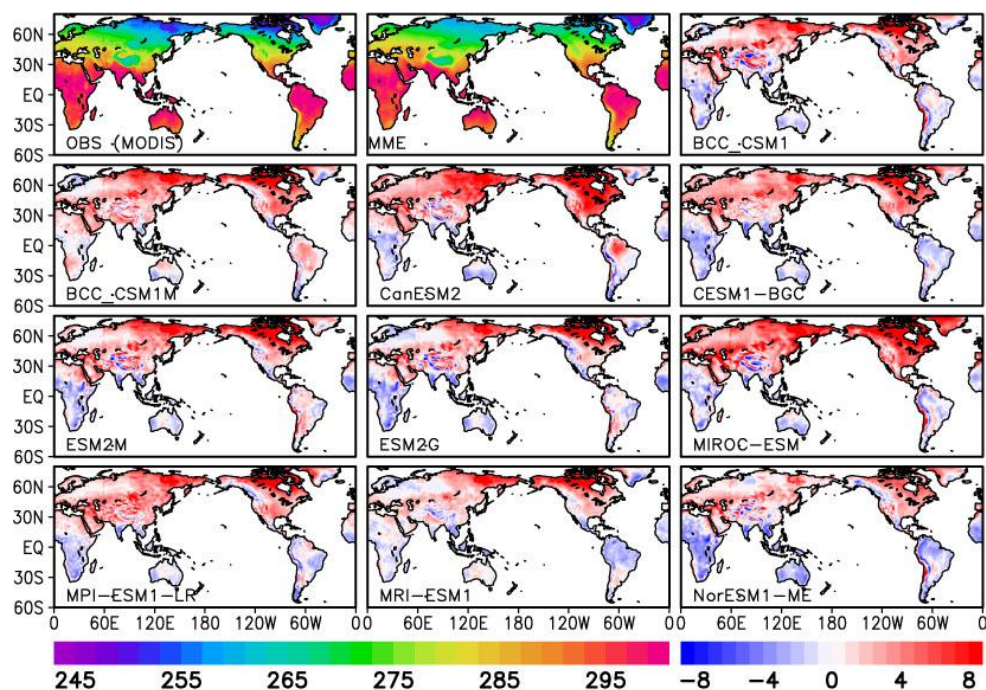


Figure S1. Spatial distribution of annual-mean surface air temperature from the CRU observation (top left), MME (top middle) and the simulation bias in each model (model minus CRU). The unit is K.

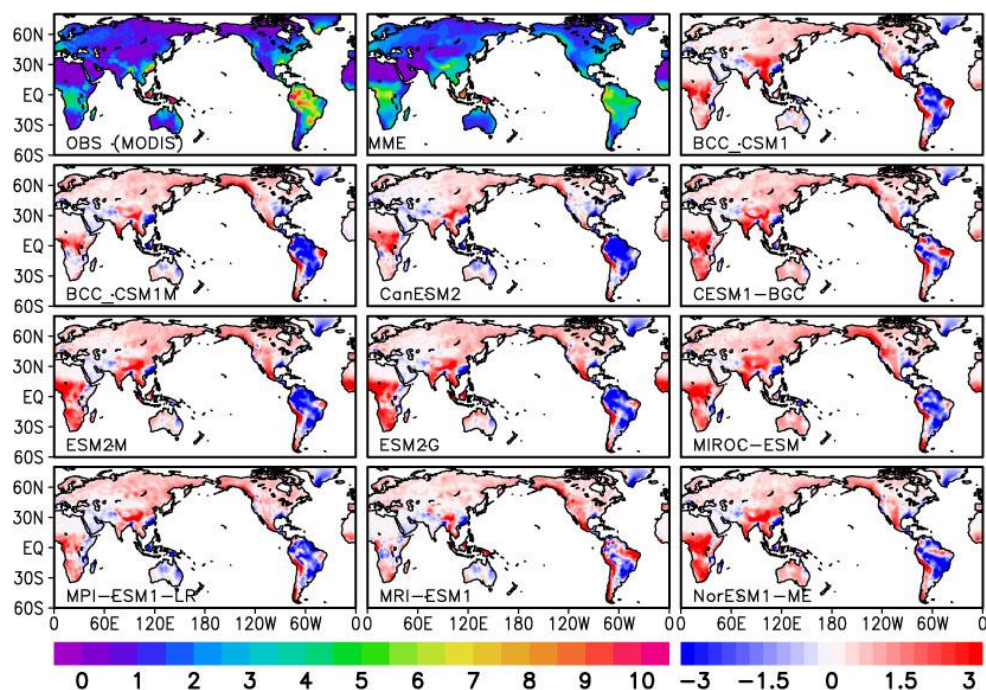


Figure S2. Spatial distribution of annual-mean precipitation from the CRU observation (top left), MME (top middle) and the simulation bias in each model (model minus CRU). The unit is mm d^{-1} .

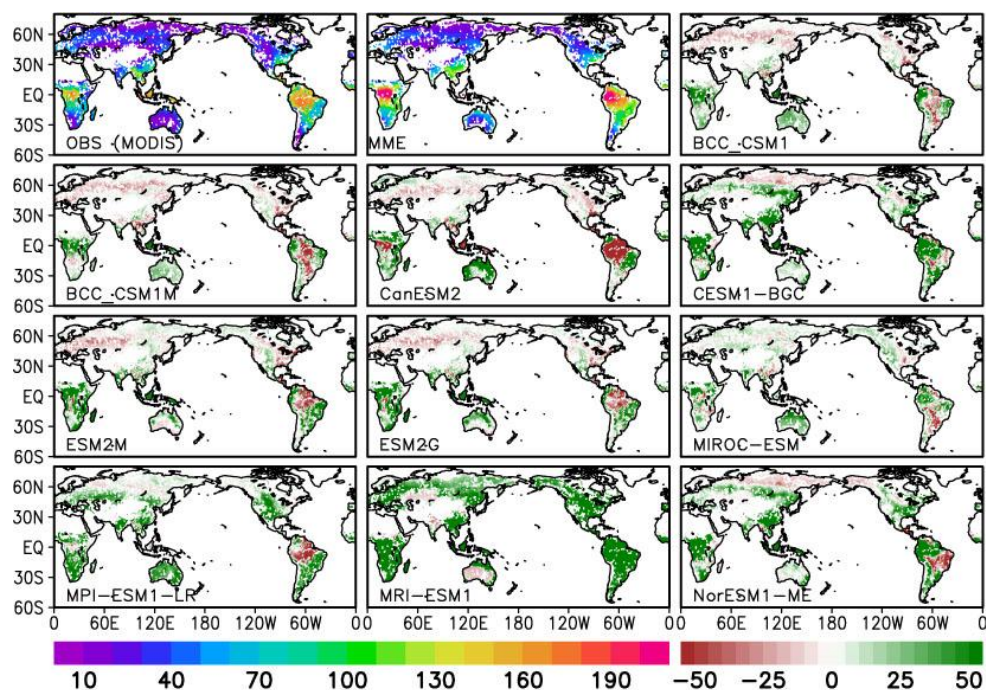
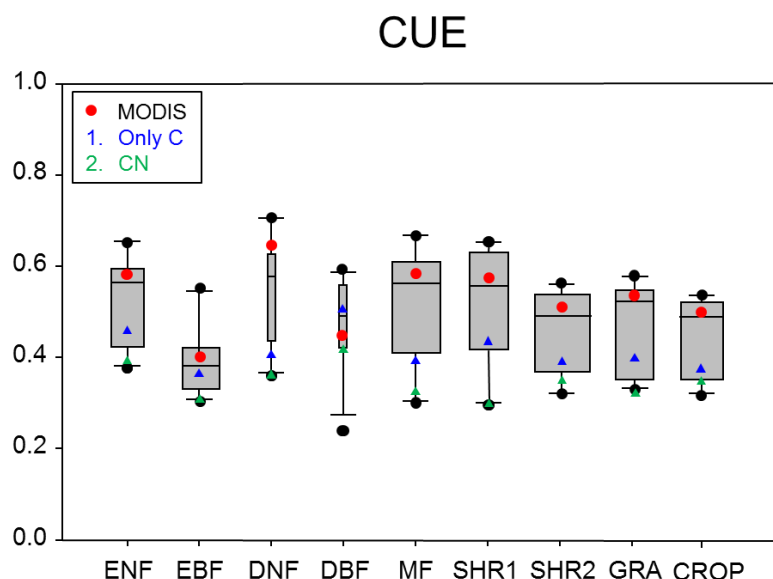


Figure S3. Spatial distribution of annual Ra from the MODIS observation (top left), MME (top middle) and the simulation bias in each model (model minus MODIS). The unit is $\text{gC m}^2 \text{mon}^{-1}$.



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 917 **Figure S4.** Simulated CUE averaged for each PFT in the two model sensitivity experiments
 918 using NCAR CEMS-BGC. CN (green triangles) indicates the run with interactive CN cycle
 919 and Only C (blue triangles) indicates the run that the nitrogen limitation effect is disabled.
 920 MODIS is also shown in red dots. The box widths are proportional to the root mean square of
 921 number of grids. The coefficients of proportionality box widths in each PFTs are: ENF (0.80),
 922 EBF (0.48), DNF (0.12), DBF (0.11), MF (1.25), SHR1 (0.91), SHR2 (1.78), GRA (0.70) and
 923 CROP (0.73).

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