Importance of carbon dioxide physiological forcing to future climate change

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An increase in atmospheric carbon dioxide (CO_2) concentration influences climate both directly through its radiative effect (i.e., trapping longwave radiation) and indirectly through its physiological effect (i.e., reducing transpiration of land plants). Here we compare the climate response to radiative and physiological effects of increased CO_2 using the National Center for Atmospheric Research (NCAR) coupled Community Land and Community Atmosphere Model. In response to a doubling of CO_2, the radiative effect of CO_2 causes mean surface air temperature over land to increase by 2.86 ± 0.02 K ($\pm$1 standard error), whereas the physiological effects of CO_2 on land plants alone causes air temperature over land to increase by 0.42 ± 0.02 K. Combined, these two effects cause a land surface warming of 3.33 ± 0.03 K. The radiative effect of doubling CO_2 increases global runoff by 5.2 ± 0.6%, primarily by increasing precipitation over the continents. The physiological effect increases runoff by 8.4 ± 0.6%, primarily by diminishing evapotranspiration from the continents. Combined, these two effects cause a 14.9 ± 0.7% increase in runoff. Relative humidity remains roughly constant in response to CO_2-radiative forcing, whereas relative humidity over land decreases in response to CO_2-physiological forcing as a result of reduced plant transpiration. Our study points to an emerging consensus that the physiological effects of increasing atmospheric CO_2 on land plants will increase global warming beyond that caused by the radiative effects of CO_2.

global warming | runoff | evapotranspiration | hydrological cycle | plant stomata

Increased atmospheric CO_2 content affects global climate not only through its greenhouse radiative effect, but also through its effect on plant physiology. Plant stomata open less widely under elevated CO_2 concentrations, leading to reduced plant transpiration (1–3). A decrease in canopy transpiration tends to reduce evapotranspiration (the sum of canopy evaporation, canopy transpiration, and soil evaporation), triggering changes in atmospheric water vapor and clouds, and affecting surface radiative fluxes, thus producing changes to temperature and the water cycle. This driver of climate change, referred to as "CO_2-physiological forcing," has been detected in both field experiments (4, 5) and climate modeling studies (3, 6–11).

In this study, we examine the climate effect of CO_2-physiological forcing using a coupled global atmosphere-land surface model (12, 13). While previous studies have looked at the response of temperature and runoff to CO_2-physiological forcing, the focus of this study is to examine the nature of climate response to CO_2-physiological forcing in terms of both magnitude and pattern, and contrast it with the effect of CO_2-radiative forcing. Most previous modeling studies on the climate effect of CO_2-physiological forcing (6–11) were performed within the modeling framework of the Met office Hadley Center models using the "MOSES" scheme (7) as the underlying land surface model. Here we employ the National Center for Atmospheric Research (NCAR) Community Land Model version 3.5 (CLM3.5) (12) coupled with the Community Atmosphere Model version 3.5 (CAM3.5) (13) to investigate the physiological effect of doubling atmospheric CO_2, relative to the radiative effect. This study provides an independent evaluation of the role of CO_2-physiological forcing in CO_2-induced climate change.

Results

We performed four 100-year simulations using the CLM3.5/CAM3.5 model coupled with a mixed-layer version of the CCSM3 ocean/thermodynamic sea-ice model (refer to the *Methods* section for detailed descriptions of the model used and simulations performed). Results presented here are annual mean climate change averaged over the last 70 yr of 100-year simulations involving an atmospheric CO_2 concentration of 800 ppm relative to a model control simulation forced with an atmospheric CO_2 concentration of 400 ppm. The model has reached quasiequilibrium for the last 70-year simulations: The drift in surface air temperature is at most on the order of 1×10^{-3} K per year and the interannual variability as measured by the standard deviation of global mean surface temperature is 0.07 K (Fig. S1). The effect of CO_2-physiological forcing is represented by simulated climate change in which the calculations of plant physiology used a CO_2 value of 800 ppm, but the calculations of radiative transfer used the control concentration of 400 ppm. Similarly, the effect of CO_2-radiative forcing is represented by simulated climate change in which the calculations of radiative transfer used a CO_2 concentration of 800 ppm, but the calculations of plant physiology used a CO_2 concentration of 400 ppm. The combined effect of CO_2 radiative and physiological forcing is represented by simulated climate change in which the calculations of both plant physiological and radiative transfer used a CO_2 concentration of 800 ppm. We note that the focus of this study is to investigate climatic response to changes in plant physiology (through reduced opening of plant stomata with increasing CO_2) and does not include additional effects from potential changes in leaf area index and vegetation distributions, both of which are fixed in the simulations performed here.

Fig. 1 shows the simulated response of latent heat flux, low cloud cover, and net solar flux at the surface to a doubling of atmospheric CO_2 in association with the radiative, physiological, and the combined radiative and physiological forcing. The latent heat flux increases almost everywhere in response to CO_2-radiative forcing because warming tends to increase the absolute water vapor pressure deficit in the boundary layer, driving additional evaporation. In contrast, in response to CO_2-physiological forcing, there is a general decrease in latent heat flux over land, particularly over heavily vegetated areas such as Central and Southern Africa and the Amazon basin. This decrease in latent heat flux is mainly a result of decreased canopy transpiration due

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GEOPHYSICS

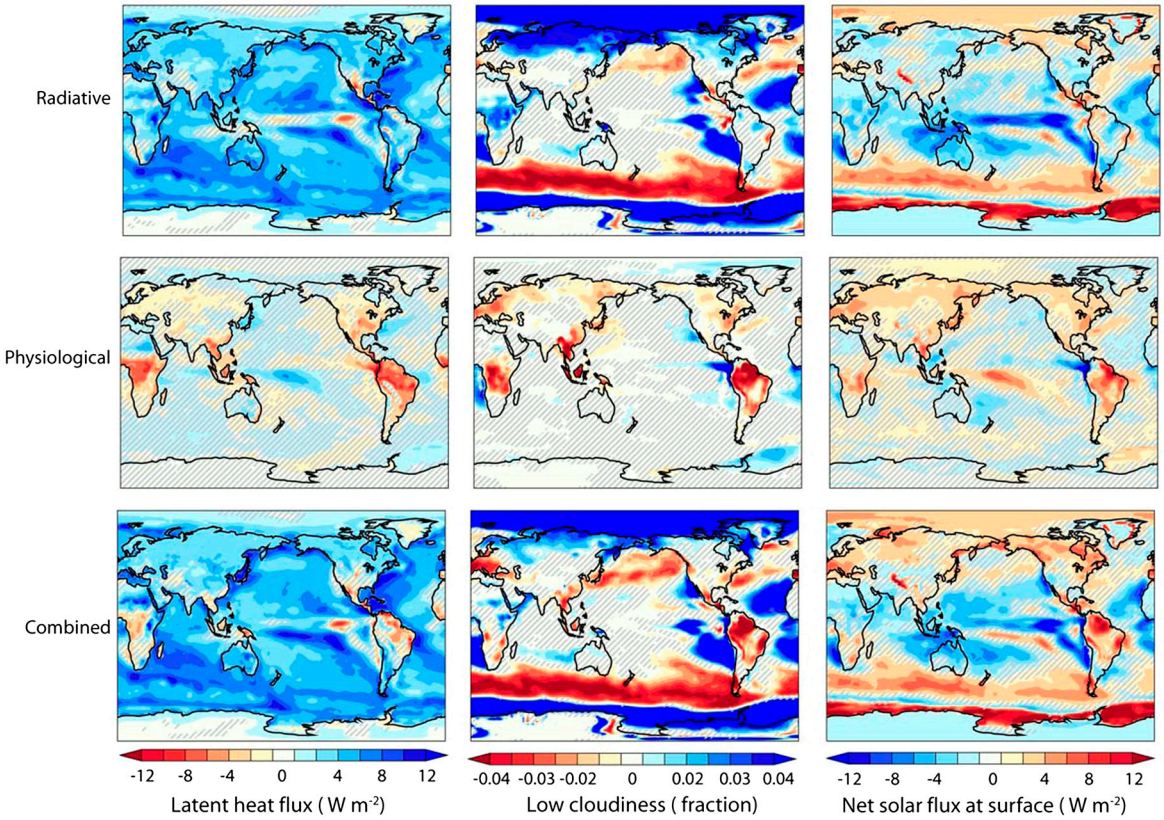

Fig. 1. Changes in latent heat flux, low-level cloudiness, and net solar flux at surface in response to CO_2-radiative forcing, CO_2-physiological forcing, and combined CO_2-radiative and physiological forcing. They are averaged annual mean changes in response to a doubling of atmospheric CO_2 calculated from the last 70-yr results of 100-yr simulations. Hatched areas are regions where changes are *not* statistically significant at the 5% level using the Student t-test.

to less widely opened plant stomata and the resultant increase in stomatal resistance at higher atmospheric CO_2 concentrations (Fig. S2 and Table S1). Averaged over land, the latent heat flux to the atmosphere increases by 2.85 ± 0.09 Wm^{-2} in association with CO_2-radiative forcing, compared to a decrease of 1.54 ± 0.08 Wm^{-2} in association with CO_2-physiological forcing (Table 1). These changes in latent heat flux in response to CO_2-radiative and physiological forcing affect cloud cover and radiative fluxes at the surface. In response to CO_2-radiative forcing there is a general increase in low-level cloudiness over the land, increasing planetary albedo and causing less solar radiation to reach the surface (Fig. 1 and Fig. S3). In contrast, in response to CO_2-physiological forcing, low cloud cover decreases over most of the land surface, reducing planetary albedo and causing more solar radiation to reach the surface (Fig. 1 and Fig. S3).

It can be seen from Figs. 2 and 3 that the inclusion of CO_2-physiological forcing modifies changes in temperature and greatly modifies changes in the hydrological cycle that is caused by CO_2-radiative forcing alone. Our simulations show that over 19.2% of the land surface (including parts of the boreal forest regions and parts of the Amazon and Southern Africa) more than 20% of the total surface warming (the warming caused by the combined CO_2-radiative and physiological effect) is caused by the CO_2-physiological effect (Fig. 3). Averaged over the global land, for a doubling of atmospheric CO_2 the effect of CO_2-physiological forcing contibutes to a surface warming of 0.47 ± 0.04 K, accounting for 14.1 ± 1.2% of the surface warming caused by the combined CO_2-radiative and physiological effect (3.33 ± 0.03 K) (Table 1). Over the surface ocean, the warming caused by CO_2-physiological forcing is 7.5% of that caused by the combined CO_2-radiative and physiological effect.

Continental runoff, which is the movement of water from land to oceans in the form of rivers and streams, represents freshwater availability and in steady state is equal to the excess of precipitation relative to evapotranspiration over land. At the global scale, the CO_2-radiative effect increases runoff by 5.2 ± 0.6% (Table 1) primarily by increased precipitation over the land (Fig. S4), whereas the physiological effect of CO_2 doubling leads to a 8.4 ± 0.6% increase in surface runoff (Table 1) mainly as a result of diminished evapotranspiration from the continents (Fig. S4). At the regional scale, the effect of CO_2-physiological forcing on runoff is particularly pronounced in the Amazon and Central and Southern Africa (Fig. 2). In these regions, the inclusion of CO_2-physiological forcing either enhances the projected increase in runoff associated with CO_2-radiative forcing or reverses the sign of runoff change that is projected to decrease in response to CO_2-radiative forcing alone. Some areas, particularly the eastern Amazon basin, show a reduction in runoff in response to CO_2-physiological forcing. This reduction in runoff is a result of reduced precipitation in these areas, which more than offsets the effect from reduced evapotranspiration (Fig. S4).

Changes in relative humidity show distinctly different responses to CO_2-radiative and physiological forcing (Fig. 2), suggesting that water vapor responds differently to these two forcings. In response to CO_2-radiative forcing, near-surface relative humidity changes by less than 1% over most of the Earth's surface, indicating that the change in atmospheric water vapor is primarily controlled by temperature-induced feedbacks following the Clausius-Clapeyron relationship (14, 15). In contrast, relative humidity decreases over most of the land area in response to CO_2-physiological forcing with decreases as large as 7% observed over parts of the Amazon and Central Africa (Fig. 2). This decrease in relative humidity is associated with the diminished source of water vapor to the atmosphere as a result of decreased canopy transpiration. The different responses of water vapor to CO_2-radiative and physiological forcing can also be seen from

Table 1. Climate responses to CO_2-radiative forcing, CO_2-physiological forcing, and the combined effect of CO_2-radiative and physiological forcing, as a result of CO_2 doubling.

	RAD – CTR	PHYS – CTR	RAD + PHYS – CTR
	Change in surface energy balance (Wm^{-2})*		
Latent heat flux over globe	4.26 ± 0.05	−0.29 ± 0.04	4.12 ± 0.05
Latent heat flux over land	2.85 ± 0.09	−1.54 ± 0.08	1.59 ± 0.09
Sensible heat flux over globe	−1.17 ± 0.02	0.58 ± 0.02	−0.62 ± 0.02
Sensible heat flux over land	−0.30 ± 0.05	2.11 ± 0.04	1.75 ± 0.05
Surface net shortwave flux over globe	−0.65 ± 0.04	0.54 ± 0.04	−0.09 ± 0.04
Surface net shortwave flux over land	−0.85 ± 0.08	1.62 ± 0.08	0.82 ± 0.08
Surface net longwave flux over globe	−3.68 ± 0.04	0.25 ± 0.03	−3.53 ± 0.03
Surface net longwave flux over land	−3.36 ± 0.09	1.06 ± 0.07	−2.46 ± 0.08
	Change in key climate variables		
Surface air temperature (K)	2.50 ± 0.02	0.22 ± 0.02	2.78 ± 0.02
Surface air temperature over ocean (K)	2.36 ± 0.02	0.15 ± 0.02	2.55 ± 0.02
Surface air temperature over land (K)	2.86 ± 0.02	0.42 ± 0.02	3.33 ± 0.03
Precipitation (%)	5.21 ± 0.06	−0.32 ± 0.05	4.96 ± 0.06
Precipitation over land (%)	6.13 ± 0.26	0.38 ± 0.24	7.35 ± 0.29
Precipitable water (%)	16.80 ± 0.18	0.87 ± 0.12	18.17 ± 0.16
Runoff (%)	5.16 ± 0.60	8.38 ± 0.61	14.87 ± 0.70
Low cloudiness (fraction)	0.0060 ± 0.0003	−0.0022 ± 0.0003	0.0037 ± 0.0003
Low cloudiness over land (fraction)	0.0105 ± 0.0004	−0.0102 ± 0.0003	0.0003 ± 0.0003

RAD – CTR represents the effect of CO_2-radiative forcing; PHYS – CTR represents the effect of CO_2-physiological forcing; RAD + PHYS – CTR represents the combined effect of CO_2-radiative and CO_2-physiological forcing from a doubling of CO_2. All results are annual mean values averaged from the last 70-yr results of 100-yr simulations. Percent changes represent values in the experiment minus the control cases, divided by the value in the control case. Fractional changes represent the fraction in the experiment minus the fraction in the control. Uncertainties are represented by ±1 standard error calculated from the last 70-yr results of 100-yr simulations. Also refer to Table S1 for a list of changes in other fields.

The effect of CO_2-physiological forcing can also be obtained by subtracting the results of RAD – CTR from the results of RAD + PHYS – CTR, which gives the effect of CO_2-physiological forcing under $2 \times CO_2$ background climate. The effect of CO_2-physiological forcing diagnosed this way is in broad agreement with the results of PHYS – CTR. However, there is some nonlinearity in the system. For example, the effect of CO_2-physiological forcing on surface temperature diagnosed from the difference between RAD + PHYS – CTR and RAD – CTR is 0.28 K, which is somewhat higher than the value of 0.22 K diagnosed from the results of PHYS – CTR.

*Shortwave fluxes are positive downward (from the atmosphere to the surface). Other fluxes are positive upward (from the surface to the atmosphere).

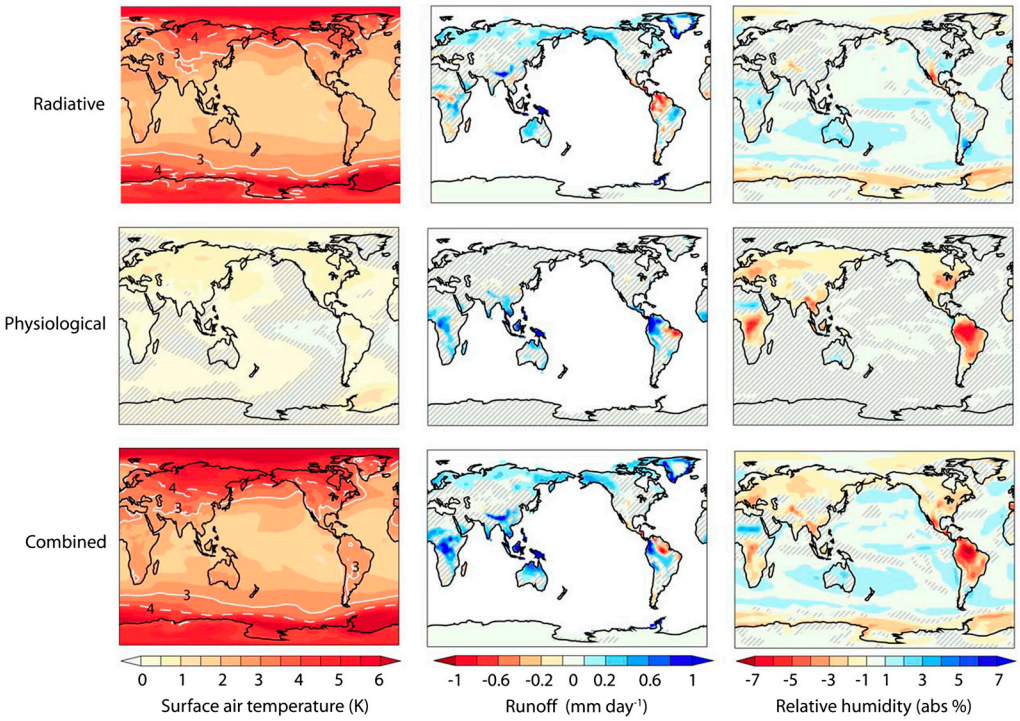

Fig. 2. Changes in surface air temperature, runoff, and near-surface relative humidity in response to CO_2-radiative forcing, CO_2-physiological forcing, and combined CO_2-radiative and physiological forcing. They are averaged annual mean changes in response to a doubling of atmospheric CO_2 calculated from the last 70-yr results of 100-yr simulations. Hatched areas are regions where changes are *not* statistically significant at the 5% level using the Student t-test. Isolines for temperature changes of 3K (*white solid lines*) and 4K (*white dashed lines*) are plotted for the case of CO_2-radiative and combined CO_2-radiative and physiological forcing to highlight the differences between these two.

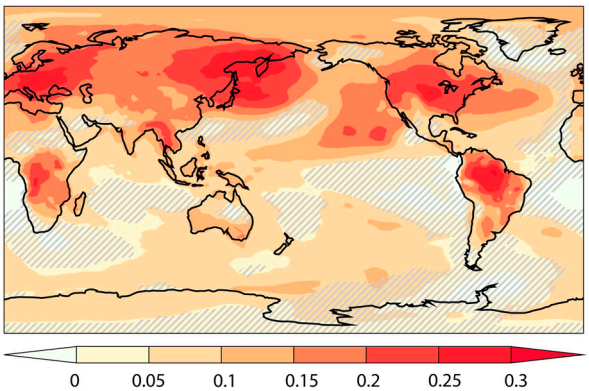

Fig. 3. Fraction of total surface warming (warming caused by the combined CO_2-radiative and physiological effects) associated with the physiological forcing of CO_2. The fractional contribution of warming due to CO_2-physiological forcing is calculated as the ratio between changes in surface air temperature in response to the CO_2-physiological forcing and temperature change in response to the combined effect of CO_2-radiative and physiological forcing. These changes are averaged annual mean values in response to a doubling of atmospheric CO_2 calculated from the last 70-yr results of 100-yr simulations. Hatched areas are regions where changes are *not* statistically significant at the 5% level using the Student t-test.

changes in water vapor content per degree of warming (Fig. S5). Globally averaged, precipitable water increases by $6.7 \pm 0.1\%$ per degree of warming in response to CO_2-radiative forcing, following the Clausius-Clapeyron relationship that governs the relationship between temperature and saturation water vapor pressure. In contrast, in response to CO_2-physiological forcing, precipitable water increases by $4.0 \pm 0.5\%$ per degree of warming, which is only about 60% of what would be predicted from the Clausius-Clapeyron relationship. This response suggests that in addition to temperature-induced feedbacks, water vapor change in association with CO_2-physiological forcing is strongly controlled by its diminished source from reduced canopy transpiration (refer to *SI Text* for a detailed analysis of water vapor response).

Discussion

We have investigated the climate effects of CO_2-physiological forcing, relative to that of radiative forcing, under a fixed distribution of vegetation type and leaf area index. Changes in both leaf area index and vegetation structure would have additional effects on temperature and the hydrological cycle, but these effects depend strongly on the strength of vegetation feedbacks and the timescales involved (6, 9, 16). It was reported in an early study (6) that when the vegetation dynamics reaches new equilibrium under doubling CO_2 concentrations, the net effect of plant response to a doubling CO_2 is a cooling of 0.1 K over land because surface cooling from increased leaf area index offsets surface warming caused by CO_2-physiological forcing. But a study from multicentury simulations forced by increasing CO_2 emissions reported a land warming of 1.4 K as a result of decreased surface albedo associated with the expansion of boreal forest (16). Recently, it was reported that at the time of CO_2 doubling the influence of CO_2-physiological forcing on runoff is not significantly modified by changes in leaf area index and vegetation distribution (9).

Our results highlight the importance of CO_2-physiological forcing in the projection of changes in temperature and the hydrological cycle. The results obtained here are in general agreement with previous studies based on the "MOSES" land surface scheme coupled with different versions of the Hadley center climate model (6, 7, 9, 10) (Table 2). The effect of CO_2-physiological forcing on surface temperature is quite consistent between different studies: in response to a doubling of CO_2, mean surface warming over land in association with CO_2-physiological forcing accounts for 11% to 16% of the warming caused by the combined effect of CO_2-radiative and physiological forcing. The relative strength of CO_2-physiological forcing on continental runoff differs more between models: in response to a doubling of CO_2, increases in runoff in association with CO_2-physiological forcing account for 27% to 65% of the runoff increase caused by the combined effect of CO_2-radiative and physiological forcing. Discrepancies in modeled changes in both evapotranspiration and precipitation (Table 2) are responsible for discrepancies in the effect of CO_2-physiological forcing on runoff between models. Nevertheless, our results, together with previous findings, consistently point to the importance of CO_2-physiological forcing in the projection of changes in global temperature and the hydrological cycle.

Our results have important implications for the conventional Global Warming Potential (GWP) concept. GWP is something of a misnomer; it is really a "Global Radiative Forcing Potential" as it measures the time integrated radiative forcing resulting from the radiative effects of greenhouse gases in the atmosphere, ignoring the warming effects from other mechanisms, such as warming associated with plant physiological forcing. Our results indicate that a substantial fraction of the warming from carbon dioxide emissions results from CO_2-physiological forcing that is not considered in the GWP measure. Thus, using a measure to evaluate the relative importance of different greenhouse gases based on the potential of an emission to warm the Earth's surface, rather than the GWP, would decrease the relative importance of non-CO_2 greenhouse gases by about 10% if based on global mean

Table 2. Comparison of model-simulated climate responses to the physiological effect of doubling CO_2

	This study*	Sellers et al. (1996)	Betts et al. (1997)	Cox et al. (1999)	Betts et al. (2007)	Boucher et al. (2009)†
Evapotranspiration over land (mm day^{-1})	−0.054 ± 0.004	−0.045		−0.07		−0.04
Surface air temperature over land (K)	0.47 ± 0.04	0.3	0.2	0.39		0.52
Fractional contribution of surface warming over land from CO_2-physiological forcing‡	16.4 ± 0.7%	10.7%		11.3%		12.9%
Runoff (mm day^{-1})	0.082 ± 0.005			0.04	0.04	0.03
Fractional contribution of runoff increase from CO_2-physiological forcing‡	65.2 ± 11%			57.1%	37.2%	27.3%
Precipitation over land (mm day^{-1})	0.028 ± 0.01	−0.01	−0.02	−0.03	0.01	−0.01

*To be consistent with the method used in other studies, the CO_2-physiological effect shown here is calculated from the difference between the results of RAD + PHYS − CTR and RAD − CTR listed in Table 1.

†The CO_2-physiological effect reported by Boucher et al. (10) was calculated from the transient simulations under the IS92a emission scenario, which have a CO_2 increase somewhat more than a doubling.

‡The fractional contribution of changes in temperature and runoff due to CO_2-physiological forcing is calculated as the ratio between changes in temperature and runoff in response to CO_2-physiological forcing and their changes in response to the combined effect of CO_2-radiative and physiological forcing.

temperature and by about 14% if based on global mean land temperature. (This calculation is merely a rough estimate based on equilibrium warming, as a more detailed evaluation would depend on the specifics of how the measure is defined, thermal lags in the climate system, and other issues.) If the goal is to provide a measure to help determine more cost-effective ways to balance emissions of various greenhouse gases to diminish global warming, it might be useful to base a measure on the potential of a gas to produce warming, rather than on the potential to produce radiative forcing. Radiative forcing is an important part, but is only part, of the picture. A metric that is based on radiative forcing alone will also fail to take into consideration other factors including changes in the hydrological cycle. For many applications, what is really desired is a measure that can estimate damage resulting from a greenhouse gas emission, but such inclusive measures are in practice difficult to implement.

To estimate the contribution of CO_2-physiological forcing to historical warming, additional simulations were performed in which the effect of CO_2-physiological forcing was assessed at a CO_2 level of 390 ppm, relative to a preindustrial level of 280 ppm. In our simulations for a CO_2 increase from 280 to 390 ppm, surface warming associated with CO_2-physiological forcing is 0.14 ± 0.02 K, accounting for $11.3 \pm 1.3\%$ of the 1.24 ± 0.02 K warming caused by the combined CO_2 radiative and physiological effects. This estimate is for equilibrium climate change including only the effect of CO_2. The current temperature increase, which has not reached equilibrium in response to anthropogenic forcings because of the thermal inertial of the ocean, should be smaller. Ensemble transient simulations using fully coupled atmosphere and ocean models are needed to better quantify the effect of CO_2-physioloigical forcing on historical and future climate change.

Our results show that temperature and the hydrological cycle respond quite differently to CO_2-radiative and physiological forcing. The effect of these two forcings is roughly additive. That is, the combined effect of CO_2-radiative and physiological forcing can be well represented by the linear sum of these two effects (Table 1 and Fig. S6). In addition to surface climate, atmospheric climate in its vertical distribution shows distinctly different responses to CO_2-radiative and physiological forcing (Fig. S7). Because reduced plant transpiration, as a result of increased atmospheric CO_2 concentration, diminishes a source of water vapor to the atmosphere, water vapor change in response to CO_2-physiological forcing is less than what would be predicted from the Clausius-Clapeyron relationship governing temperature-induced water vapor change. This finding is consistent with a previous study on CO_2-physiological forcing (10) and has important implications for our understanding of changes in water vapor associated with climate change. Through changes in plant transpiration and/or ground evaporation, CO_2-physiological forcing and/or land use change will affect atmospheric water vapor via changes in its sources, in addition to the temperature-induced feedback. Therefore, climate change triggered by CO_2-physiological forcing and/or land use change would cause different responses in atmospheric water vapor and relative humidity from that triggered by changes in radiative forcing. The distinct signature of water vapor change may allow the detection of climate change signals caused by CO_2-physiological forcing and/or land cover change, as compared to that caused by changes in greenhouse gas and aerosol radiative forcing.

Methods

Model. The atmosphere model used here, CAM3.5 (13), has a horizontal resolution of 1.9° latitude by 2.5° longitude and has 26 vertical levels. To allow for interactions between the atmosphere and ocean, the model is coupled to a mixed-layer version of CCSM3 ocean model. For the mixed-layer ocean model simulations, the mixed-layer depths were prescribed to climatological values, and the prescribed ocean heat transport was derived from the net energy flux over the ocean surface in a climatological simulation with prescribed sea surface temperature. The atmosphere model is coupled with a land surface model, CLM3.5 (12), which is an improved version of CLM3 (17). CLM3.5 represents the land surface by sixteen different plant functional types (PFT) and simulates a number of biophysical processes for each PFT, such as stomatal physiology and photosynthesis, interactions of energy and water fluxes with vegetation canopy and soil, and the surface hydrology. Leaf stomatal resistance, which is needed for the calculation of water vapor flux, is related to leaf surface temperature, CO_2 concentration, and water vapor pressure at the leaf surface (18). Compared to CLM3, CLM3.5 has a more realistic simulation in the partitioning of evapotranspiration, which is of great importance for a reliable simulation of the climate effect from CO_2-physiological forcing (19) (also see *SI Text*).

Simulation and Analysis. Four 100-year simulations were performed using the coupled CAM3.5/CLM3.5 model and the annual mean results of the last 70 yr of the simulations were used for analysis: (*i*) a control simulation (CTR) in which both atmospheric radiative transfer and plant physiology were forced by an atmospheric CO_2 concentration of 400 ppm (here we use a round number of 400 ppm to approximately represent the modern-day atmospheric CO_2 concentration); (*ii*) a CO_2-radiative forcing simulation (RAD) in which the radiative transfer model was forced by $2 \times CO_2$ concentration of 800 ppm, but the calculations of plant physiology were carried out with $1 \times CO_2$ of 400 ppm; (*iii*) a CO_2-physiological forcing simulation (PHYS) in which the calculation of plant physiology was forced by $2 \times CO_2$ of 800 ppm, but the calculation of radiative transfer was carried out with $1 \times CO_2$ of 400 ppm; (*iv*) a simulation in which the calculations of both the radiative transfer and plant physiology were forced with $2 \times CO_2$ of 800 ppm (RAD + PHYS). The difference between RAD and CTR represents the effect of CO_2-radiative forcing, and the difference between PHYS and CTR represents the effect of CO_2-physiological forcing. In addition, the difference between RAD + PHYS and CTR provides the effect of combined CO_2-radiative and physiological forcing.

Statistical analysis was performed on the last 70-yr results of 100-yr model simulations. Because of autocorrelation in time series, the actual number of degrees of freedom is less than (or equal to) the number of sample years (70 here). Here, we calculated the actual degrees of freedom by taking into account autocorrelation in time series (20). Then the standard error was calculated and the Student t-test was performed using the calculated actual number of degrees of freedom.

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