LETTERS

Projected increase in continental runoff due to plant responses to increasing carbon dioxide

Richard A. Betts[1], Olivier Boucher[1], Matthew Collins[1], Peter M. Cox[1,2], Peter D. Falloon[1], Nicola Gedney[3], Deborah L. Hemming[1], Chris Huntingford[4], Chris D. Jones[1], David M. H. Sexton[1] & Mark J. Webb[1]

In addition to influencing climatic conditions directly through radiative forcing, increasing carbon dioxide concentration influences the climate system through its effects on plant physiology[1]. Plant stomata generally open less widely under increased carbon dioxide concentration[2], which reduces transpiration[1,3–6] and thus leaves more water at the land surface[7]. This driver of change in the climate system, which we term 'physiological forcing', has been detected in observational records of increasing average continental runoff over the twentieth century[8]. Here we use an ensemble of experiments with a global climate model that includes a vegetation component to assess the contribution of physiological forcing to future changes in continental runoff, in the context of uncertainties in future precipitation. We find that the physiological effect of doubled carbon dioxide concentrations on plant transpiration increases simulated global mean runoff by 6 per cent relative to pre-industrial levels; an increase that is comparable to that simulated in response to radiatively forced climate change (11 ± 6 per cent). Assessments of the effect of increasing carbon dioxide concentrations on the hydrological cycle that only consider radiative forcing[9–11] will therefore tend to underestimate future increases in runoff and overestimate decreases. This suggests that freshwater resources may be less limited than previously assumed under scenarios of future global warming, although there is still an increased risk of drought. Moreover, our results highlight that the practice of assessing the climate-forcing potential of all greenhouse gases in terms of their radiative forcing potential relative to carbon dioxide does not accurately reflect the relative effects of different greenhouse gases on freshwater resources.

Physiological forcing of the hydrological cycle by CO_2 has been shown to be the major cause of historical increases in continental-scale runoff[8]. However, predictions of future runoff change due to anthropogenic climate change generally do not consider this[9–11], partly because uncertainty in precipitation change is considered to be the main limitation[9].

We performed a perturbed-physics ensemble of 224 doubled-CO_2 experiments with the HadSM3 climate model, which is a mixed-layer ocean version of the HadCM3 general circulation model[12,13] but including the MOSES land surface scheme[4,8]. The simulated runoff depends on precipitation (both amount and intensity) and evapotranspiration (the sum of evaporation and transpiration), and the latter also affects climate through the surface energy and moisture budgets[4]. Transpiration depends on canopy conductance, the large-scale aggregate of stomatal conductance that responds to temperature, humidity, soil moisture and photosynthetically active radiation, and CO_2 concentration[4,14–17].

Each of the 224 experiments used a different version of HadSM3. The versions differed in the values assigned to certain key model parameters[12], with multiple parameters perturbed concurrently[13]. Each experiment consisted of a pair of simulations using the same model version, one simulation with pre-industrial CO_2 and one with doubled CO_2. Such techniques allow the variation of results between ensemble members to give some indication of uncertainty in the predicted climate response[12,18].

In our ensemble, one perturbation was the choice of whether to include physiological responses to the CO_2 increase. All 224 ensemble members included radiative forcing due to CO_2, but 81 members also included physiological forcing while the remaining 143 members did not. These two sub-ensembles are labelled RADPHYS and RAD respectively. The number of members of RADPHYS and RAD was an arbitrary consequence of the procedure for selecting members of the 224-member ensemble for general purposes, and not a specific selection for this work alone. We were therefore able to extend the ensemble technique to examine the effect of a particular parameter, in this case the switch for the inclusion of physiological forcing, in the context of uncertainties arising from variations in the other parameters (see Methods).

In our analysis, Y_1 and Y_2 represent 20-year area mean runoff for the pre-industrial (subscript 1) and doubled-CO_2 (subscript 2) members of an individual pair of simulations, ΔY is the difference within a pair, and $\overline{Y}_1$, $\overline{Y}_2$ and $\overline{\Delta Y}$ represent the means over a sub-ensemble. Similar notation holds for precipitation P, with area means taken over land only, and for r, which is the ratio of Y to P:

$$Y = rP \qquad (1)$$

The sub-ensemble mean global runoff in the control simulations ($\overline{Y}_1$) was approximately 2% higher in RADPHYS than RAD (Table 1), but the standard deviations in Y_1 were an order of magnitude larger than this difference and a t-test showed the difference in $\overline{Y}_1$ to be not statistically significant. Global runoff increased with doubling CO_2 in all pairs of simulations in both RADPHYS and RAD; the ensemble-mean increase $\overline{\Delta Y}$ was 43 ± 15 kg m^{-2} yr^{-1} in RADPHYS, but only 27 ± 11 kg m^{-2} yr^{-1} in RAD (Table 1, Fig. 1a). This difference in $\overline{\Delta Y}$ was significant at the 0.1% level. The doubled-CO_2 runoff increase was therefore approximately 59% larger when physiological forcing is included in this set of simulations.

Global P and $\overline{P}$ also increased with doubling CO_2 in both RADPHYS and RAD (Table 1, Fig. 1b), and the sub-ensemble mean $\overline{\Delta P}$ was greater in RADPHYS. Although this might appear inconsistent with a relative reduction in the return of moisture to the atmosphere because of relatively decreased transpiration, it is consistent with the enhanced warming seen over land (Fig. 1c) arising from the reduced evaporative cooling[1,3,4]. The reduced recycling of moisture over land was offset by an increase in moisture convergence from over the oceans.

[1]Met Office Hadley Centre, Fitzroy Road, Exeter EX1 3PB, UK. [2]School of Engineering, Computing and Mathematics, Exeter University, Exeter EX4 4QF, UK. [3]Met Office, Joint Centre for Hydro-Meteorological Research, [4]Centre for Ecology and Hydrology, Maclean Building, Wallingford, Oxfordshire, OX10 8BB, UK.

Table 1 | Physiological forcing effects on global mean precipitation, runoff and runoff/precipitation ratio

	RAD	RADPHYS	RADPHYS − RAD	RAD_DV	RADPHYS_DV	RADPHYS_DV − RAD_DV
$\overline{Y}_1$	252 ± 54	257 ± 57	5	220	220	0
$\overline{Y}_2$	279 ± 49	300 ± 56	21	227	238	11
$\Delta\overline{Y}$	27 ± 11	43 ± 15	16	7	18	11
$\overline{P}_1$	682 ± 102	731 ± 104	49	706	702	−4
$\overline{P}_2$	718 ± 108	769 ± 109	51	706	691	−15
$\Delta\overline{P}$	36 ± 16	38 ± 19	2	0	−11	−11
$\overline{r}_1$	0.37 ± 0.05	0.35 ± 0.05	−0.02	0.31	0.31	0
$\overline{r}_2$	0.39 ± 0.05	0.39 ± 0.05	0.00	0.32	0.34	0.02
$\Delta\overline{r}$	0.02 ± 0.01	0.04 ± 0.01	0.02	0.01	0.03	0.02
$\dfrac{\overline{\Delta Y}}{Y_1}$ (%)	11 ± 6	17 ± 5	6	3	8	5
$\dfrac{\overline{\Delta P}}{P_1}$ (%)	5 ± 2	5 ± 3	0	0	−2	−2
$\dfrac{\overline{\Delta r}}{r_1}$ (%)	6 ± 4	12 ± 4	6	3	10	7

Y and P are given in units of kg m^{-2} yr^{-1}. Standard deviations refer to variations in the long-term means of experiments within a sub-ensemble. RAD_DV and RADPHYS_DV results are 30-year means for 2000–2030 (subscript 1) and 2070–2100 (subscript 2) in one pair of transient simulations with dynamic vegetation, with no standard deviations because only one experiment was performed.

However, $\Delta\overline{P}$ was only 6% greater in RADPHYS than RAD (significant at 5%). For a given global ΔP, the global ΔY was generally higher in RADPHYS than in RAD (Fig. 1d). $\overline{r}$ increased by 0.02 on doubling CO_2 in RAD (Table 1), possibly as a result of the warmer climate featuring more intense precipitation that exceeded the infiltration rate of the soil more often than at present-day levels of CO_2. However, $\overline{r}$ increased by 0.04 on doubling CO_2 in RADPHYS, consistent with a reduction in transpiration.

To quantify the relative contribution of changes in precipitation and evapotranspiration to the runoff changes, we approximate the total change in runoff Y in terms of separate contributions from changes in P and r, as a percentage of the baseline runoff:

$$\frac{\Delta Y}{Y_1} = \frac{\Delta P}{P_1} + \frac{\Delta r}{r_1} \qquad (2)$$

This linear approximation is found to be valid for Y and P in both RAD and RADPHYS (Table 1). The differences in the means of $\Delta Y/Y_1$, $\Delta P/P_1$ and $\Delta r/r_1$ between RADPHYS and RAD are approximately 6%, 0 and 6% respectively (Table 1). This demonstrates that increases in r are the dominant cause of the greater increase in Y in RADPHYS than RAD.

At continental scales (Fig. 2 and Supplementary Information), where P increased with doubling CO_2 such as in Asia (Fig. 2b, Supplementary Table 2), North America (Fig. 2d, Supplementary Table 4), and in most ensemble members in Europe (Fig. 2c, Supplementary Table 3) and Oceania (Fig. 2e, Supplementary Table 5), Y increased more in RADPHYS than in RAD. Where P decreased, such as in most ensemble members in South America (Fig. 2f, Supplementary Table 6) and in a large number of ensemble members in Africa (Fig. 2a, Supplementary Table 1), Y decreased less or increased more in RADPHYS than in RAD. Indeed in Europe, $\overline{P}$
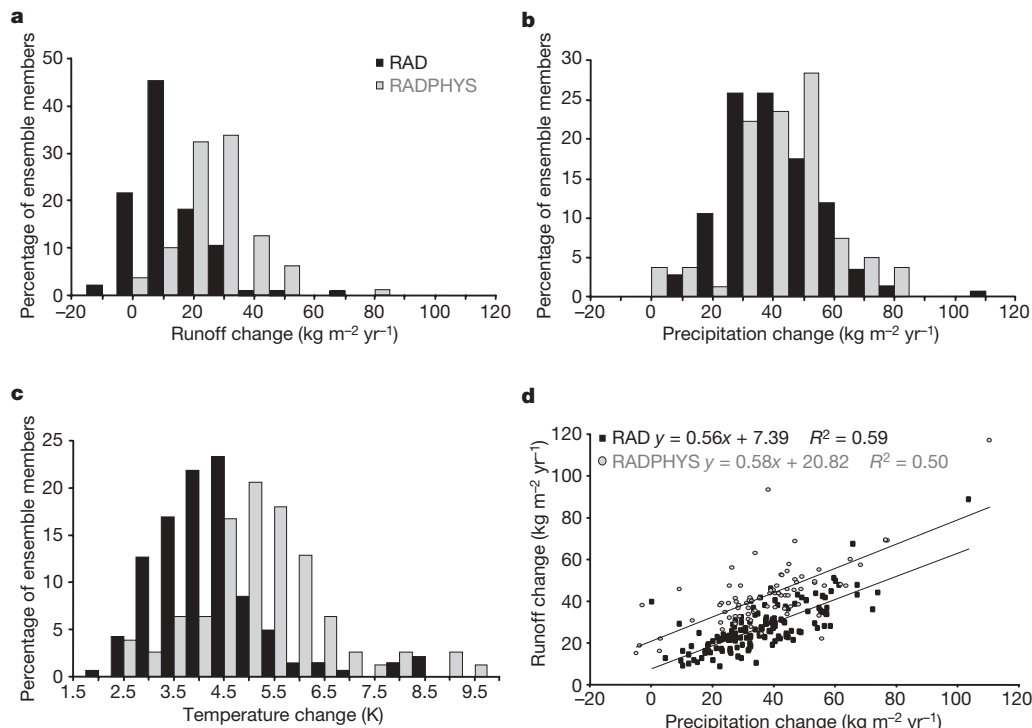

Figure 1 | Impact of physiological forcing on global mean runoff, precipitation and temperature. a, Frequency distribution of simulated changes in global mean runoff due to doubling CO_2 in a 224-member perturbed-physics global climate model ensemble, with physiological forcing included (RADPHYS) and excluded (RAD). **b,** As for **a** but for precipitation over land. **c,** As for **a** but for near-surface air temperature over land. **d,** Global mean runoff changes versus global land mean precipitation changes due to doubling CO_2 in 224 ensemble members, with physiological forcing included and excluded.

increased less in RADPHYS than RAD, whereas $\overline{Y}$ increased more in RADPHYS (Supplementary Table 3). Similarly in Africa, $\overline{P}$ decreased more in RADPHYS than RAD, whereas $\overline{Y}$ increased in RADPHYS but decreased in RAD (Supplementary Table 1). In all cases, $\overline{r}$ increased more in RADPHYS than RAD at the continental scale as well as the global scale.

A further aspect of physiological forcing is CO_2 fertilization of photosynthesis, which can affect changes in leaf area index and vegetation distribution[3,18,19]. Increased leaf area index can act to increase canopy conductance and potentially offset stomatal closure, and changes in leaf area index and vegetation type can also affect climate through changes in land surface properties such as albedo and aerodynamic roughness[3,20,22,23]. Changes in leaf area index and vegetation distribution were not included in RAD and RADPHYS. Previous studies[18,21] showed increased Y with physiological forcing for a number of models that included dynamic vegetation and variable leaf area index, but these did not include feedbacks to the atmosphere, which may bias the result. To provide a more complete assessment directly comparable with the current work, we performed two additional simulations RAD_DV and RADPHYS_DV including dynamic vegetation[24], variable leaf area index and an ocean general circulation model[25]. In RAD_DV, CO_2 acted only as a greenhouse gas, whereas in RADPHYS_DV, CO_2 changes affected stomatal closure and also fertilized photosynthesis. These were transient simulations to account for vegetation dynamics timescales, driven by the IS92a CO_2 concentration scenario[26] in which CO_2 approximately

doubles at the end of the twenty-first century compared to the present day. In both simulations, large-scale vegetation dynamics were included, but in RAD_DV the vegetation responded only to climate change, whereas in RADPHYS_DV the vegetation also responded to physiological forcing through both stomatal responses and fertilization of photosynthesis.

Both RADPHYS_DV and RAD_DV simulated increasing Y as CO_2 increased, but RADPHYS_DV showed a more rapid increase (Table 1). RAD_DV simulated very little change in global land mean P, despite an increase in overall global (land+ocean) mean precipitation, as a result of significant decreases in Amazonia and some other regions offsetting increases elsewhere. RADPHYS_DV simulated a decrease in P, largely because the decrease over Amazonia was greater than in RAD. This was partly a result of reduced transpirational return of moisture to the atmosphere, and partly a result of a northward shift in the Inter-Tropical Convergence Zone attributed to increased Northern Hemisphere warming due to a net reduction in canopy conductance and decreased surface albedo arising from increased leaf area[19]. However, despite this difference in ΔP being opposite in sign to the difference in $\Delta \overline{P}$ between the RAD and RADPHYS ensembles that excluded dynamic vegetation, the difference in $\Delta r/r_1$ between RADPHYS_DV and RAD_DV was 7%, which is similar to the 6% difference between RADPHYS and RAD. This suggests that the influence of physiological forcing on r is not significantly modified by changes in leaf area index or vegetation distribution, at least at the global scale. Nevertheless, we note the potential
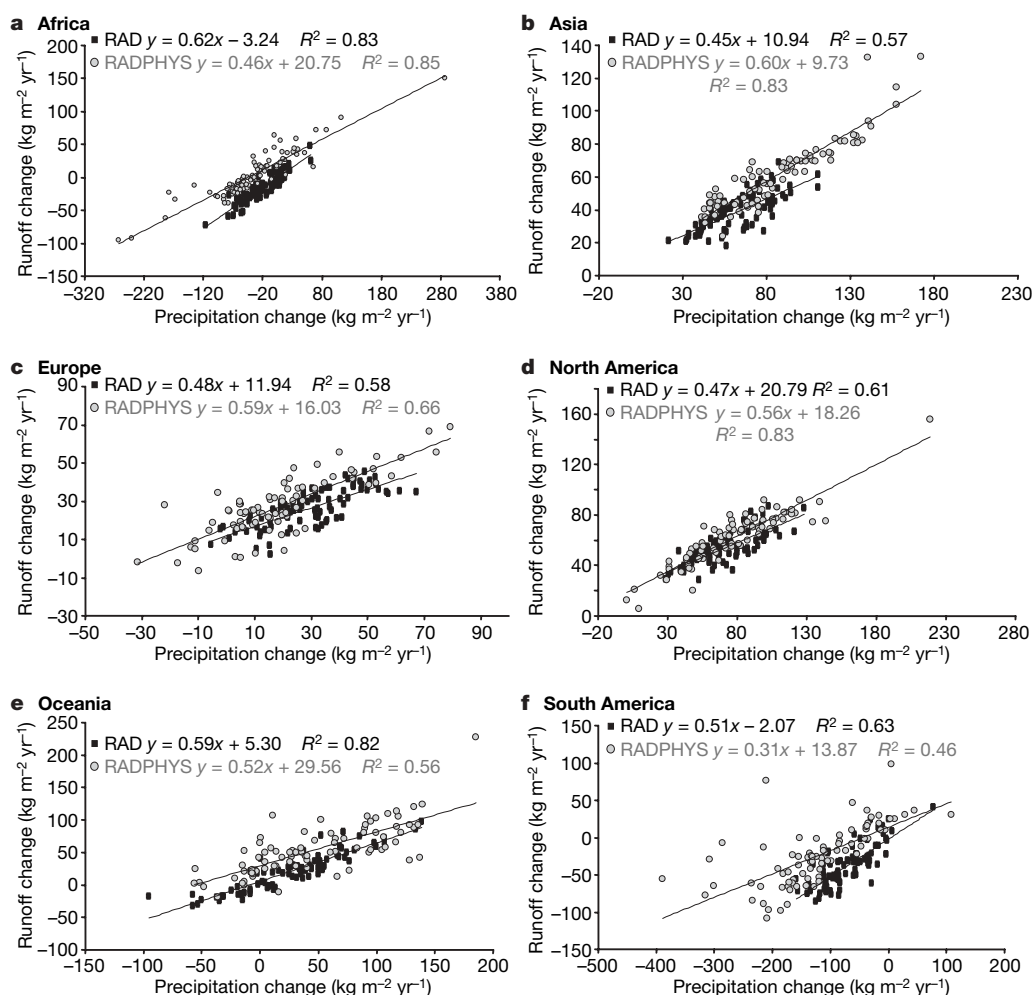

Figure 2 | Impact of physiological forcing on relationship between changes in runoff and precipitation on doubling CO_2. Continental mean runoff changes versus precipitation changes due to doubling CO_2 in 224 ensemble members, with physiological forcing included (RADPHYS) and excluded (RAD). **a**, Africa; **b**, Asia; **c**, Europe; **d**, North America; **e**, Oceania; **f**, South America.

for large impacts of vegetation dynamics on ΔY at regional scales, through both the local effects of transpiration changes and the remote effects of precipitation change induced by vegetation changes elsewhere.

Because the effect of physiological forcing on doubled-CO_2 runoff changes is important even in the context of uncertainties in precipitation change, assessments of climate change impacts on future flood and drought risk should take this into account. With greater increases and smaller decreases in runoff due to physiological forcing, the risks of rain and river flooding may increase more than has previously been anticipated, because intense precipitation events would be more likely to occur over saturated ground. In contrast, the risks of hydrological drought may not increase as much as expected on the basis of meteorological changes alone. However, reduced precipitation is not completely negated by physiological forcing, so some regions may still experience increased drought.

The strong influence of physiological forcing on runoff also raises an important issue regarding the comparison of CO_2 with other greenhouse gases. The United Nations Framework Convention on Climate Change (UNFCCC)[27] requires that concentrations of different greenhouse gases are routinely compared in terms of a 'CO_2 equivalent', which for non-CO_2 greenhouse gases is conceptualized as the concentration of CO_2 which would exert the same influence on climate. The UNFCCC and the Kyoto Protocol currently quantify this with global warming potentials (GWPs) based on radiative forcing[28].

However, this assumes that radiative forcing is the only mechanism through which greenhouse gases influence climate. Because this work and previous work[7,8,18,21] have shown that hydrological impacts are also affected to a comparable extent by physiological forcing by CO_2, and because most other greenhouse gases, such as CH_4, N_2O and the chlorofluorocarbons, do not exert physiological forcing, radiative-forcing-based metrics give an incomplete indication of the relative effects of the different greenhouse gases on hydrological impacts. For example, CH_4 has a 100-year GWP of 23, suggesting that it is 23 times 'more potent' than CO_2 in influencing climate. However, CH_4 does not exert a physiological forcing (except indirectly by producing CO_2), so its effect on hydrological impacts relative to CO_2 may be considerably less than that implied by the GWP. O_3 is another example of a greenhouse gas that is likely to exert a physiological forcing, because it affects plant functioning directly as a poison. Moreover, atmospheric aerosols can affect surface evaporation through changes in the surface radiation budget[29], and can also affect P through changes in cloud droplet size[28]. Other chemical species such as ammonia can affect plant physiology (and hence hydrology) but do not exert radiative forcings. Water resources and flood risk are among the most frequently cited issues of concern over climate change[10,30], so we consider that the conventional GWP-based concept of 'CO_2 equivalent' is incomplete and additional metrics for comparing greenhouse gases in terms of hydrological impacts are required.

METHODS SUMMARY

The perturbed-physics ensemble technique involves performing a large number of simulations with multiple climate model versions, each with different values assigned to key parameters involved in the simulation of climate processes. Here we used an ensemble of 224 different versions of the HadSM3 climate model[12,13], each with its own unique combination of parameter values or settings. One parameter varied within the ensemble determines whether plant physiological processes respond to atmospheric CO_2 changes (hereafter the physiological forcing switch, PF). Arbitrarily, PF was 'on' in 81 members of the ensemble (RADPHYS), and 'off' in the remaining 143 (RAD). Two simulations were performed with each ensemble member, one simulation at climatic equilibrium with pre-industrial CO_2 and the other at climatic equilibrium with doubled CO_2. Each pair of simulations was termed one 'experiment'. In RAD, with PF 'off', plant physiological processes were simulated with the pre-industrial CO_2 concentration.

In Fig. 1d, each point shows the 20-year equilibrium mean runoff change versus the 20-year equilibrium mean precipitation change due to doubling CO_2 for one experiment. In Fig. 1a–c, the grey and black bars show percentages of experiments in the RADPHYS and RAD sub-ensembles respectively for which the runoff, precipitation or temperature changes lie between the increments shown on the x axis. Comparison between the grey and black bars lying between the same increments shows the relative frequency of a particular change in these quantities in experiments with and without PF. Further simulations RADPHYS_DV and RAD_DV were transient simulations additionally including changes in vegetation type and leaf area due to CO_2 and climate changes.

Our results rely on the accuracy of the parameterized transpiration sensitivity to CO_2 concentrations. We did not explicitly vary plant physiological parameters in our ensembles (aside from turning PF 'on' and 'off'), so we did not explore uncertainties in the response to physiological forcing to the same extent as those in the response to radiative forcing. However, our simulated reductions in transpiration under doubled CO_2 are consistent with experimental work using 'free-air CO_2 enrichment' (FACE) techniques[5,6]. Our model provides a near-optimal fit to observed increases in continental runoff[8] and is intermediate in the range of other models' responses of runoff to increasing CO_2 (refs 18 and 21).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Author Contributions R.A.B. proposed the study, performed the dynamic vegetation simulations and led the analysis and writing. D.L.H. performed statistical analysis of the ensemble simulations and contributed expertise on field experiments on plant physiology. P.D.F. analysed the dynamic vegetation simulations. P.M.C. developed the MOSES and TRIFFID models and contributed to the interpretation. C.D.J., N.G., C.H. and O.B. contributed to the analysis and provided further expertise on modelling plant physiology, hydrology and land–atmosphere interactions. M.C., D.M.H.S. and M.J.W. designed and performed the ensemble simulations and advised on their interpretation. All co-authors contributed to the text.

METHODS

The perturbed-physics ensemble technique has previously been used to begin to quantify the uncertainties in climate predictions arising from uncertainties in the values assigned to key parameters input to the HadSM3 climate model[12]. Most of the parameters are numeric quantities which have a range of possible values but which are assigned a particular value in the standard version of HadSM3[12,13]. Some parameters act as logical switches which determine whether particular processes are represented within the model; a particular example is the switch for plant physiological responses to changes in atmospheric CO_2 (PF), which is enabled in the standard version of HadSM3 but can be disabled if required. If this process is disabled, the plant physiological process calculations are assigned a fixed CO_2 concentration as an input term, so any changes in plant physiology are a response to changes in meteorological and hydrological changes only.

Each of the 224 slightly different versions of HadSM3 had its own unique combination of parameter values or settings. These combinations can be thought of as points in a 31-dimensional parameter space defined by the values of the numeric parameters and the 'on/off' settings of the logical switches. The values of numeric parameters were varied between maximum and minimum plausible values as judged by experts[12,13], with intermediate values as used in the standard version of HadSM3 also being used, The combinations of parameter values were selected partly to provide representative coverage of this parameter space, and not to examine the responses to any particular parameter. For the purposes of generating the ensemble, the two settings of the physiological forcing switch are considered equally likely. The ensemble was not designed to systematically examine the effect of switching PF "on" or "off", so there were no pairs of ensemble members which differed only in the setting of the PF switch individual. That is, the members of RADPHYS had no directly parallel equivalents in RAD.

While the two sub-ensembles therefore do not provide a perfect controlled experiment for examining the effects of physiological forcing, because combinations of other parameter values also differ, there is sufficient evidence to suggest that these other differences exert random effects on the climate and do not introduce any systematic bias in runoff or its response to doubling CO_2. The numbers of members in the RADPHYS and RAD sub-ensembles were sufficient to ensure that the differences between the two sub-ensemble mean changes were statistically significant at 1% for runoff and temperature and 5% for precipitation, but there was no statistically significant bias in the control simulations. Moreover, previous work[4] with a single pair of simulations with the same atmosphere–land model provides a controlled experiment supporting the results of our ensemble. That work[4] showed an increase in runoff of 26 ± 7 and $11 \pm 7 \, kg \, m^{-2} \, yr^{-1}$ with and without physiological forcing respectively (with standard deviations in that study referring to annual means in a single simulation).

An intercomparison of the responses of six vegetation models including our own[19] showed that all the models produced increased runoff due to physiological forcing by CO_2, and our model was intermediate in the range of responses. One recent FACE experiment[6] showed a localized warming of 1.4 K over a 20-m-diameter plot as a result of reduced transpiration due to increasing CO_2 from 380 p.p.m. to 550 p.p.m. The mean difference in global land average warming between RADPHYS and RAD was 0.96 K, for an increase in CO_2 from 280 to 540 p.p.m. This smaller increase in warming for a larger CO_2 rise may partly reflect the fact that our global land average results include areas with no vegetation.