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1 **Extending a first-principles primary production model to predict wheat yields**

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12 **Keywords**

13 wheat; photosynthesis; crop yield; crop model; CO₂ fertilization; harvest index

14 **Highlights**

- 15 1. A novel, simply formulated crop model with quantified uncertainties successfully predicts
16 wheat yields at research sites in China.
- 17 2. The model captures the time course of GPP and variations in biomass and yield across sites
18 and between years.
- 19 3. Sensitivity analyses and future projections indicate a positive response of wheat yield to rising
20 CO₂, partially counteracted by a negative response to warming.

21 **Data statement**

22 The climate and flux data from WeiShan can be obtained by contacting Huimin Lei
23 (leihm@tsinghua.edu.cn). The flux data for YuCheng , the climate, LAI, crop data used the in this
24 manuscript are publicly available from the National Ecosystem Research Network of China CNERN
25 (<http://www.cnern.org.cn/>). All climate data driving the PC model runs for future and the model outputs
26 of LPJmL, EPEIC, GEPIC are publicly available from Inter-Sectoral Impact Model Intercomparison
27 Project-2b (ISIMIP2b: <https://www.isimip.org/protocol/#isimip2b/>). The PC model code will be
28 available from Mendeley data.

29 **Abstract**

30 Climate exerts a major influence on crop development and yield. Despite extensive modelling efforts,
31 there is still considerable uncertainty about the consequences of a changing climate for the yields of
32 major crops. Existing crop models are complex and rely on many assumptions and parameters,
33 motivating a quest for more parsimonious models with stronger theoretical and empirical foundations.
34 This paper presents a prototype of such a model for wheat, informed by measurements of gross primary
35 production (GPP), biomass and yield at research sites across the wheat-growing regions of China. First,
36 GPP was predicted using a recently developed first-principles model driven only by climate, carbon
37 dioxide (CO₂) concentration, and light absorbed by leaves. Modelled GPP was shown to agree well
38 with eddy-covariance measurements. Second, the data were used to show that above-ground biomass
39 (AB) is proportional to time-integrated GPP, and that grain yield shows a saturating relationship with
40 AB. Simple empirical equations based on these findings were combined with modelled GPP to predict
41 yield, including propagated errors due to parameter uncertainty in both the GPP model and the

42 empirical equations. The resulting ‘hybrid’ model, applied in a variety of climates, successfully
43 predicted measured interannual variations in AB and yield. Third, the model was extended to include
44 a phenology scheme, a mass-balance equation relating mean leaf area index to accumulated GPP over
45 growth phase, and an independently observed response of leaf mass-per-area to CO₂. Sensitivity
46 analyses and scenario runs with this extended model showed a positive but saturating (at ~600 ppm)
47 response of yield to rising CO₂, consistent with experimental evidence. This positive effect was
48 partially counteracted by a net negative response of yield to increasing temperature, caused by
49 increasing photorespiration and an accelerated growth cycle.

50 **1. Introduction**

51 An adequate food supply is an essential basis for economic development and social stability in the
52 context of increasing population and continuing anthropogenic climate change (Porter et al., 2014). As
53 one of the world’s four major crops (with maize, rice and soybean), wheat provides about a quarter of
54 the world’s cereal production (FAOSTAT, 2018) which, in turn, provides two-thirds of human caloric
55 intake (Zhao et al., 2017). Wheat was introduced from the Near East and been cultivated in China since
56 the late 6th to early 5th millennium BP (Betts et al., 2014). China is now both the largest producer and
57 the largest consumer of wheat (Wang et al., 2009). Current wheat production in China exceeds 134 Mt
58 of grain per year. This is more than 17% of the total global wheat production, and about 22% of the
59 total cereal production of China (FAOSTAT, 2018). Thus, even a small fluctuation in China's wheat
60 production could potentially impact not only the Chinese economy but also global food security.

61 The growth and harvestable yield of wheat are determined by environmental factors (Asseng et
62 al., 2004) but also strongly influenced by management (He et al., 2015). Light, CO₂, temperature, water

63 and nutrient availability define the basic conditions for the growth and development of the crop. Light
64 and CO₂ directly affect photosynthesis (Gerbaud and Andre, 1980); temperature further influences
65 growth and development processes including germination, anthesis and harvest (Asseng et al., 2011;
66 He et al., 2015; Liu et al., 2018; Porter and Gawith, 1999; Tao et al., 2012); water and nutrient
67 availability principally influence foliage cover (Nielsen and Halvorson, 1991; Pan et al., 2019) and
68 therefore the absorption of light for photosynthesis. However, the basic conditions of wheat growth,
69 especially temperature and CO₂ concentration, are changing. Temperatures in China have risen by
70 1.2°C over the past few decades (Cao et al., 2017; Piao et al., 2010) and continued warming is expected
71 in the coming decades (Kirtman et al., 2014). Winter is warming faster than summer (Piao et al., 2010;
72 Wu et al., 2017) and this situation is potentially unfavorable to the production of wheat (Brooking,
73 1996). On the other hand, atmospheric CO₂ already exceeds 400 ppm, more than 40% above its pre-
74 industrial level and is expected to continue rising (Collins et al., 2014). For C₃ crops (including wheat)
75 the effect of rising CO₂ level on photosynthesis is positive (Ainsworth and Rogers, 2007; Boylan, 2016;
76 Sage et al., 1989), leading to higher photosynthetic productivity and potentially also grain yield
77 (Lawlor and Mitchell, 1991). Improved management practices (e.g. fertilization, irrigation) and crop
78 breeding have also contributed to increased wheat yield (Qin et al., 2015; Yu et al., 2019) under current
79 climate conditions, and this trend is expected to continue.

80 The combined effects of changes in climate, CO₂ and management are highly uncertain (Challinor
81 and Wheeler, 2008) and numerical models are needed to project future trends in yield in different
82 regions, and thereby to facilitate adaptation in the food production system. Such models should
83 integrate knowledge from experiments and observations with theoretical understanding. Crop models
84 have been under development for at least 40 years, and there are now many models with the technical

85 capacity to simulate the growth and development of wheat (Blanc, 2017; Huang et al., 2016; Palosuo
86 et al., 2011). However, current crop models require detailed input information that is challenging to
87 collect over large scales and potentially subject to change in a dynamic environment. Moreover, inter-
88 model comparisons have revealed large differences between model predictions of both current yields
89 and future trends (Liu et al., 2019; Nelson et al., 2014; Ostberg et al., 2018). This situation parallels
90 that for natural vegetation models (Prentice et al., 2015), and suggests that current crop models contain
91 untested and potentially incorrect assumptions. Recently, however, progress has been made in
92 developing simpler vegetation models, based on theoretical principles but drawing extensively on
93 empirical data to test each model component (Franklin et al., 2017; Wang et al., 2017). Here we adopt
94 this novel approach to develop a prototype model to predict wheat growth and yield.

95 The starting point for this model ('PC', for P crop: see Fig. 1) was the universal C₃ primary
96 production model 'P' (Stocker et al., 2019; Wang et al., 2017). The P model is a theoretically derived
97 and extensively tested light use efficiency (LUE) model that predicts gross primary production (GPP)
98 as a function of climate, absorbed light and CO₂ on time steps of a week to a month. Further model
99 development and testing of the PC model, presented here, used measurements of GPP, biomass and
100 yield at research sites across the wheat-growing regions of China. In the first step of the analysis, the
101 original P model was applied to predict GPP at two flux-tower sites situated in wheat crops in order to
102 test its performance. In the second step, simple empirical equations were fitted to experimental data at
103 several field research sites in order to relate accumulated GPP to aboveground biomass (AB), and AB
104 to grain yield. These equations were combined with the P model to predict yields for different sites and
105 years; these predictions were compared to observed yields. Uncertainties in predicted yields due to key
106 parameters of the P model, and to the fitted coefficients of the empirical equations, were quantified. In

107 the third step, the model was extended to represent the responses of yield to environmental change by
108 the inclusion of (a) a general scheme to predict phenology, (b) a mass-balance equation quantifying
109 leaf area index (LAI) consistent with a given GPP, and (c) an observed relationship between leaf mass-
110 per-area (LMA) and the CO₂ concentration experienced during crop growth. These extensions allowed
111 modelled light absorption to be influenced by changes in growing-season length, and changes in
112 modelled GPP to feed back to LAI. The extended model was applied at six field sites to project future
113 wheat yields under different combinations of increasing CO₂ and temperature, in a sensitivity analysis
114 for combinations of CO₂ and temperature increase, and in alternative scenario runs for future CO₂ and
115 temperature change.

116 **2. Material and methods**

117 **2.1 The P model**

118 The P model is based on the standard biochemical model of C₃ photosynthesis (Farquhar et al.,
119 1980), with additional formulations that allow photosynthetic capacities and stomatal behaviour to
120 acclimate to environmental conditions on weekly to monthly time scales (Wang et al., 2017).
121 Instantaneous photosynthetic rates according to the standard model are the lesser of the electron
122 transport-limited rate (A_J) and the carboxylation-limited rate (A_C). A_C is proportional to the Rubisco
123 capacity (V_{cmax}). In the P model, V_{cmax} is assumed to acclimate to growth conditions such that the two
124 rates are co-limiting under average daytime conditions (Maire et al., 2012; Smith et al., 2019). A_J is
125 proportional to the absorbed photosynthetic photon flux density (PPFD) at low PPFD, increasing with
126 PPFD towards a light-saturated rate that is proportional to the electron-transport capacity (J_{max}). In the
127 P model, acclimation of J_{max} parallels that of V_{cmax} and their ratio is set to maximize the benefit (A_J)

128 minus the cost of maintaining J_{\max} . Both A_C and A_J are functions of the leaf-internal CO₂ partial
 129 pressure (c_i), whose ratio (χ) to the ambient CO₂ partial pressure (c_a) is determined by stomatal
 130 responses to the relative rates of carbon gain and water loss. In the P model, χ is determined by the
 131 least-cost criterion (Prentice et al., 2014), which minimizes the combined costs of maintaining the
 132 Rubisco and water transport capacities. The three constraints (on V_{\max} , J_{\max} and χ) lead to an
 133 expression for weekly to monthly GPP under field conditions that has the mathematical form of a LUE
 134 model. That is, accumulated GPP is proportional to absorbed PPFD:

$$135 \quad \text{GPP} = \Phi_0 I_{\text{abs}} m \sqrt{[1 - (c^* / m)^{2/3}]} \quad (1a)$$

136 where

$$137 \quad m = (c_i - \Gamma^*) / (c_i + 2\Gamma^*) \quad (1b)$$

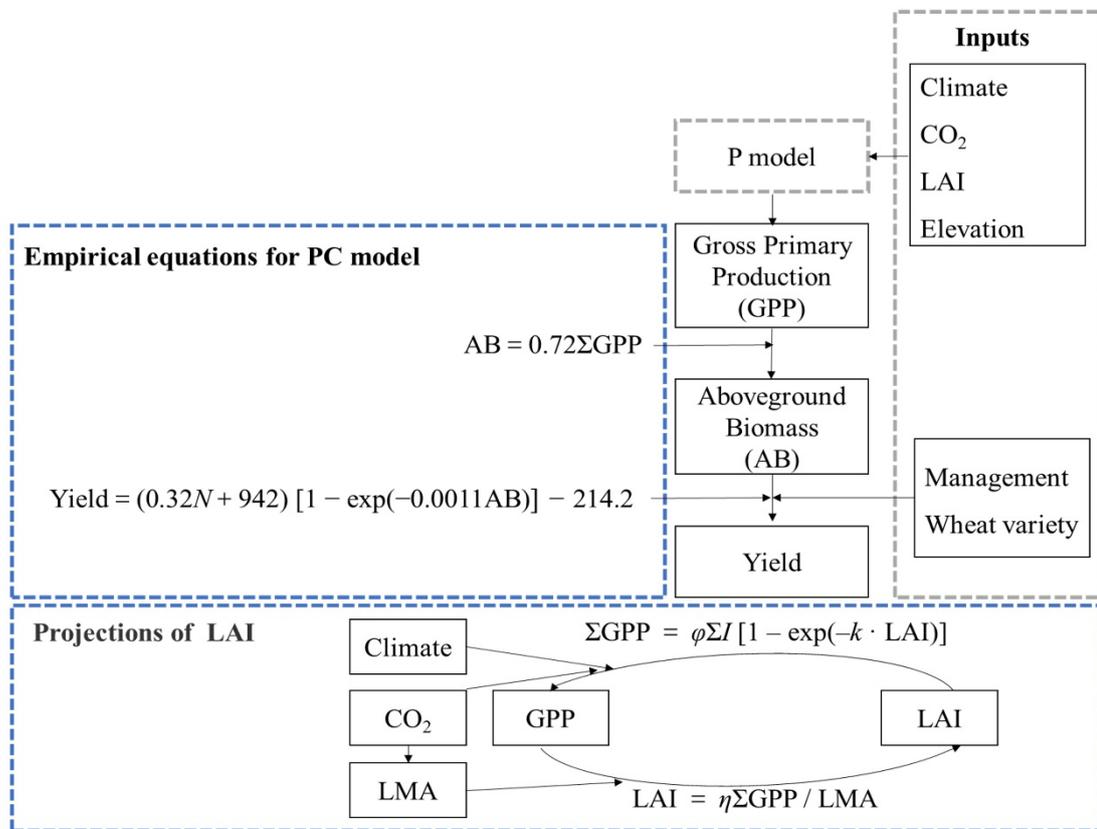
$$138 \quad c_i / c_a = \Gamma^* / c_a + (1 - \Gamma^* / c_a) \zeta / (\zeta + \sqrt{D}) \quad (1c)$$

$$139 \quad \zeta = \sqrt{[\beta (K + \Gamma^*) / 1.6\eta^*]} \quad (1d)$$

140 Here, Φ_0 is the intrinsic quantum yield (mol CO₂ mol⁻¹); I_{abs} is the PPFD intercepted and absorbed by
 141 the canopy (mol m⁻² s⁻¹); c_a is the ambient atmospheric CO₂ partial pressure (Pa); Γ^* is the
 142 photorespiratory compensation point (Pa); η^* is the viscosity of water, relative to its value at 25 °C
 143 (dimensionless); D is the vapour pressure deficit (Pa); K is the effective Michaelis-Menten coefficient
 144 of Rubisco (Pa); and $c^* = 0.41$ and $\beta = 146$ are dimensionless constants, where c^* has been estimated
 145 from observed $J_{\max} : V_{\max}$ ratios and β from observed stable carbon isotope ratios (Wang et al., 2017).

146 The P model thus calculates GPP as the product of I_{abs} , which is the product of incident PPFD and
 147 $f\text{APAR}$ (the fraction of incident PPFD absorbed by foliage) and LUE. LUE is the product of Φ_0 , m and

148 the square-root term in equation (1a). The parameters Γ^* , η^* and K depend on temperature (Bernacchi
 149 et al., 2001; Wang et al., 2017) and Γ^* and K depend on atmospheric pressure (Farquhar et al., 1980).
 150 The inputs to the model are air temperature (T), relative humidity (RH), incident PPFD, $fAPAR$,
 151 elevation (to calculate atmospheric pressure) and c_a (the product of the current year's mole fraction of
 152 CO_2 with atmospheric pressure). When driven by satellite-derived $fAPAR$ data, the model has been
 153 shown to reproduce monthly GPP well at eddy-covariance flux tower sites in natural vegetation
 154 worldwide (Stocker et al., 2019; Wang et al., 2017) and geographic patterns, seasonal cycles and
 155 interannual variability of GPP at flux tower sites located in different biomes, including croplands
 156 (Balzarolo et al., 2018).



157
 158 **Figure 1: The structure of the PC model.** ΣGPP : accumulated gross primary production over
 159 growing season ($g\ C\ m^{-2}$); N : total application of nitrogen ($kg\ N\ hm^{-2}$). LAI: leaf area index
 160 (dimensionless). φ : light use efficiency (%). ΣI : the sum of incident light over the growth phase (mol

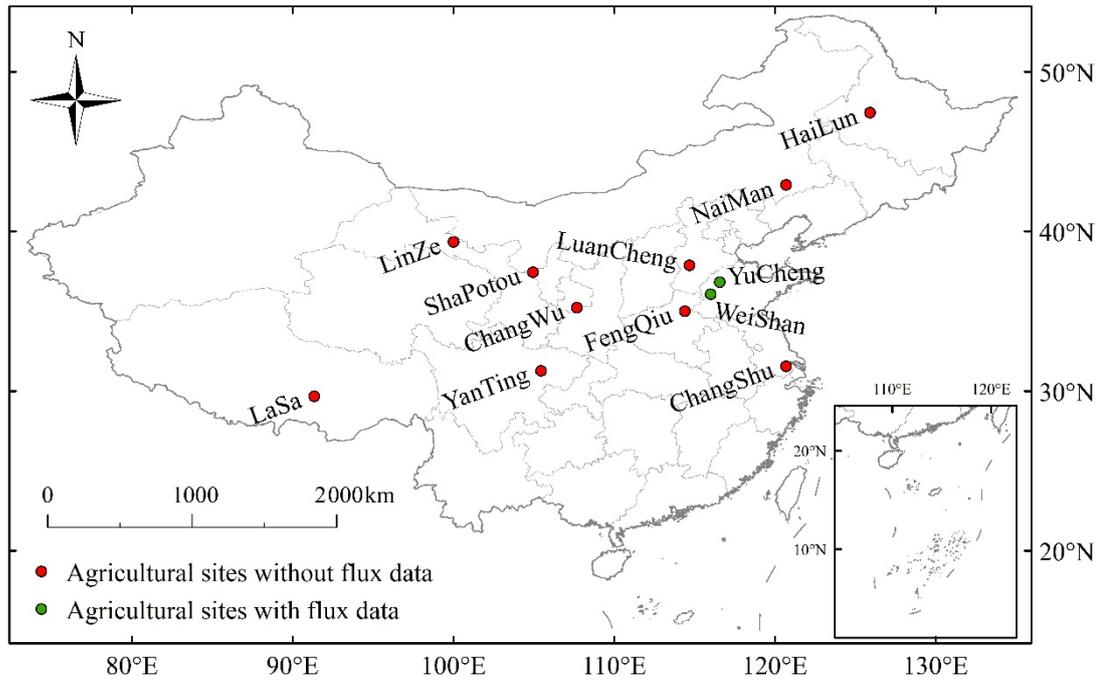
161 photo m^{-2}). k : a dimensionless constant, ($k = 0.5$). η : the fraction of ΣGPP allocated to leaves
162 (dimensionless). LMA: leaf mass per area (g m^{-2}). Climate here comprises temperature, relative
163 humidity and incident photosynthetic photon flux density. Boxes with grey dash line indicate the
164 already published model or known information, whereas the boxes with blue dash line indicate the
165 new model and its extension developed here.

166 We ran the P model on a weekly time step. The model has already been shown to work well on a
167 ten-daily time step (Balzarolo et al., 2018). We applied the ‘BRC’ model set-up (Stocker et al., 2019),
168 which differs from the original published version (Wang et al., 2017) by incorporating an observed
169 temperature-dependence of Φ_0 (Bernacchi et al., 2003):

$$170 \quad \Phi_0 = (0.352 + 0.021T - 0.00034T^2) / 8 \quad (2)$$

171 **2.2 Sites and field data**

172 Data from 12 agricultural sites in the main wheat-growing area of China (see Fig. 2) were used
173 for the second step of model development and testing (see Table 1 and Table 2). More than 90% of
174 wheat production occurs in the areas where these sites are located (Wang et al., 2009), so they are
175 representative of the environmental conditions for wheat production in China.



176

177

Figure 2: Locations of sites providing experimental data.

Site	Code	Longitude (E, °)	Latitude (N, °)	Elevation (m)	Mean annual air temperature (°C)	Mean annual precipitation (mm)
WeiShan	WS	116.83	36.23	20	13.3	532
YuCheng	YC	116.57	36.82	22	13.2	530
ChangShu	CS	120.7	31.55	3.1	16.6	1321.2
ChangWu	CW	107.68	35.23	1220	9.1	580
LuanCheng	LC	114.68	37.88	50.1	12.2	536.8
FengQiu	FQ	114.4	35	67	13.9	605
YanTing	YG	105.45	31.27	420	17.3	836
HaiLun	HL	125.92	47.45	240	4	550
LaSa	LA	91.33	29.67	3688	6	425
LinZe	LZ	100	39.35	1384	1.5	550
NaiMan	NM	120.7	42.92	358	5	425
ShaPotou	SP	104.95	37.45	1250	9.6	1250

Site code	Data span	PPFD (mol m ⁻² day ⁻¹)	T (°C)	RH (%)	CO ₂ (ppm)	LAI	Elevation (m)	AB (g m ⁻²)	Yield (g m ⁻²)	Fertilization Irrigation	Wheat variety	Flux data (g C m ⁻² day ⁻¹)	Usage
WS	2006	√	√	√	√	√	√					√	a
YC	2004-2015	√	√	√	√	√	√	√	√	√	√	√*	a, b, c, d
CS	2004-2015	√	√	√	√	√	√	√	√	√	√		c, d
CW	2004-2015	√	√	√	√	√	√	√	√	√	√		c, d
FQ	2004-2015	√	√	√	√	√	√	√	√	√	√		c, d
LC	2004-2015	√	√	√	√	√	√	√	√	√	√		c, d
YG	2004-2015	√	√	√	√	√	√	√	√	√	√		c, d
HL	2005-2006		√				√	√	√	√	√		c
LS	2004-2015		√				√	√	√	√	√		c
LZ	2006		√				√	√	√	√	√		c
NM	2006		√				√	√	√	√	√		c
SP	2006		√				√	√	√	√	√		c

179 **Table 2: Data details and use.** √: data are available; a: sites were used to test the P model; b: sites were used to derive the GPP to AB
180 relationship; c: sites were used to derive the AB to yield relationship; d: sites were used to test the final model. * Two years (2004-2005) during
181 the data span are available for the flux data at YuCheng.

182 Two flux tower sites (WeiShan, YuCheng; see Table 2 and Fig. 2) were used to test the GPP
183 predictions. One full year of observations from WeiShan (2006) and two years of observations from
184 YuCheng (2004, 2005) were available. The climate data (PPFD, T and RH) and canopy coverage (here
185 estimated from LAI by Beer's law), required as input to the P model, were obtained from on-site
186 measurements for WeiShan provided by the original authors (Lei and Yang, 2010) and downloaded
187 from the National Ecosystem Research Network of China (CNERN: <http://www.cnern.org.cn/>) for
188 YuCheng. CO₂ concentrations used are the annual global average obtained from the United States
189 National Oceanic & Atmospheric Administration (NOAA:
190 <https://www.esrl.noaa.gov/gmd/ccgg/trends/>).

191 There are no data on AB or grain yield from WeiShan, although this information is available for
192 YuCheng. We therefore used the two years of data from YuCheng to derive the relationship between
193 GPP and AB. We obtained experimental data from ten additional agricultural sites providing
194 information on AB and grain yield from CNERN. CNERN also provided data on climate (including
195 PPFD, T and RH), LAI, dates of the growing period, wheat varieties planted and management practices
196 (including irrigation and the supply of total nitrogen, phosphate and potassium) for all of these sites.
197 However, the records cover different periods (see Table 2): some sites only have data for one year (LZ,
198 SP, NM); one site has data for two years (HL); the remaining sites have records spanning multiple
199 years (CS, CW, FQ, LC, YG, LS). We used all the available data from these ten sites and YuCheng
200 together (584 data points) to estimate the allocation relationship between AB and grain yield. We used
201 data from six sites (CS, CW, FQ, LC, YG, YC) with records for more than two years to test the final
202 model. We could not use the Lasa site for testing because there are no LAI data from this site.

203 Climate data were pre-processed on a weekly time step, with PPFD summed and T and RH
204 averaged. Then vapour pressure deficit (D , kpa) was calculated according to the following equation
205 (Campbell and Norman, 2012):

$$206 \quad D = 610.8 \exp[17.27T/(T+237.3)] (100 - RH) / 100 \quad (3)$$

207 The fraction of absorbed photosynthetically active radiation was estimated by Beer's law (Monsi, 1953)
208 from LAI:

$$209 \quad f_{\text{APAR}} = 1 - \exp(-k \cdot \text{LAI}) \quad (4)$$

210 where k is a dimensionless constant, assigned a generic value of 0.5. LAI was measured several times
211 over the growing season, but the times of measurement varied from year to year and site to site. The
212 LAI data used as input to test the P model (WS 2006, YC 2004-2005) are based on eight to ten
213 observations at each site over growing season. We interpolated the data to weekly mean values using
214 a polynomial regression of LAI against time. Measurements of LAI at the sites used to test the crop
215 model (PC model) were made more sporadically (less than five observations per growing season) and
216 therefore inadequate for polynomial regression. We derived LAI values for PC model test from the
217 MODIS LAI product (MCD15A3H: 4-day time-step and 500m resolution,
218 <https://modis.gsfc.nasa.gov/>). Since MODIS severely underestimates the observed LAI at the six test
219 sites, we calculated the relationship between observed and MODIS LAI by linear regression and used
220 the slope of this regression to rescale the MODIS LAI data and derive weekly mean LAI.

221 **2.3 Derivation of allocation relationships**

222 We hypothesized that a fixed proportion (ϵ) of accumulated GPP during the growing season would
223 be allocated to above-ground biomass (AB). We calculated GPP accumulation (ΣGPP) from the
224 beginning of the growing season to the day when AB was measured, then derived an empirical
225 relationship between AB and ΣGPP by linear regression. We used the slope of this linear regression as
226 an estimate of ϵ .

227 We hypothesized that grain yield should increase, monotonically but not necessarily linearly, with
228 AB, and that this relationship might be influenced by wheat varieties and management practices. Non-
229 linear regression was used to derive an empirical relationship between grain yield and AB, taking

230 account of the effect of nitrogen supply and wheat variety on the relationship, meanwhile testing the
231 effects of irrigation and the application of phosphate and potash. Non-linear regression was performed
232 using a mixed-effects model in the **nlm** package of R. The form of the fitted equation is as follows:

$$233 \text{ Yield} = (a \cdot N + b) [1 - \exp(c \cdot AB)] + d \quad (5)$$

234 where N is the total application of nitrogen (kg N hm^{-2}), and a , b , c and d are parameters to be fitted.
235 Wheat variety was considered as a random effect added to parameter b , thus allowing maximum yields
236 to differ by variety. The potential effects of other factors (irrigation, precipitation, mean temperature
237 during the growth season) were tested by examining the residuals from this regression. To check the
238 goodness of fit of the non-linear regression, linear regression was also performed both using all the
239 data together, and for each variety separately. The root mean squared error (RMSE) and Akaike
240 Information Criterion (AIC) were calculated as an indicator of the goodness of fit of each model.

241 **2.4 Model evaluation**

242 We tested the performance of the PC model by comparing interannual variations in predicted and
243 observed AB and grain yield over multiple years at the six test sites (CS, CW, FQ, LC, YC, YG), using
244 meteorological observations from each site to drive the model. The simulated accumulated GPP during
245 the growing season was allocated to AB using the fixed ratio (ϵ) obtained by linear regression, and AB
246 at harvest was allocated to grain yield using the non-linear relationship described above (Equation 5).
247 The growing season was defined as the period when mean daily temperature was above 0°C .
248 Interannual variation in yield provides an independent test of the model as no information on
249 interannual variability was used in the derivation of empirical relationships used in the model.

250 There are two sources of uncertainty in the model predictions: the input data (climate and LAI)
251 and the model parameters. We assumed the input data were reliable and focused on parameter
252 uncertainty. We considered each of the sources of uncertainty in the individual equations in the P model

253 independently, and combined these uncertainties using the standard error propagation formula
254 (Prentice and Thomas, 2018):

$$255 \quad u^2(y) = \sum_i (\partial f / \partial x_i)^2 u^2(x_i) \quad (6)$$

256 where $u(y)$ is the standard uncertainty (of GPP or AB or yield), $\partial f / \partial x_i$ is the sensitivity to variable x_i
257 (obtained by differentiating the individual equations), and $u(x_i)$ is the standard uncertainty of x_i .

258 **2.5 Model extension**

259 2.5.1 Phenology scheme

260 The phenology scheme for wheat was adopted from the LPJmL4 model (Bondeau et al., 2007;
261 Schaphoff et al., 2018). Sowing and maturity dates were obtained from the datasets provided in the
262 global gridded crop model inter-comparison project (Elliott et al., 2015). A phenological scalar (f_{PHU})
263 ranging from 0 at sowing to 1 at harvest was computed:

$$264 \quad f_{\text{PHU}} = \sum_1^n (T_m - T_b) / \text{PHU} \quad (7)$$

265 where n is the number of days from sowing, T_m is the daily mean air temperature ($^{\circ}\text{C}$) and T_b is the
266 base temperature (here 0°C) and used to determine LAI development, using a sigmoid curve during
267 the growth phase and a quadratic curve during the senescent phase. (In the absence of water and
268 nutrient stresses, LAI is assumed to follow this optimal curve. During the growth phase:

$$269 \quad f_{\text{LAI}_{\text{max}}} = f_{\text{PHU}} / [f_{\text{PHU}} + \exp(l_1 - l_2 \cdot f_{\text{PHU}})] \quad (8)$$

270 where LAI is a time-dependent fraction ($f_{\text{LAI}_{\text{max}}}$) of maximum LAI (LAI_{max}), and l_1 and l_2 are the first
271 and second inflection points. During the senescence phase:

$$272 \quad f_{\text{LAI}_{\text{max}}} = [(1 - f_{\text{PHU}})^2 / (1 - f_{\text{PHU}_{\text{sen}}})^2] (1 - f_{\text{LAI}_{\text{max-harvest}}}) + f_{\text{LAI}_{\text{max-harvest}}} \quad (9)$$

273 where $f_{\text{PHU}_{\text{sen}}}$ is the fraction of PHU when senescence begins, and $f_{\text{LAI}_{\text{max-harvest}}}$ is the fraction of
274 maximum LAI at harvest (here fixed to zero). The f_{PHU} values corresponding to the l_1 and l_2 inflection
275 points were derived from Figure 4 in Bondeau et al. (2007) and the parameter values of l_1 and l_2 were
276 calculated for these f_{PHU} values using the method of Neitsch et al. (2011). We used values for the l_1
277 and l_2 inflection points of 0.89 and 10, respectively.

278 2.5.2 Dynamic leaf area index

279 Prognostic calculation of LAI was enabled by fitting a linear relationship between leaf biomass
280 and AB based on data from the field sites, then solving for LAI in the mass-balance equation:

$$281 \quad (\text{LMA} / \eta) \cdot \text{LAI} = \varphi \Sigma I [1 - \exp(-k \cdot \text{LAI})] \quad (10)$$

282 where η is the fraction of ΣGPP allocated to leaves, LMA is the leaf mass-per-area (g m^{-2}), φ is the
283 modelled LUE (the ratio of modelled GPP, following equation (1), to absorbed PPF D), and ΣI is the
284 accumulated incident PPF D (mol photon m^{-2}). k is a dimensionless constant ($k = 0.5$). Equation (10)
285 indicates that the LAI demand (left hand side) must equal to its supply (right hand side). The LAI
286 demand represents the allocation of accumulated GPP to canopy to support a certain level of LAI. The
287 LAI supply represents the carbon accumulation supported by a certain level of LAI. η was estimated
288 from the observed data on leaf biomass and ΣGPP from the YuCheng site in 2004 and 2005, LMA was
289 set at 35.7 g m^{-2} corresponding to the mean observed value at YuCheng and allowed to increase linearly
290 with CO_2 using the observed slope (0.05 g m^{-2} per ppm) from Thilakarathne et al. (2013).

291 2.6 Model application

292 2.6.1 Sensitivity analysis

293 Using 2005 as a baseline (baseline temperature is the weekly mean temperature over the growing
294 season and baseline CO_2 is 380 ppm), we ran simulations with the extended model, including

295 prognostic phenology and dynamic LAI and LMA, with temperature increasing by 0.05° increments
296 up to 5° above the baseline temperature and CO₂ concentration increasing by increments of 5 ppm up
297 to 500 ppm above the baseline CO₂ concentration. These changes were superimposed on the weekly
298 mean temperatures and on the annual CO₂ concentration. All other inputs (radiation, relative humidity,
299 management practices and wheat variety) were fixed at their 2005 values.

300 **2.6.2 Future scenarios**

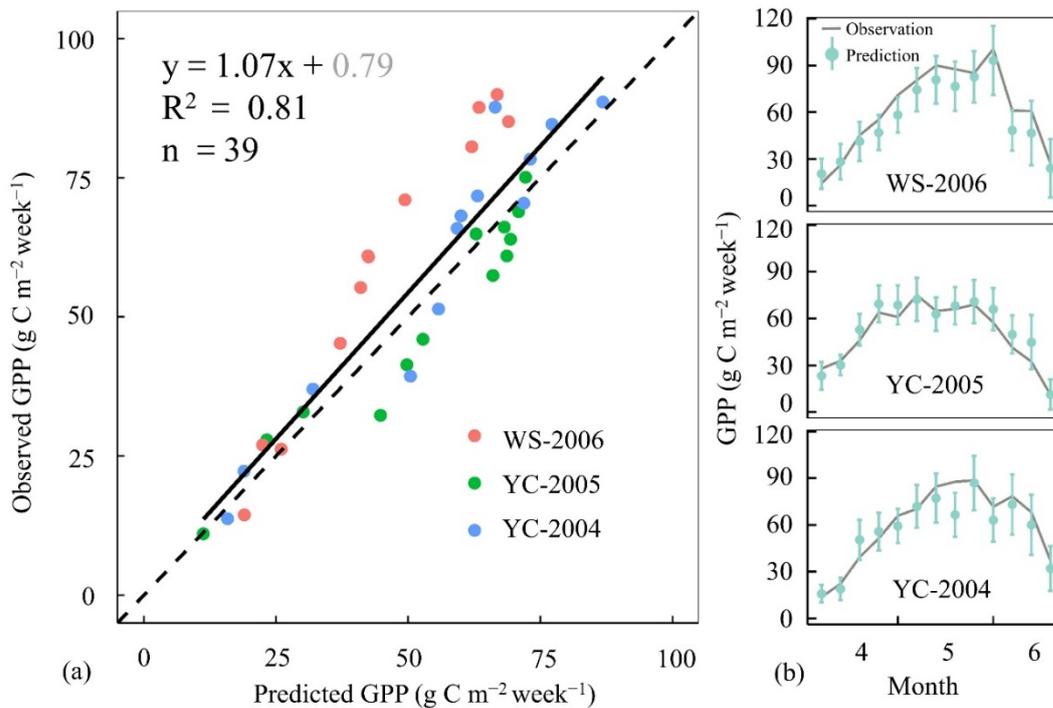
301 We used the model to examine the consequences of potential future climate changes on wheat
302 yields, following the protocol used by the Inter-Sectoral Impact Model Intercomparison Project-2b
303 (ISIMIP2b: <https://www.isimip.org/protocol/#isimip2b/>). Climate data, including daily mean
304 temperature, photosynthetically active radiation (assumed to be half of downward shortwave radiation)
305 and relative humidity from the MIROC5 simulations, and CO₂ concentrations, for two scenarios
306 (RCP2.6 and RCP6.0) were used to run the PC model at six test sites (CS, CW, FQ, LC, YC, YG) from
307 2006 to 2099. Management practices and wheat varieties were unchanged from 2005.

308 The LPJmL (Bondeau et al., 2007; Muller and Robertson, 2014; Schaphoff et al., 2018), GEPIC
309 (Liu et al., 2007) and PEPIC (Liu et al., 2016) crop models have been used to simulate future wheat
310 yields in ISIMIP2b. We compared our future projections of yield with results from these three models.
311 In ISIMIP2b, these models ran simulations with full irrigation and no irrigation. In order to eliminate
312 the effect of variable water supply, we compared our results with those from the full-irrigation run. We
313 extracted simulated wheat yields at our six test sites from the results of each model for the RCP2.6 and
314 RCP6.0 scenarios. Further information about these three models, including input data, leaf area,
315 phenological development, yield formulation and stresses considered, is given in Table S1.

316 **3. Results**

317 **3.1 Modelled versus observed GPP**

318 Predicted weekly GPP values were consistent with the observations from the flux towers, both in
319 their magnitudes (Fig. 3a) and their patterns over the growing season (Fig. 3b). Observed and predicted
320 GPP were highly correlated ($R^2 = 0.81$, $RMSE = 10.1 \text{ g C m}^{-2} \text{ week}^{-1}$) and the slope of the relationship
321 was close to 1:1 (slope = 1.07 ± 0.08) with a non-significant offset (intercept = $0.79 \pm 4.67 \text{ g C m}^{-2}$
322 week^{-1}).



323

324 **Figure 3: Comparison of predicted and observed gross primary production at two sites. (a)**

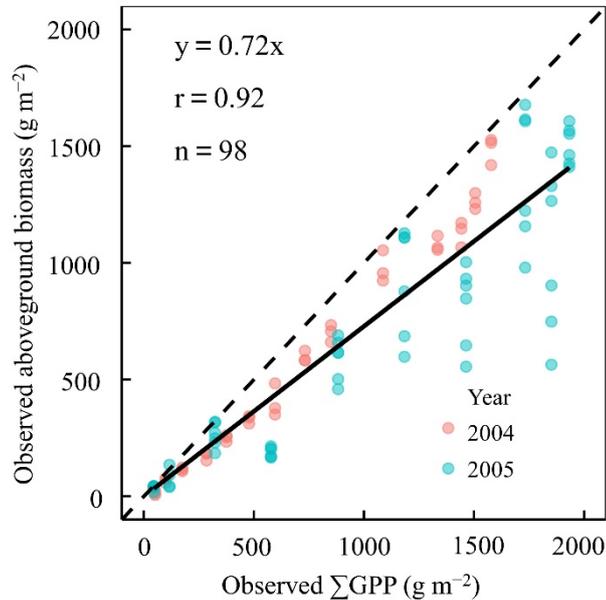
325 Scatterplot. The thick black line is the linear regression. The grey number is not significant; **(b)** GPP

326 during the growing season (weekly sums). WS-2006, YC-2005 and YC-2004, represents WeiShan in

327 2006, YuCheng in 2005 and YuCheng in 2004, respectively.

328 **3.2 The relationship between AB and GPP**

329 A strong linear relationship (Fig. 4) was shown between AB and accumulated GPP ($r = 0.92$) with
330 an estimated 72% (slope, $\varepsilon = 0.72$) of accumulated GPP allocated to AB. The intercept was statistically
331 significant, but small enough to be neglected.



332

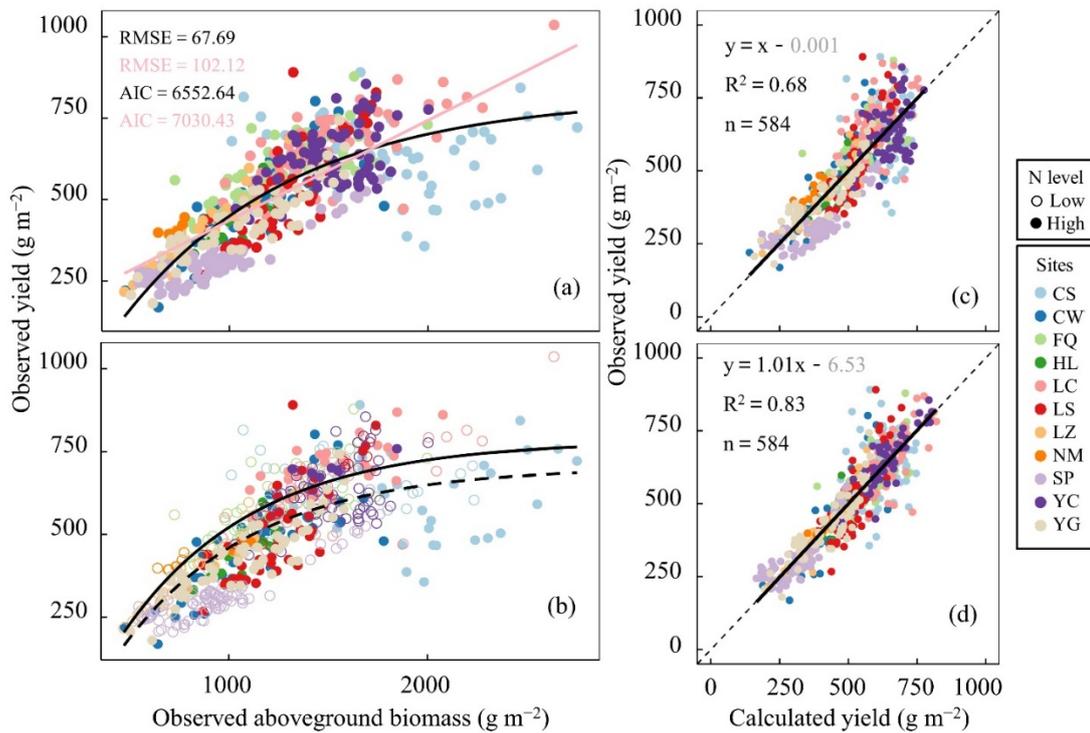
333 **Figure 4: The proportion of accumulated gross primary production (GPP) allocated to**
334 **aboveground biomass.** The data are observations during the wheat growth season at YuCheng from
335 2004 to 2005. All values were accumulated from green-up to measurement time.

336 **3.3 The relationship between yield and AB**

337 Yield was shown to be a saturating function of AB (Fig. 5a). Nitrogen addition affected the overall
338 level of allocation (Fig. 5b), with higher nitrogen supply causing high allocation to AB. The
339 relationship was affected by wheat variety, and a saturating relationship can also be shown within each
340 of the varieties that covers a large range of AB (range $> 1800 \text{ g m}^{-2}$), with a substantially smaller
341 RMSE and AIC compared to linear fits (Fig. S1). Moreover, the slopes of linear regressions fitted to
342 each variety separately decline with the mean value of AB for the variety (Fig. 7 and Fig. S2). In other
343 words, at the high end of AB values, the increment in yield diminishes with the increment in AB. These

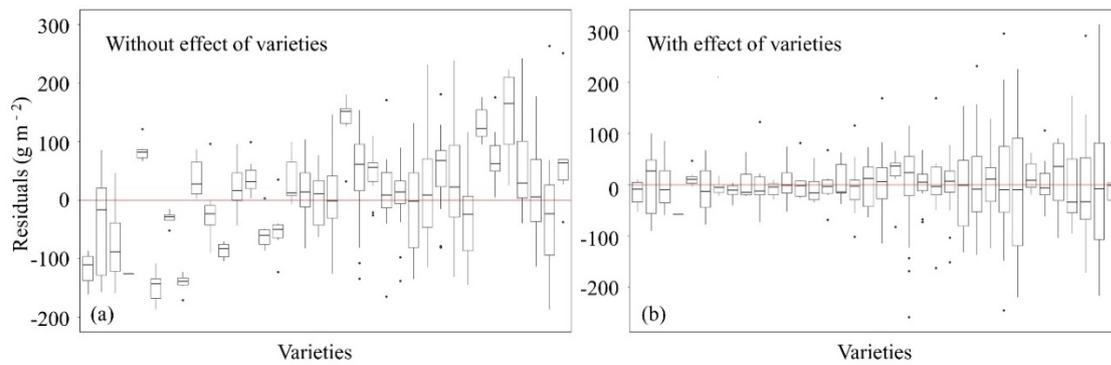
344 results indicate that the non-linear, saturating relationship of yield to AB applies generally, both within
 345 and across varieties.

346



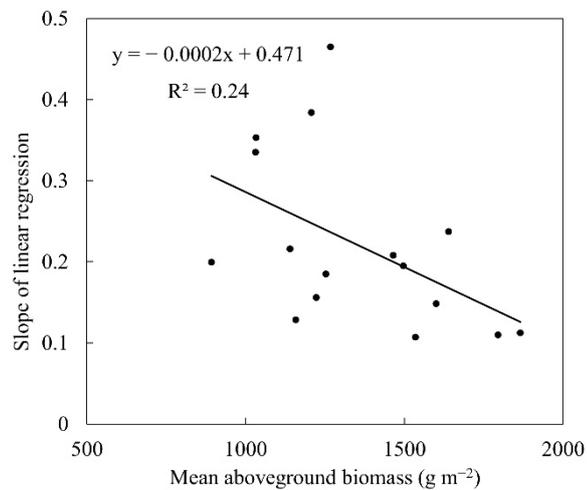
347

348 **Figure 5: Results of the mixed-effects model. (a)** Yield versus aboveground biomass (AB). Pink
 349 line is linear regression and black line is non-linear regression. **(b)** Yield trend with AB, including the
 350 effect of nitrogen addition. The solid line is the fitted curve of yield with AB at high nitrogen level
 351 (pure nitrogen added = 300 kg hm⁻²) and the dotted line is at low nitrogen level (pure nitrogen added
 352 = 100 kg hm⁻²). The open and closed circles represent the observations with total application of pure
 353 nitrogen at levels above and below 200 kg hm⁻², respectively. **(c)** Scatterplot including AB and nitrogen
 354 as predictors. **(d)** Scatterplot including AB, nitrogen and variety as predictors. Grey numbers are non-
 355 significant.



356

357 **Figure 6: The relationship between residuals and wheat varieties. (a)** Without the random
 358 effect of variety; **(b)** with this effect. Each box represents a wheat variety. The red line is zero and the
 359 black dots are outliers.



360

361 **Figure 7: The fitted slope and mean value of aboveground biomass based on the linear**
 362 **regression of yield against aboveground biomass within each variety.** (See Fig. S2 for the separate
 363 linear regressions.)

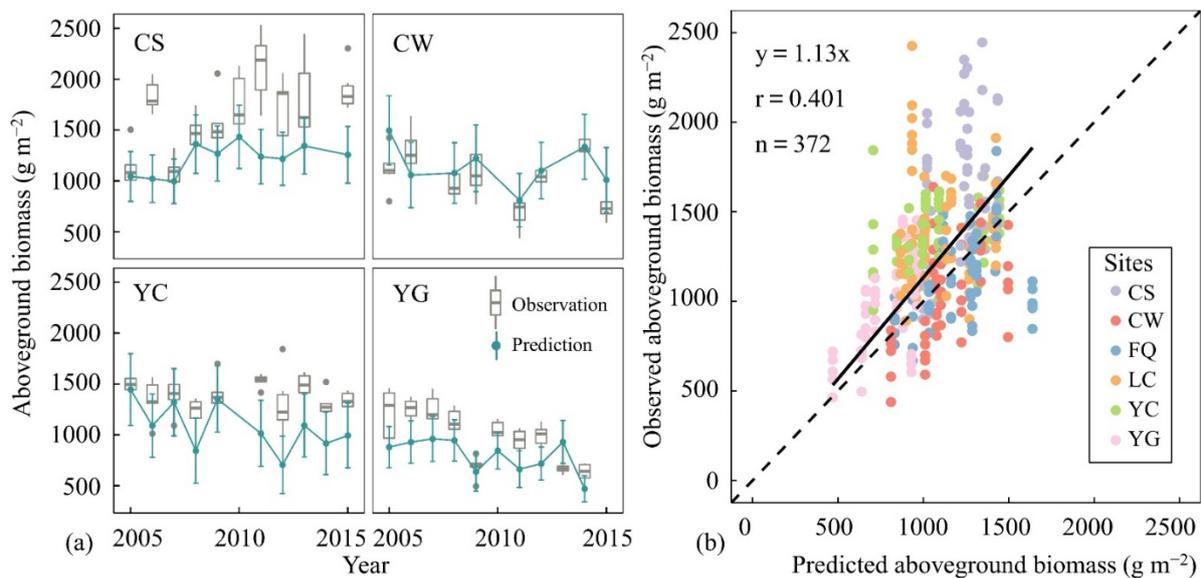
364 The comparison between simulated and observed yields improved when variety was taken into
 365 account (Fig. 5c compared to Fig. 5d). Residuals of the non-linear regression were reduced (Fig. 6),
 366 and the correlation between predicted and observed yield improved (R^2 increased from 0.68 to 0.83).
 367 Irrigation, mean temperature over the growing season, and the supply of phosphate and potassium had

368 no significant effects on the relationship between AB and yield ($P > 0.05$) on yield (Fig. S3), indicating
369 that the first-order effects of these factors are already subsumed in AB.

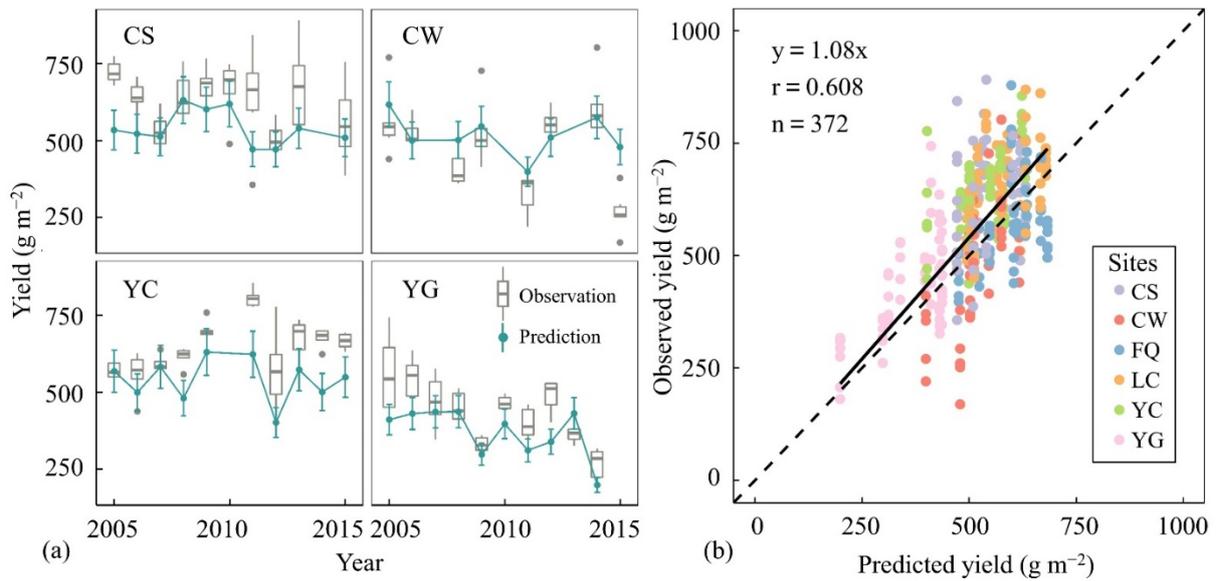
370 3.4 Model evaluation

371 3.4.1 Prediction of AB and yield variations

372 The model captured the pattern of interannual variation in AB (see Fig. 8) and, although there
373 were some anomalous years, the predicted AB was generally within the range of the observations. The
374 correlation between predicted and observed AB was moderate ($r = 0.40$). The simulated and observed
375 yields matched reasonably well ($r = 0.61$) and interannual variations in grain yield were captured (Fig.
376 9 and Table S2), with observations almost always within the uncertainty range of the predictions.



377
378 **Figure 8: Comparisons of observed and modelled aboveground biomass. (a)** Interannual
379 variation at four sites: ChangShu, ChangWu, YuCheng, YangTing. **(b)** Scatterplot of predicted and
380 observed AB at all sites.



381

382

383

Figure 9: Comparisons of observed and modelled yield. (a) Interannual variations at four sites: ChangShu, ChangWu, YuCheng, YangTing. **(b)** Scatterplot of predicted and observed yield at all sites.

384

3.4.2 Uncertainty analysis

385

Uncertainty in model predictions could originate either in the input data (climate, LAI) or in the model. We assumed that the input data were reliable, and used YuCheng 2005 as a case study to analyse the uncertainties due to the following model parameters:

387

388

- The two most uncertain quantities (β , c^*) in the P model (Prentice and Thomas, 2018). β is the ratio of the unit costs for the maintenance of carboxylation and transpiration capacities, evaluated at 25°C. It determines the value of the ratio of leaf-internal to ambient CO₂ (an index of stomatal behaviour) under standard conditions. c^* is the unit cost of maintaining electron-transport capacity and determines the extent to which optimum carboxylation capacity is lowered because of the cost of maintaining an equivalent capacity for electron transport (Equation 1).

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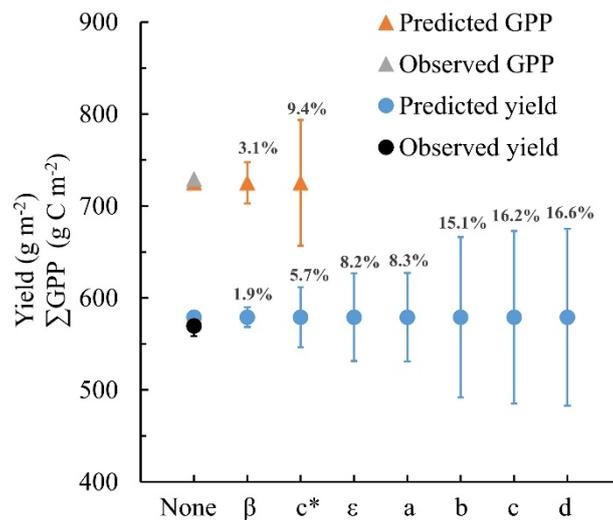
395

- The proportionality constant (ε) between biomass and accumulated GPP.

396

- The four main parameters (a , b , c , d) from the formula relating yield to AB (Equation 5).

397 The calculated uncertainties with respect to different model parameters for predicted GPP and
 398 yield are shown in Fig. 10. When the parameters were varied by $\pm 10\%$, the total uncertainty of
 399 predicted GPP was $\sim 9\%$. The largest source of this uncertainty ($\sim 6\%$) was associated with the
 400 parameter c^* , which is an important control on the magnitude of simulated GPP. This parameter also
 401 contributes substantially ($\sim 4\%$) to the uncertainty in simulated yield. The other parameter contributing
 402 substantially ($\sim 7\%$) to this uncertainty is the main slope parameter (b), which is the principal control
 403 over the yield attained for a given biomass.



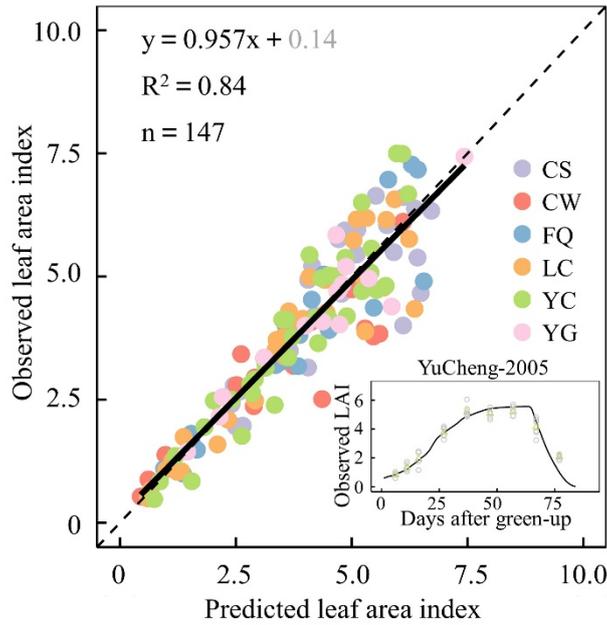
404

405 **Figure 10: The impact of parameter uncertainty on the prediction of GPP accumulation and**
 406 **yield.** YuCheng 2005 was selected as a case study. Triangles represent GPP and dots represent yield.
 407 The x -axis represents the progressive inclusion of $\pm 10\%$ uncertainty in successive parameters,
 408 indicated by their symbols.

409 3.5 Model extension and application

410 3.5.1 Testing the phenology scheme

411 The phenology scheme was shown to reproduce seasonal patterns of LAI today (Fig. 11)
 412 reasonably well ($R^2 = 0.84$).

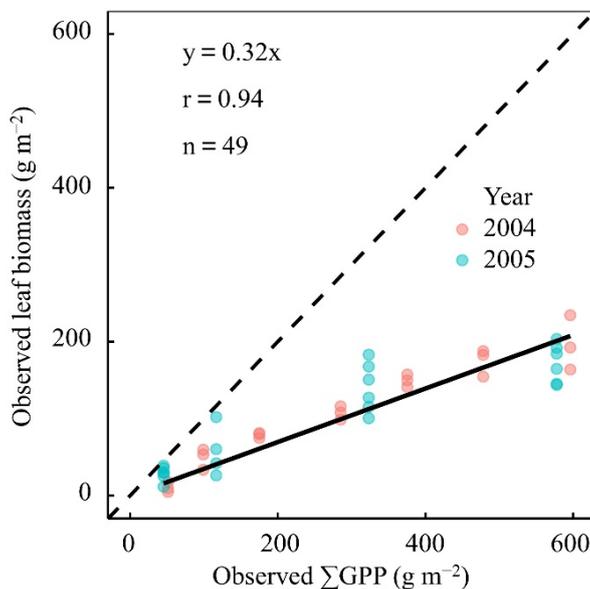


413

414 **Figure 11: Observed versus predicted leaf area index (LAI) with the LPJmL4 phenology**
 415 **scheme.** The inset shows the observed (circles, green is mean value) and predicted (line) seasonal time
 416 course of LAI at the YuCheng site in 2005. The grey number is not significant.

417 **3.5.2 The relationship between leaf biomass and accumulated GPP**

418 A strong linear relationship ($r = 0.94$) was found between leaf biomass and accumulated GPP,
 419 allowing us to estimate $\eta = 0.32$ (Fig. 12) and thereby solve equation (10) for mean LAI over growth
 420 phase.



421

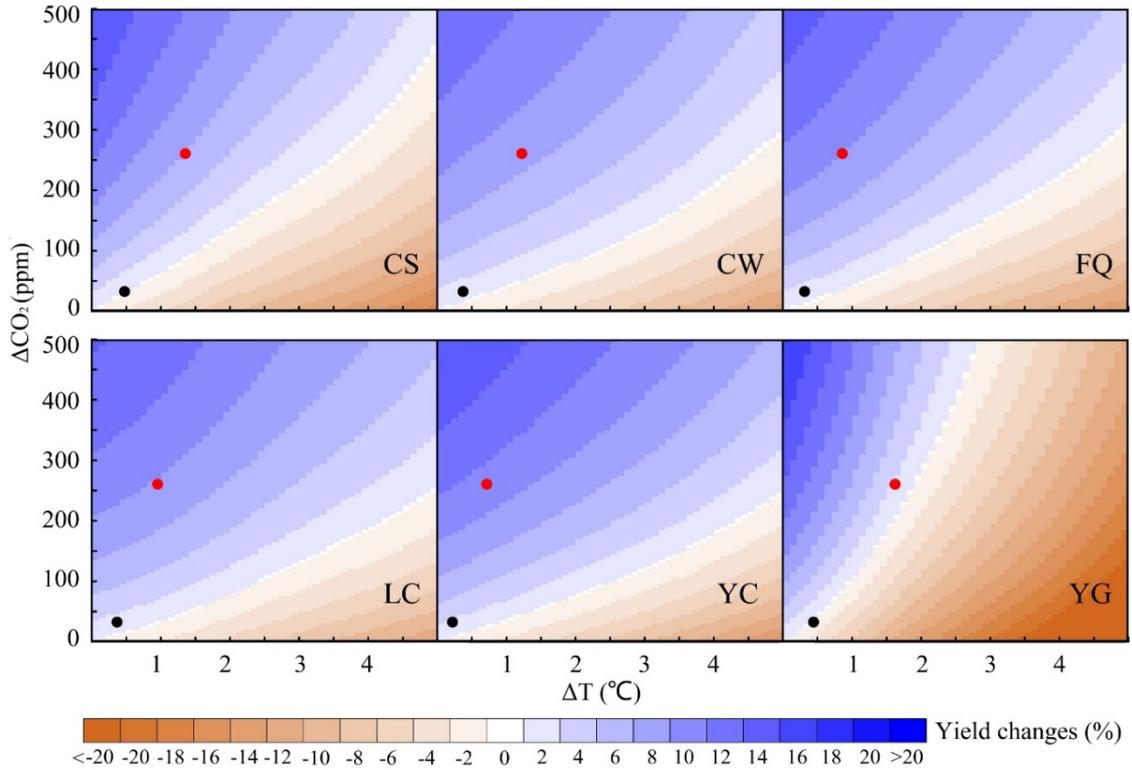
422 **Figure 12: The proportion of gross primary production (GPP) allocated to leaves.** The data
423 are observations during the wheat growth phase in 2004 and 2005 at YuCheng. All values were
424 accumulated from green-up to measurement time.

425 Projections of changing LAI as a function of CO₂ concentration are shown in Figure 14b and
426 Figure S4. Modelled LAI increases in response to increasing CO₂, but when the effect of increasing
427 LAI on LMA is considered, the increase is much smaller and reaches a maximum at around 600 ppm.
428 This behaviour is consistent with the maximum yield enhancement indicated by raised CO₂
429 experiments, as summarized in the meta-analysis by Broberg et al. (2019).

430 3.5.3 Sensitivity analyses

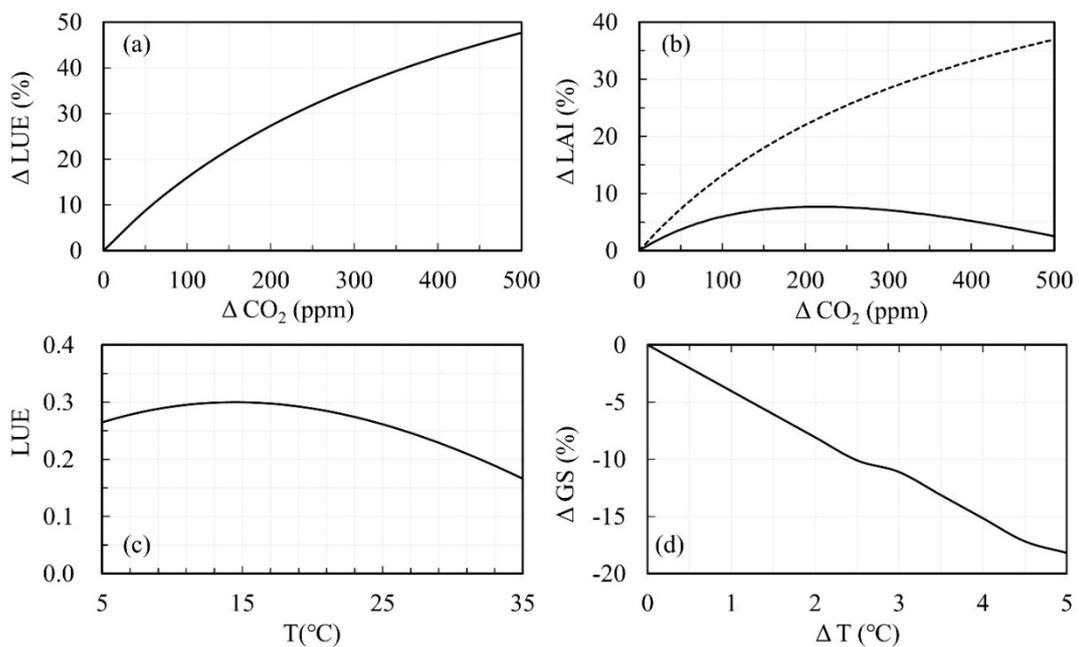
431 Modelled grain yields increase with rising CO₂ concentration, and decrease with increasing
432 temperature, when other variables are kept fixed (Fig. 13). Higher temperature shortens the growing
433 season (Fig. 14d) leading to a reduction in total absorbed light. In addition, the response of modelled
434 LUE to rising temperature follows a unimodal curve (see Fig. 14c) such that increasing temperature
435 above the optimum reduces GPP (Long, 1991). Lower GPP means lower yield. On the other hand,
436 rising CO₂ monotonically increases LUE, GPP and yield; and rising GPP leads to rising LAI,
437 amplifying this effect. But the net effect of CO₂ is limited by an increase in LMA.

438 For these scenarios and sites, the modelled positive effect of rising CO₂ concentration on yield
439 was greater than the negative effect of increasing temperature. However, the modelled reductions in
440 yield caused by rising temperature differed among the sites (Fig. 13). Modelled wheat yields in warmer
441 regions today, like YG and CS, are more sensitive to warming than cooler regions such as LC.



442

443 **Figure 13: The response of predicted yield to rising CO₂ and increasing temperature at six**
 444 **sites.** Dots mean increasing on temperature and mean rising on CO₂ concentration in the last decade
 445 (2090-2099) comparing with the first decade (2006-2015) under two future scenarios (RCP2.6, the
 446 black dot, and RCP6.0, the red dot). The temperature is the mean value over growing season.

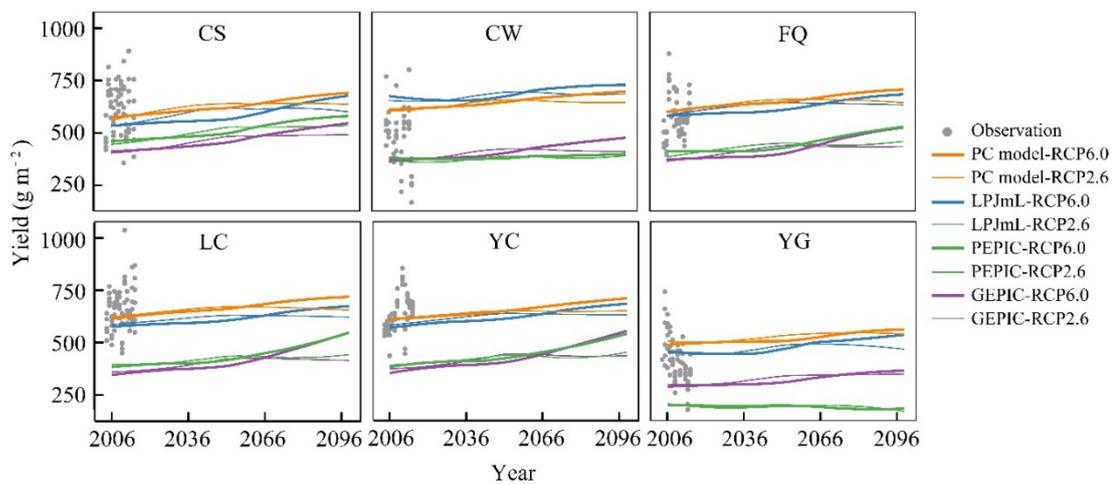


447

448 **Figure 14: The response of light use efficiency (LUE), leaf area index (LAI) and growing**
 449 **season length (GS) to CO₂ concentration and temperature (T).** Using the climate and CO₂
 450 measurements from YuCheng 2005 as a baseline condition. **(a)** The response of LUE change to CO₂
 451 increment. **(b)** The response of LAI change to CO₂ increment. Solid line includes the effect of CO₂ on
 452 LMA; dash line excludes this effect. **(c)** The response of LUE to temperature. **(d)** The response of
 453 changes in growing season length to temperature increment.

454 3.5.4 Comparison with future scenario runs by other crop models

455 We compared future scenarios with the PC model to ISIMIP2b model runs performed with the
 456 same scenarios using complex crop models. PC and LPJmL simulated contemporary yields reasonably
 457 well across all the sites, but the PEPIC and GEPIC models showed unrealistically low yields except at
 458 site CS. PC showed an increase in wheat yield ~6.6% in the RCP2.6 and ~15.1% in the RCP6.0
 459 simulations by the end of the 21st century (Fig. 15). Although the different crop models predict different
 460 absolute magnitudes of wheat yields, the trend and the interannual variations are similar among all
 461 models. Moreover, the magnitude of increase shown by PC is similar to that shown with LPJmL. All
 462 models showed increases in wheat yield at individual sites over the 21st century, with the exception of
 463 the PEPIC model at the YG site.



465 **Figure 15: Comparison of different crop models: future scenarios at six sites.** The climate
466 data to drive the crop models were derived from the MIROC5 climate model. Lines represent modelled
467 interannual yield trends; Points represent measured yields.

468 **4. Discussion**

469 The P model has been extensively tested against GPP derived from flux measurements in natural
470 vegetation (Stocker et al., 2019; Wang et al., 2017) and has also been shown to perform well in
471 simulating the GPP of croplands (Balzarolo et al., 2018). The present study has confirmed that the P
472 model can predict the GPP of irrigated and fertilized wheat crops in China (Fig. 3); that above-ground
473 crop biomass can be modelled as a fraction of accumulated GPP (Fig. 4); and that yield can be modelled
474 as a saturating function of AB (Fig. 5). Further extensions and tests of the model in a wider range of
475 environmental and economic settings will be needed to allow application to model wheat crops under
476 water and/or nutrient stresses (which are expected to result in different relationships among GPP, AB
477 and yield), or in a wider range of climates.

478 The ratio of above-ground biomass production to GPP is typically 0.41 (natural) to 0.53 (managed)
479 for forests, ~0.2 for natural grasslands and 0.6 to 0.7 for managed grasslands (Carnieli et al., 2015).
480 Values of this ratio, up to ~0.8, have been found for intensively managed crops (Carnieli et al., 2015;
481 Chen et al., 2018; Huang et al., 2018). The value of 0.72 estimated in our study is in the upper part of
482 the expected range. This is not unreasonable. As an annual crop, wheat does not require strong roots
483 for support. In addition, the study sites are irrigated (to eliminate water stress) and fertilized (to reduce
484 or eliminate nutrient stress), so the below-ground carbon allocation needed to acquire nutrients and
485 water is minimal. Modern varieties of wheat are highly efficient in converting GPP to biomass because
486 selective breeding has aimed to increase the GPP allocation to biomass, and ultimately to grain.

487 Most crop models assume that grain yield is a fixed proportion of above-ground or total biomass,
488 the so-called harvest index (HI) (Donald, 1962; Hay, 1995). However, the grain yield data analysed

489 here follow a saturation function with AB (Fig. 5), so that HI declines with increasing AB. The level
490 of AB at which saturation occurs is largely determined by the wheat variety (Fig. 6 and Fig. S1). The
491 maximum yield given by $(a \cdot N + b)$ in equation (5) is influenced by the wheat variety and the amount
492 of nitrogen added. The actual yield is also determined by the amount of biomass accumulated and,
493 therefore, by the GPP during the growing season – which depends on CO₂, climate, canopy
494 development and incident PPFD. The negative intercept (d) quantifies the requirement for a certain
495 minimum biomass accumulation before any carbon is allocated to seeds. When a linear regression was
496 fitted instead of a saturating function, the estimate of d became positive, which is biologically
497 impossible as it suggests a positive yield when AB is zero (Fig. S2).

498 It follows from this simple empirical representation of the experimental data that improving grain
499 yield is not simply a case of adding more fertilizer (which also comes with significant monetary and
500 environmental costs). Moreover, yields will also not automatically increase in proportion to the effect
501 of CO₂ on photosynthesis, because the saturating nature of this relationship implies a “diminishing
502 return” on increases in AB. The differences among varieties are potentially important here. They
503 suggest that a key target for crop improvement should be the ability of the plants to allocate more
504 carbon to grain as AB increases, and thereby to profit from higher CO₂ levels.

505 Both the current level and the trend in yield over the 21st century simulated by the PC model are
506 similar to that shown by the LPJmL model (Fig. 15). This similarity is probably due to the fact that the
507 LPJ component of LPJmL, is also, ultimately, based on the standard model of photosynthesis and the
508 acclimation of V_{cmax} – the latter process now supported by a wealth of evidence (Smith et al., 2019).
509 However, the PC model is simpler, has fewer parameters and is more transparent, with major
510 advantages both for the credibility of the results and the ease with which uncertainties can be quantified
511 and traced to their source.

512 Quantification of prediction uncertainties in complex models requires extensive computation to
513 estimate the sensitivity to their many parameters. In contrast, the PC model consists of a single central

514 equation (1a), which can readily be differentiated with respect to its (far fewer) parameters. This
515 process allows uncertainties to be attached to predictions without excessive computational demands
516 and allows the major sources of uncertainty to be pinpointed. We have shown that the parameter c^* ,
517 related to the metabolic costs of maintaining electron transport capacity, and parameter b , related to
518 the potential maximum yield, accounts for a large fraction of the prediction uncertainty (Fig. 10) –
519 indicating the importance of further work to improve these aspects of the model.

520 Studies have suggested that rising temperatures could greatly reduce the grain yield of wheat
521 (Asseng et al., 2014; Asseng et al., 2011; Zhao et al., 2017; Zhao et al., 2016), because of the shortened
522 growing season. However, many studies have neglected the effects of rising CO₂ on C₃ photosynthesis,
523 which has the potential to mitigate the impact of rising temperatures on production by improving LUE,
524 particularly as the temperature optimum shifts to higher temperatures with rising CO₂. The effects of
525 elevated CO₂ have been shown by Free Air Carbon dioxide Enrichment (FACE) experiments, with
526 positive impacts on wheat yields and net assimilation rates (Broberg et al., 2019).

527 The primary mechanism by which increasing CO₂ increases GPP is through the improvement of
528 LUE. This mechanism is amplified by the positive feedback by which increased GPP allows greater
529 LAI, which in turn implies greater light absorption and GPP. On the other hand, LMA increases with
530 CO₂, resulting in a diminished response and, according to our model, a peak of the positive response
531 of LAI to CO₂ above ~600 ppm (Fig. 14b and Fig. S4). However, we see no peak in the positive
532 response of yield to CO₂. This appears to be because $fAPAR$ is comparatively insensitive to changes
533 in LAI at the high end. However, according to our simulations, a positive but saturating response of
534 yield and LUE to CO₂ are found at high CO₂ levels (Fig. 13 and Fig. 14a). This appears to be
535 inconsistent with the yield response shown in the meta-analysis of enhanced CO₂ experiments by
536 Broberg et al. (2019). However, the response shown in that paper is small, solely derived from chamber
537 rather than FACE experiments, and seems to reflect the reduced sensitivity of higher yield wheat
538 varieties to CO₂ changes.

539 The magnitude of yield enhancement simulated by our model is consistent with the findings of
540 Broberg et al. (2019) for the mid-range of wheat yields. Field warming experiments, summarised in
541 Zhao et al. (2016), show negative responses of yield to warming of between 0.5 to 3.0°C at individual
542 sites in northwestern and northern China, with an average response of -4.4% per °C in northwestern
543 China to -2.8% per °C in northern China. Across our study sites (which are in the same region), we
544 predict a net negative response to increased temperature of between -2.3 and -5.7 per °C. This
545 response is caused by the reduction in the length of the growing season and the negative impact of
546 temperature on LUE. The modelled response of yield to combinations of raised CO₂ and temperature,
547 as shown by sensitivity analysis, reflects a combination of net positive effects of CO₂ and net negative
548 effects of rising temperature. Scenario runs show that, under the scenarios tested, the positive effects
549 of CO₂ on yield however outweigh the negative effects of temperature, consistent with the findings of
550 other crop models for China (Liu et al., 2019). Warmer regions are more sensitive to warming than
551 cooler regions (also consistent with Liu et al. (2019)), indicating that wheat production in warmer
552 regions of China will be more challenged by climate change.

553

554 **5. Conclusions**

555 The yield of irrigated and fertilized wheat crops at research sites across the wheat-growing region
556 of China was simulated successfully using a parsimonious model based on a combination of first-
557 principles theoretical considerations governing GPP with empirical analyses of the relationships
558 amongst GPP, AB and yield. The model reproduced the general magnitude and patterns of interannual
559 variability in both AB and yield. When driven by future climate and CO₂ scenarios, it produced results
560 similar to those of the most credible of the more complex crop models.

561 The model also provided insights into how wheat yields may respond to global environmental
562 change. The effect of rising CO₂ on photosynthesis does not imply proportionately increased yield.
563 The model results suggested that the positive response of yield to rising CO₂ may saturate at around

564 600 ppm. The model also predicted a negative effect of warming on wheat yields. Sensitivity analysis
565 showed this negative effect to be stronger in regions with warmer climates today. Nonetheless, in
566 common with other crop models, the simulations indicated an increase of ~6.6% in wheat yields under
567 the RCP2.6 and ~15.1% under the RCP6.0 scenarios of future CO₂ and climate.

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