ORIGINAL ARTICLE

Modelling the impact of improved photosynthetic properties on crop performance in Europe

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Abstract

Using the GECROS model, we simulated the effect of improvements in photosynthesis a range of growth parameters, including yield, and on the ε_c (the conversion efficiency of absorbed solar energy to the chemical energy of biomass) and ε_i (the efficiency of solar energy interception or absorption by the canopy) parameters of the Monteith crop growth equation, for wheat and potato (which use C3 photosynthesis) and maize (which uses C4 photosynthesis). In the case of the C3 crops, the improvements in photosynthesis were via 20% increases in the parameters V_{cmax} (carboxylation capacity of Rubisco), J_{max} (electron transport capacity), $S_{c/o}$ (Rubisco specificity), κ_{2LL} (efficiency of converting incident light into electron transport) and g_m (mesophyll conductance), while for the C4 crop, it was via 20% increase in V_{cmax}, J_{max} and $S_{c/o}$ and a 20% decrease in g_{bs} (the conductance that controls the leak of CO_2 from the bundle sheath cells in C4 leaves). The changes were applied individually and in combination. The responses were modelled using climate data collected over a 10-year period from 66 sites around Europe. Improvements in photosynthesis did result in increases in yield but with considerable variation between the parameters that were adjusted. The greatest increases were obtained for increases in J_{max} and κ_{2LL} (up to an average 11% increase for total plant biomass), and these increases were found across all Europe. Increases in both these parameters have a predominant effect on the light-use efficiency for subsaturating irradiances. Improvements in the other parameters produced smaller increases.

1 | INTRODUCTION

Photosynthesis is the engine of crop productivity, but it is also a complex process that is highly responsive to the environment and has a complex relationship to crop growth. Deliberately improving photosynthesis as a means to improve crop yield is not a new idea, dating back to about 40 years ago (Austin, 1989; Gifford & Evans, 1981; Zelitch, 1975) but actually realising that goal at that time was impossible owing to technical and scientific barriers. The last 20 years, however, have seen a re-awakened interest in using improvements in photosynthesis to improve crop primary production and yield (von Caemerrer & Evans 2010; Gifford & Evans, 1981; Lawson et al., 2012; Zhu et al., 2010). The complexity of photosynthesis means that it cannot realistically be viewed as a single trait, but rather that it should be seen as a super trait that is the product of many more elemental traits. The obvious

question that follows from this is, which of the subtraits of photosynthesis are most limiting for crop production? In this paper, we will make use of a crop yield model, GECROS, that has within it a photosynthesis model (Yin & Struik, 2017). We will use a modelling approach to explore the effect on various crop yield-related parameters of a uniform improvement of a range of parameters for C3 and C4 photosynthesis. This will be done for a range of sites in Europe, and in this way we will identify the limiting photosynthetic traits for these sites.

This approach depends on being able to model photosynthesis and fortunately steady-state photosynthesis at the leaf level can be modelled well if some basic physiological parameters are known; this is a feature that we will exploit in our study. The Farquhar–von Caemmerer–Berry model (Farquhar et al., 1980; von Caemmerer & Farquhar, 1981), hereafter the FvCB model, can model assimilation if the properties and amount of leaf Rubisco, and the photosynthetic electron transport rate, are known. In addition, electron transport rate can be estimated from photosynthesis-irradiance response models (Harbinson & Yin, 2017; Thornley & Johnson, 2000), with the (absolute) light-limited quantum yield and (possibly) leaf light absorption data also being needed to define the light-limited slope of the light-response curve (Ehleringer & Bjorkman, 1977; Hogewoning et al., 2012). Leaves also function within canopies, which are complex structures within which incident solar irradiance is absorbed, transmitted and scattered, and water vapour and CO_2 move by diffusion and mass transport to and from sites of release and uptake. The accurate modelling of canopies is still not routinely possible and these modelling problems currently require solutions by simplification. Scaling from the leaf level to the canopy level is still most commonly done by simplifying canopy structure (e.g. using the two-leaf approach of de Pury & Farquhar, 1997 as we will use here) rather than by integrating the photosynthetic contribution of individual leaf areas in response to a simulation of the within-canopy environment. Furthermore, going beyond the steady-state situation and modelling leaf-level photosynthetic responses to environmental fluctuations, such as readily changing irradiance, is, however, still not feasible at a mechanistic level nor systematically using empirical models. Scaling fluctuating light responses from the leaf to the canopy is particularly challenging given the complexity of modelling the within canopy fluctuating environment (e.g. light flecks and canopy or leaf movement). Despite the problems of modelling the crop canopy, models that simulate the distribution and intensity of fluctuating light within canopies have been developed (e.g. Burgess et al., 2021; Retkute et al., 2018), and our understanding of the physiology, measuring and modelling

of the dynamics of photosynthetic responses to fluctuating light is similarly improving (e.g. Kaiser et al., 2018; Morales et al., 2018; Murchie et al., 2018). Mixing these intrinsically detailed, fine-scale models with the larger scale of the GECROS model still remains to be done and is likely to be computationally demanding.

While steady-state photosynthesis can be well-modelled if some basic parameters are known, these parameters are dependent on factors external and internal to the plant. For example, changes in temperature will have an effect on the parameters of the FvCB model but do so in a predictable way so this effect can be calculated (Bernacchi et al., 2001). In other cases, the effect on photosynthesis is indirect and may be difficult to model. Thus making it difficult to connect photosynthesis to growth. Abiotic stress, for example drought or low temperatures, can act to slow growth, producing end-product or sink-limitation of photosynthesis. When this happens photosynthetic carbon gain may cease to be a limiting factor for growth, rather growth can limit carbon gain in a way that may not be easy to model (Dingkuhn et al., 2020). Also, in any year crop yields can be affected in a more catastrophic way by extreme events (drought, flood), pests and diseases, and management of nutrition and irrigation. Any of these can result in a limitation of growth (Muller et al., 2011). Our analysis has not attempted to include modelling of these more or less exceptional cases affecting yield but rather has presumed that yield will be photosynthesis (i.e. carbon gain) led to some extent, and in this case modelling of photosynthesis is an effective way of predicting growth. The reason for excluding these effects external to photosynthesis is simply allow us to focus on the responses of photosynthesis and thus get an idea of what could be achieved within a production system that was photosynthesis limited.

To predict the impact of altering some well-understood and important properties of photosynthesis on different crop yield-related parameters, we will use the embedded photosynthesis model of GECROS. This photosynthesis model is based on that of Farquhar et al. (1980). This also takes account of the impact of environmental factors on photosynthesis insofar as they can be simulated. The accuracy of GECROS as a crop modelling tool has been validated using, e.g. rice (Gu et al., 2014; Kadam et al., 2019), potato (Khan et al., 2014) and other crops including wheat and maize (Lenz-Wiedemann et al., 2010). In this study, we will model the responses of wheat, potato and maize. We will use existing climate data as an input to the model. This study builds on previous modelling exercises that showed that improvements in photosynthesis could result in yield increases (Long et al., 2006; Yin & Struik, 2017; Zhu et al., 2010) and proof-of-principle results in which

improvements in photosynthesis resulted in yield (measured as biomass) increases (Kromdijk et al., 2016; López-Calcagno et al., 2020; Simkin et al., 2015, 2017). In this paper, we will deal with photosynthetic traits in more detail and show whether location in Europe can affect the value of trait improvement in terms of yield.

2 | MATERIALS AND METHODS

2.1 | The crop growth model, GECROS

The crop model GECROS was first published by Yin and van Laar (2005) and predicts the effects of climatic factors (radiation, temperature, wind speed and vapour pressure) and the amounts of available soil water and nitrogen on crop biomass and yield (Figure 1). The model describes the interactive responses of key physiological processes to environmental variables, and thus encapsulates the biological processes and environmental interactions that drive crop dynamics and give rise to emergent feedback phenomena. Since its first release, the model has been updated several times, with the latest version being described by Yin and Struik (2017)—this is the version we will use here. Here, we will summarise the modules used for (i) modelling carbon assimilation and growth processes, and (ii) modelling nitrogen uptake, root-shoot relations, sink demand and senescence.

2.1.1 | Modelling carbon assimilation and growth processes

Photosynthesis and transpiration—Instantaneous leaf photosynthesis (A) was calculated using analytical algorithms that are based on the FvCB model (Farquhar et al., 1980) for C_3 photosynthesis, and the equivalent models for C_4 photosynthesis (von Caemmerer & Furbank, 1998), combined with a phenomenological model of stomatal conductance g_s. This analytical approach was also combined with a temperature and leaf N-dependent model of mesophyll conductance g_m. Analytic cubic polynomials (see Yin & Struik, 2009) simultaneously solve stomatal conductance (g_s), internal [CO_2] level and leaf photosynthesis rate (A) at any given temperature. The value of g_s obtained by this means was used in the Penman–Monteith equation (Monteith, 1973) for surface energy balance to model leaf transpiration and leaf temperature, with the leaf temperature estimate being then used to re-calculate leaf photosynthesis and transpiration. Leaf N content affects photosynthesis, g_s, g_m and transpiration and more basic photosynthetic parameters (i.e. maximum Rubisco carboxylation rate V_{cmax}, maximum rate of linear electron transport J_{max}). Upscaling from the leaf to canopy photosynthesis and transpiration was achieved using the sun/shade model of de Pury and Farquhar (1997). Canopy extinction and reflection coefficients for direct and diffuse radiations were calculated using the approaches of
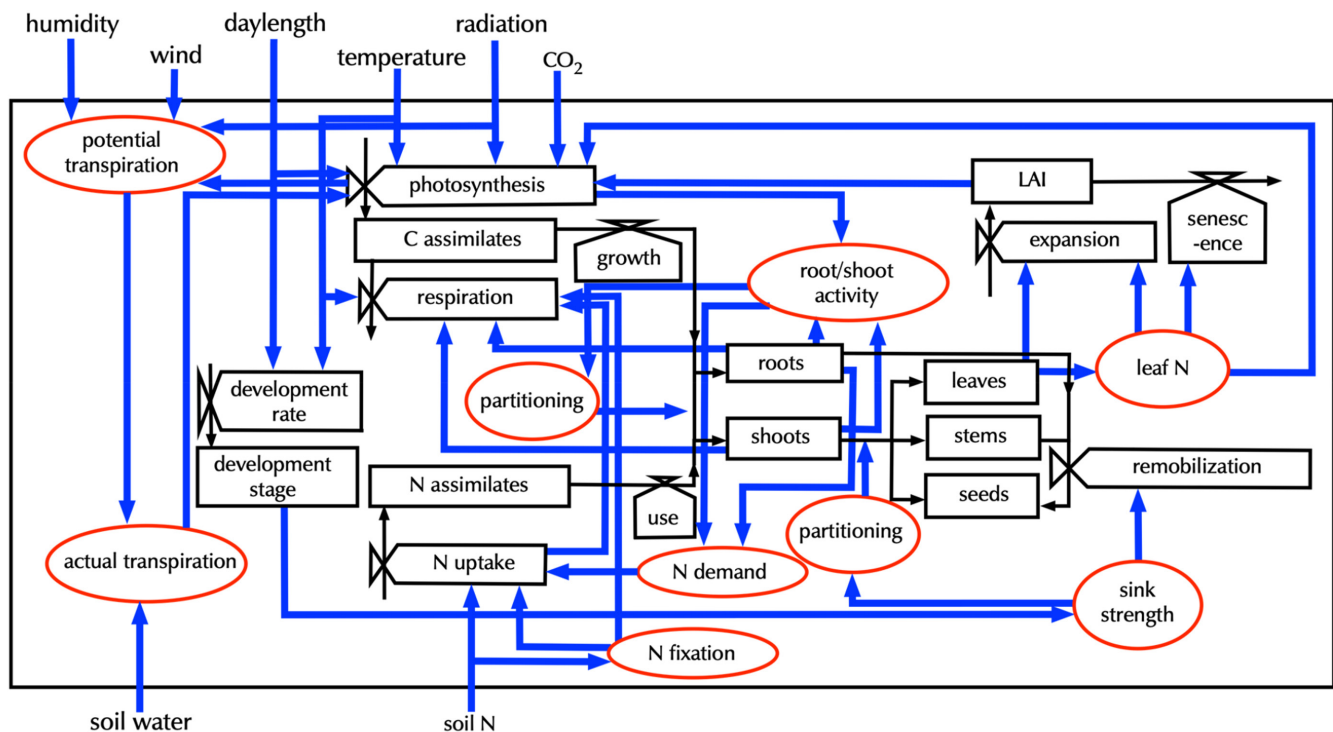

FIGURE 1 Relational diagram describing physiological processes and their interactions as affected by environmental variables, quantified in the GECROS model. Based on Yin and van Laar (2005)

Goudriaan (1988) and Anten (1997). Temporal upscaling from instantaneous rates to daily integrals was performed using the 5-point Gaussian integration (Goudriaan, 1986) to account for (a)symmetric diurnal course of radiation and temperature, to which photosynthesis and transpiration respond nonlinearly. These approaches for spatial and temporal extensions are valid only in the absence of water stress. In the presence of water stress (i.e. when water availability does not satisfy the requirement for potential transpiration), the available water, whose diurnal course is assumed to follow that of radiation, is partitioned between sunlit and shaded leaves according to their relative share of their potential transpiration to obtain their actual instantaneous transpiration. This actual transpiration is transformed into the actual level of g_s (see equation 18 of Yin and Struik (2017)), and the actual g_s was then used as an input to the analytical quadratic model (Yin & Struik, 2017) to estimate the instantaneous actual photosynthesis of the sunlit and shaded leaves. The Gaussian integration is again used to obtain the daily total of the actual photosynthesis.

Crop respiration—Crop respiration was modelled using the framework of Cannell and Thornley (2000), which recognises individual relationships between respiration and each process it supports. The following component processes were recognised: growth, symbiotic N_2 fixation, root nitrogen uptake, nitrate reduction, other ion uptake, phloem loading and residual maintenance component. Growth efficiency is obtained from the chemical composition of plant material based on carbon fraction and glucose requirement of these chemical components. Most of the other processes can be similarly well quantified (Cannell & Thornley, 2000). In the model, maintenance respiration was assumed to be related to crop N content.

2.1.2 | Modelling nitrogen uptake, root-shoot relation, sink demand and senescence

Nitrogen uptake—Usually N uptake is the minimum of crop N demand and soil N supply; the latter is presented in a soil model. Crop N demand (N_{dem}) is modelled from an equation based on the analysis of Hilbert (1990) for balanced growth conditions. This analysis assumes that achieving the optimum plant N:C ratio for a maximised relative C gain requires that relative root activity for N uptake and relative shoot activity for C assimilation are balanced.

Partitioning between root and shoot—The partitioning of newly formed C and N assimilates between root and shoot is modelled from the equations of Yin and Schapendonk (2004). The equations are based on classical root-shoot functional balance theory, with the incorporation of a mechanism that allows plants to control root-shoot partitioning in order to maximise their relative C gain. When incorporated into a crop model, these equations reproduce the plasticity of root: shoot ratios in response to environmental conditions (Yin & Schapendonk, 2004).

Sink demand—Assimilates distributed to the shoot need to be further modelled for partitioning among the shoot organs. It is assumed that the strength of growing organs as sinks for available C determines the partitioning, and any surplus assimilate goes to the pool of reserves, which can be later remobilised if there is assimilate deficit. To achieve this the differential form of the asymmetric determinate growth function of Yin, Goudriaan, Lantinga, Vos et al. (2003) is used to describe the dynamics of sink demand. Note that sink activity is difficult to model mechanistically and realistically so projecting future sink activities is beyond the scope of this exercise.

LAI and senescence—Leaf area index (LAI) is modelled as the minimum of C- and N-determined LAI. The former (L_C) is the same as LAI calculated from biomass accumulated in leaves. The latter (L_N) is modelled using an equation developed by Yin et al. (2000) describing LAI in relation to the amount of canopy leaf nitrogen. An important aspect of this approach is to produce a simple yet robust method to predict the onset and quantity of leaf senescence: the rate of the LAI decrease due to senescence can be formulated as $\left[L_C - \min\left(L_C, L_N\right)\right]/t_c$, where t_c is the time constant. A similar approach was used for describing root senescence, based on root N content.

2.2 | The photosynthetic parameters that were adjusted in the modelling

2.2.1 | C3 photosynthesis

Photosynthesis is well summarised by models that, to varying degrees of completeness, can simulate its activity. The FvCB model (Farquhar et al., 1980; von Caemmerer & Farquhar, 1981) is widely seen as a simple and effective description of the biochemistry of photosynthesis. This is especially so for the properties of Rubisco and its interaction with photosynthetic electron transport. This model simulates the response of assimilation to CO_2 concentration in the substomatal cavity (strictly it should be at the site of carboxylation of RuBP, i.e. in the chloroplast). It focuses on the biochemistry of the primary CO_2 fixing reaction (Rubisco) but also includes a limitation that can be attributed to limitations by photosynthetic electron transport or the regeneration metabolism of the Calvin cycle. This limitation is not mechanistically modelled in detail in the basic FvCB model, which encompasses at a

manageable scale of model-complexity the basic physiology of photosynthesis at the cellular level. It is sufficiently well-designed and flexible that it can be connected to other models that describe processes, such as the diffusion of CO_2, needed to produce more complete, and more complex, models of photosynthesis. Its simplicity and utility means that the model has been very widely used in photosynthesis research. The model is also widely used to parameterise measured leaf photosynthetic responses so photosynthesis *in folio* is well-understood in terms of the parameters of the model. Adjustments to these parameters are therefore an excellent way to experiment *in silico* with improvements to photosynthesis. The parameters of the FvCB model that we will adjust are:

- V_{cmax}—the maximum rate of Rubisco catalysed carboxylation of RuBP. This reaction is assumed to be RuBP saturated (i.e. not limited by RuBP supply) and so is a first-order enzyme catalysed reaction that follows Michaelis–Menten kinetics. This determines the assimilation rate under low-CO_2 conditions and probably under high-light conditions at the ambient-$[CO_2]$.

- J_{max}—light-saturated rate of potential electron transport rate. This determines the assimilation rate corresponding to a rate of carboxylation that is limited by the supply of RuBP and not that of CO_2. In fact, RuBP supply can be limited by several factors. It can be limited by electron transport (e.g. when irradiance limits or when electron transport capacity has reached its maximum) but it can also be limited by the regeneration phase of the Calvin cycle. The FvCB model takes a simple approach assuming being limited by electron transport. As RuBP supply can be limited by other factors than electron transport J_{max} can be a physiologically complex parameter.

- $S_{c/o}$—the specificity factor of Rubisco for catalysing the carboxylation rather than the oxygenation of RuBP. In one parameter the specificity factor combines four subparameters and summarises the effectiveness of Rubisco as a catalyst for the carboxylation relative to the oxygenation reaction

$$S_{c/o} = (K_o V_{cmax}) / (K_c V_{omax})$$

where K_o is the Michaelis–Menten constant for the oxygenation reaction (bigger means the reaction is less sensitive to O_2), K_c the Michaelis–Menten constant for the carboxylation reaction, V_{cmax} as defined above, and V_{omax} the maximum rate of the oxygenation reaction.

- κ_{2LL}—this is another parameter of the irradiance response equation, a parameter defining the light-limited efficiency of converting irradiance into linear electron transport (Yin et al., 2009). Strictly this refers to the quantum efficiency of linear electron transport and is thus typically seen as being PSII-centred (PSI also carries out cyclic electron transport), but it is a lumped parameter and can be used more generally as a measure of the conversion of incident light into linear electron transport. For example, an increase in the spectral range of photosynthetically active radiation can be simulated by an increase in κ_{2LL}.

- g_m—the mesophyll conductance. This concerns the diffusion of CO_2 from the substomatal cavity to the site of carboxylation in the chloroplast and represents a diffusive resistance. Note that to drive the flux of CO_2 the concentration of CO_2 must be lower in the chloroplast than in the substomatal cavity. This decrease in the concentration of CO_2 decreases the fixation of CO_2 because it makes CO_2 concentration more limiting for the carboxylation reaction catalysed by Rubisco and it decreases the ratio of the carboxylation and oxygenation reactions catalysed by Rubisco. This internal diffusive resistance is more commonly measured by its reciprocal, the mesophyll conductance, g_m.

2.2.2 | C4 photosynthesis

There is an analogue of the FvCB C3 photosynthesis model for the C4 photosynthesis which like the FvCB model provides a simple tool for simulating C4 photosynthesis (von Caemmerer, 2000; von Caemmerer & Furbank, 1998). Four key parameters of the C4 photosynthesis model were adjusted in the analysis of the potential improvement of yield-related parameters in response to improvements in photosynthesis: V_{cmax}, J_{max}, $S_{c/o}$ and g_{bs}. Of these, V_{cmax}, J_{max} and $S_{c/o}$ are the same as for C3 photosynthesis and describe the action of the C3 photosynthesis in the bundle sheath cells. The remaining parameter, g_{bs}, describes the resistance to leakage (expressed as its reciprocal, a conductance) of CO_2 from the high CO_2 concentration within the bundle sheath cells. A higher g_{bs} results in a higher loss of this CO_2 from bundle sheath cells, representing an inefficiency of the CO_2-concentrating mechanism, a C4 process. So a lowering of this conductance (a greater restriction to loss) is better.

2.3 | Simulation procedure

While the GECROS model has algorithms to simulate crop production under water-limited conditions, we assumed there would be no water limitation to allow us to explore the effect of photosynthesis improvements alone.

Using GECROS, we explored the response of yield-related parameters to a 20% change in each of the above photosynthetic parameters, and to the changes with all five or four parameters combined. Baseline parameter values were taken from Yin and Struik (2017). 20% was chosen because improvements in crop model photosynthesis brought about by GM techniques typically result usually in improvement in photosynthetic parameters comparable to the ones we used. For example, Simkin et al. (2015) recorded a 25% increase in the maximum assimilation rate in a A/C_i response for mature leaves of tobacco transformed with ictB (see Figure 3b; Simkin et al. 2017) recorded a 40% increase in the maximum assimilation rate in light-response curve and a 28% increase in the maximum assimilation rate at light saturation in a light-response measurement in tobacco with increased Rieske FeS complex; and Driever et al. (2017) reported a 17% increase in maximum assimilation rate in wheat at a CO_2 mole fraction of 400 ppm, and a 12% increase at 1300 ppm, following a 60% increase in SBPase (see Figure 3a). Natural variation for traits of the kind we explore in this paper also shows a variation of around 20%; examining the variation of Rubisco parameters in domesticated wheat and wild relatives of wheat Prins et al. (2016) found a 20% variation in V_{cmax} at 25°C, which increased to a 33% variation at 35°C (see Figure 1; in this case, the midpoint value between the maximum and minimum values was taken as the reference value), and for $S_{c/o}$, the variation was 10% at 25°C and 16% at 35°C (see their Figure 2, calculation as for V_{cmax}), while in a study of wheat Elizabete Carmo-Silva et al. (2017) found a 27% variation for J_{max} and a 24% variation for V_{cmax} (Carmo-Silva et al., their Figure 6), again taking the midpoint of the distribution of values as the reference. Using the same percentage of change for all photosynthesis parameters also allowed us to assess the simulated relative importance of these parameters in affecting crop yield.

The simulation was implemented to examine the responses of wheat, potato and maize to 20% increases in the above photosynthesis parameters. This analysis used past 10-year (1991–2000) weather data from 66 European sites (weather data from Institute for Environmental and Sustainability of the European Commission's Joint Research Centre and tabulated by Yin, Vos, & Lantinga 2003; Table S1); but the atmospheric [CO_2] concentration was set to 400 ppm. The results obtained from GECROS were aboveground biomass, total plant biomass, storage organ biomass (this includes grain production—storage organs are considered to be the useful yield of the crop), whole season photosynthesis, whole season intercepted photosynthetically active radiation, the radiation interception efficiency and the energy conversion efficiency. While GECROS produces a wide range of outputs

we will predominantly emphasise total plant biomass, and the radiation interception efficiency and the energy conversion efficiency, i.e. the terms ε_i and ε_c in the Monteith yield equation (Long et al., 2006; Monteith & Moss, 1977).

3 | RESULTS

We first show results for the overall effect of improved photosynthesis by averaging simulation output across the 66 sites. We then assess whether there is some geographical variation in crop responses to photosynthesis improvement.

3.1 | Simulated overall average effects of improving photosynthesis on crop traits
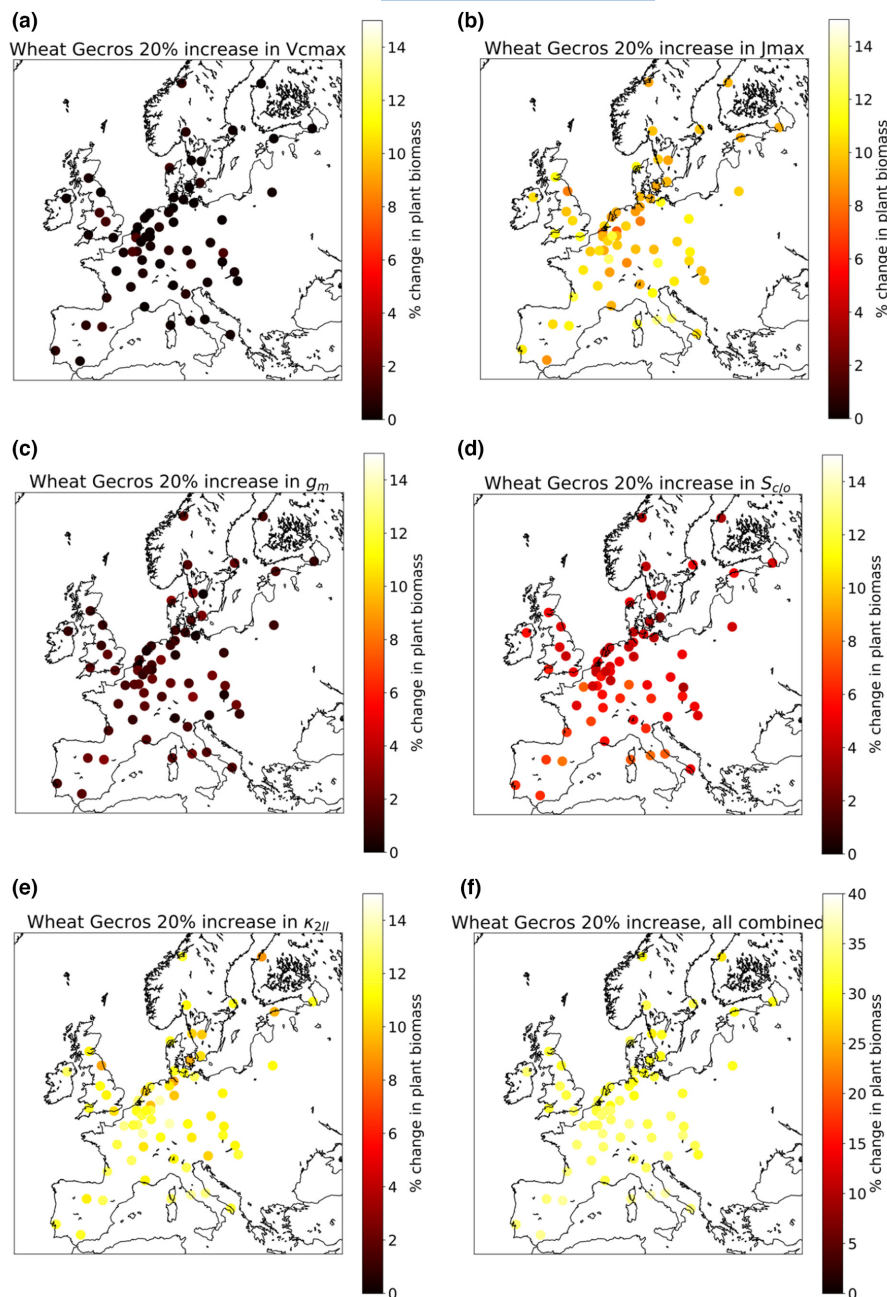
The baseline results of yield parameters simulated using the default photosynthetic parameter values for the three crops (Tables 1–3) generally agreed with the expected values of these crops in the absence of (a)biotic stresses.

The impact on crop yield parameters of wheat and potato (both C3 crops) resulting from 20% increases in V_{cmax}, J_{max}, g_m, $S_{c/o}$, κ_{2LL} and all five combined are shown in tabular (Tables 1 and 2) and graphical form (Figures S1 and S2). The impact on the yield parameters for maize (a C4 crop) to 20% increases in V_{cmax}, J_{max} and $S_{c/o}$, a 20% decrease in g_{bs}, and all four changes combined are shown in tabular (Table 3) and graphical form (Figure S3).

These results from GECROS show that for the C3 and C4 species the mean effect of increasing V_{cmax} is only minor (Tables 1–3, Figures S1a, S2a and S3a). In both C3 and C4 species it results in only small increases in whole season photosynthesis, with the biggest effect on maize (0.22%), then wheat (0.12%) and then potato (0.07%), and small increases in ε_c, with the biggest increase with maize (0.23%), then wheat (0.19%) and then potato (0.11%). These small effects of an increase in V_{cmax} on photosynthesis parameters are paralleled by similarly small effects on growth. This implies that, at least in the modelled situation, crop assimilation and yield are rarely Rubisco limited in wheat, potato or maize.

Increasing J_{max} (i.e. RuBP supply, limited most often by electron transport or the regeneration phase of the Calvin cycle; Tables 1–3, Figures S1b, S2b and S3b), on the other hand, results in significant effects on photosynthesis; whole season photosynthesis increases by 7.3% in maize, 6.4% in wheat and 5.2% in potato, and ε_c increases by 8.6% in wheat, 7.8% in potato and 6.3% in maize. This resulted in notable increases in growth; total plant biomass increased by 10.1% in wheat, 8.2% in potato and 8.1% in

FIGURE 2 The geographical distribution of wheat yield responses across Europe to increases (i.e. improvements) in photosynthetic parameters calculated by GECROS

maize. Increasing J_{max} increased the total amount of intercepted PAR (and ε_i) slightly for all three species, with the greatest effects for wheat (ε_i increased by 1.3%) and maize (ε_i increased by 1.6%). The increase in storage organ biomass was less than the increase in total plant biomass for wheat (5.2% vs 10.1%) and potato (4.6% vs 8.2%) but bigger for maize (14.3% vs 8.1%).

An increase in mesophyll conductance (g_m, a parameter, which is only significant in C3 photosynthesis) produces only small increases in yield (total plant biomass) (Tables 1 and 2, Figures S1c and S2c) with ε_c and ε_i being essentially unaffected. Improving (i.e. increasing) $S_{c/o}$ (a Rubisco parameter whose increase will improve both light-limited and light-saturated assimilation)

moderately increases biomass in wheat (5.2%) and potato (3.4%), and slightly increases it in maize (1.5%) (Figures 2d, 3d and 4d; Tables 1–3, Figures S1d, S2d and S3d). ε_c is similarly affected, while ε_i is relatively unaffected.

Increasing the efficiency with which irradiance drives linear electron transport (κ_{2LL}) produces large increases in whole season canopy photosynthesis and ε_c; whole season canopy photosynthesis increased by 7.8% in wheat and 4.5% in potato and ε_c increased by 10.9% and 7.0% for wheat and potato, respectively. ε_i was relatively unaffected in both species. The increase in photosynthesis resulted in increased biomass production, by 11.5% in wheat and 6.5% in potato. As with increases

TABLE 1 The baseline simulation results and average percentage increase in yield parameters estimated by GECROS for wheat in response to 20% increases in photosynthetic parameters

Wheat	Above-ground biomass	Total plant biomass	Storage organ biomass	Whole season canopy photosynthesis	Whole season intercepted PAR	ε_i	ε_c
Baseline	$1723\,\mathrm{g\,m^{-2}}$	$1936\,\mathrm{g\,m^{-2}}$	$917\,\mathrm{g\,m^{-2}}$	$4631\,\mathrm{g\,CO_2\,m^{-2}}$	$752\,\mathrm{MJ\,m^{-2}}$	70%	$2.59\,\mathrm{g\,MJ^{-1}}$
+20% V_{cmax}	0.06	0.16	0.16	0.12	−0.04	−0.04	0.19
+20% J_{max}	6.90	10.14	5.14	6.40	1.35	1.35	8.65
+20% g_m	0.72	1.48	1.01	1.06	−0.05	−0.05	1.52
+20% $S_{c/o}$	2.95	5.23	3.00	3.51	0.28	0.27	4.91
+20% κ_{2LL}	6.58	11.46	6.57	7.80	0.56	0.55	10.90
+20% All	20.29	32.77	17.50	22.55	2.08	2.06	30.10

TABLE 2 The baseline simulation results and average percentage increase in yield parameters estimated by GECROS for potato in response to 20% increases in photosynthetic parameters

Potato	Above-ground biomass	Total plant biomass	Storage organ biomass	Whole season canopy photosynthesis	Whole season intercepted PAR	ε_i	ε_c
Baseline	$1736\,\mathrm{g\,m^{-2}}$	$1897\,\mathrm{g\,m^{-2}}$	$1294\,\mathrm{g\,m^{-2}}$	$4244\,\mathrm{g\,CO_2\,m^{-2}}$	$786\,\mathrm{MJ\,m^{-2}}$	73%	$2.44\,\mathrm{g\,MJ^{-1}}$
+20% V_{cmax}	0.07	0.07	0.12	0.07	−0.05	−0.05	0.11
+20% J_{max}	6.12	8.23	4.65	5.19	0.35	0.33	7.85
+20% g_m	0.71	0.87	0.87	0.69	−0.19	−0.19	1.05
+20% $S_{c/o}$	2.69	3.41	2.69	2.34	−0.26	−0.27	3.65
+20% κ_{2LL}	5.31	6.50	5.40	4.51	−0.47	−0.49	7.02
+ 20% All	17.06	23.51	14.51	15.99	0.25	0.22	23.17

TABLE 3 The baseline simulation results and average percentage increase in yield parameters estimated by GECROS for maize in response to 20% increases or decreases in photosynthetic parameters

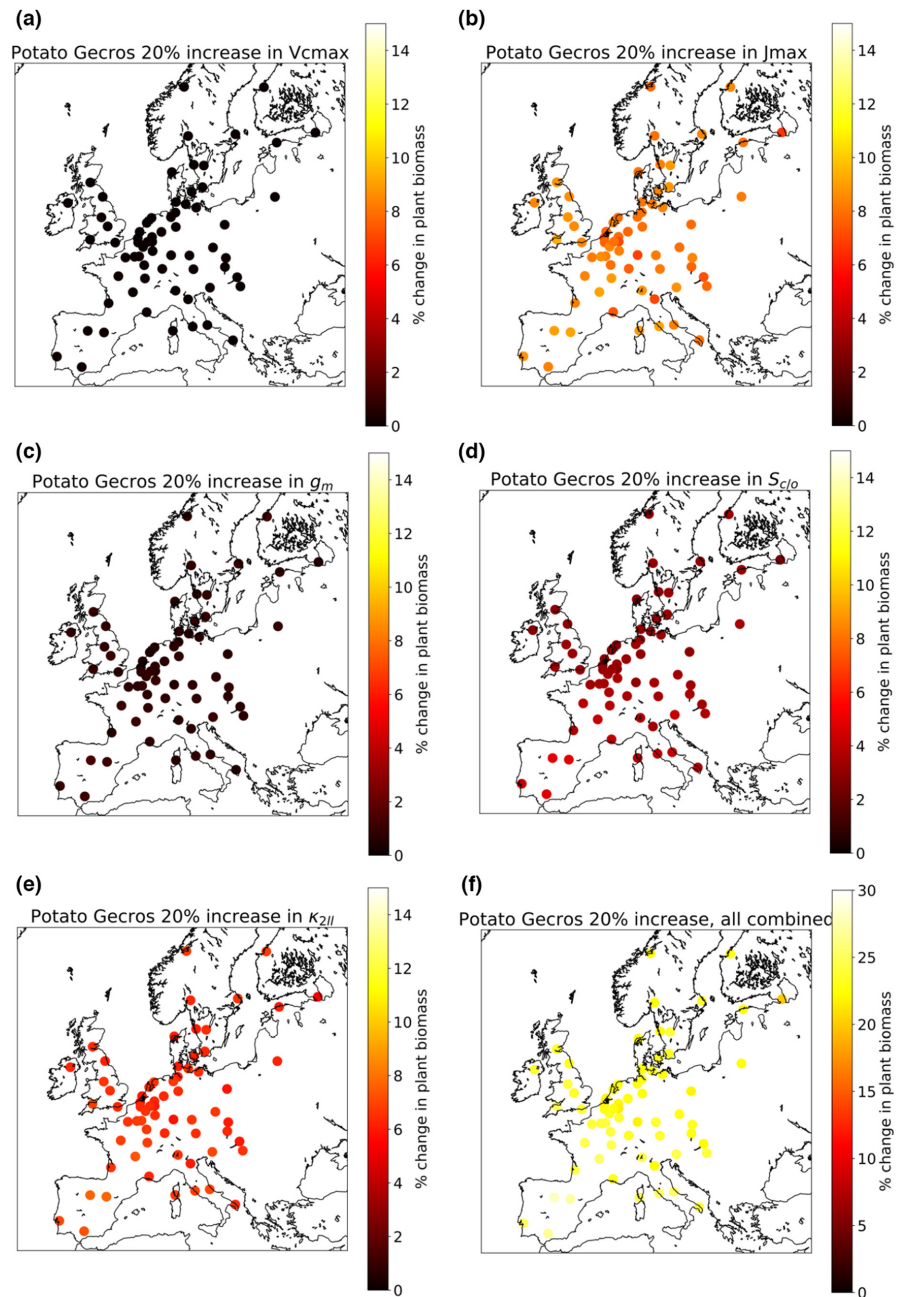| Maize	Above-ground biomass	Total plant biomass	Storage organ biomass	Whole season canopy photosynthesis	Whole season intercepted PAR	ε_i	ε_c
Baseline	$2334\,\mathrm{g\,m^{-2}}$	$2461\,\mathrm{g\,m^{-2}}$	$1131\,\mathrm{g\,m^{-2}}$	$5807\,\mathrm{g\,CO_2\,m^{-2}}$	$770\,\mathrm{MJ\,m^{-2}}$	71%	$3.21\,\mathrm{g\,MJ^{-1}}$
+20% V_{cmax}	0.22	0.22	0.48	0.22	−0.01	−0.01	0.23
+20% J_{max}	8.83	8.10	14.27	7.33	1.63	1.62	6.32
−20% g_{bs}	1.18	1.11	1.94	1.05	0.13	0.13	0.98
+20% $S_{c/o}$	1.56	1.46	2.41	1.36	0.21	0.21	1.25
20% in All	11.62	10.71	19.09	9.85	1.83	1.82	8.67

to J_{max}, the impact on storage organ biomass for wheat and potato was less than the impact on total plant biomass. Note that the increase in the κ_{2LL} parameter was only applied to the C3 crops owing to the complex electron transport/assimilation relationship in C4 plants; there are two cell types involved in photosynthesis in C4 plants with different electron transport properties in each.

The leakiness of the bundle sheath cells for CO_2 decreases the efficiency of C4 photosynthesis so decreasing this leakiness—decreasing g_{bs}—improves whole canopy photosynthesis by just 1.0% and plant biomass accumulation by 1.5% (Table 3, Figure S3c).

The photosynthetic properties modelled largely act independently of each other; only the change in $S_{c/o}$ overlaps with the effects of V_{cmax} and J_{max} via the ratio of the velocities of oxygenation and carboxylation that is a parameter in the functions for V_{cmax} and J_{max}. A combined increase in all the parameters used in the C3 analysis, therefore, results in an increase in total plant biomass

accumulation and ε_c that is greater than obtained when the parameters were individually increased (Tables 1 and 2, Figures S1f and S2f). The increase in total biomass for wheat was 33% while for potato it was 23.5% (as before the increase in the storage organ biomass was lower), whole season photosynthesis increased by 22.5% for wheat and 16.0% for potato, while ε_c increased by 30% for wheat and 23% for potato (ε_i barely changed). The consequence of combining the parameter improvements for maize (Table 3 and Figure S3f) was less than for the C3 plants—total plant biomass increased by 10.5% (though storage organ biomass increased by 19%) while ε_c increased by 8.5%.

3.2 | The geographical dimension of yield responses

Climate and weather are not constant across Europe, so we used climate data from a range of European locations to explore how yield would be affected by improvements to photosynthesis across Europe. There is some geographical variation in the responses of total plant biomass (Figures 2–4) but supports the mean response of total plant biomass shown in Tables 1–3 and Figures S1–S3. Generally increasing V_{cmax} results in only a very weak increase in plant biomass for wheat (Figure 2a), potato (Figure 3a) and maize (Figure 4a)
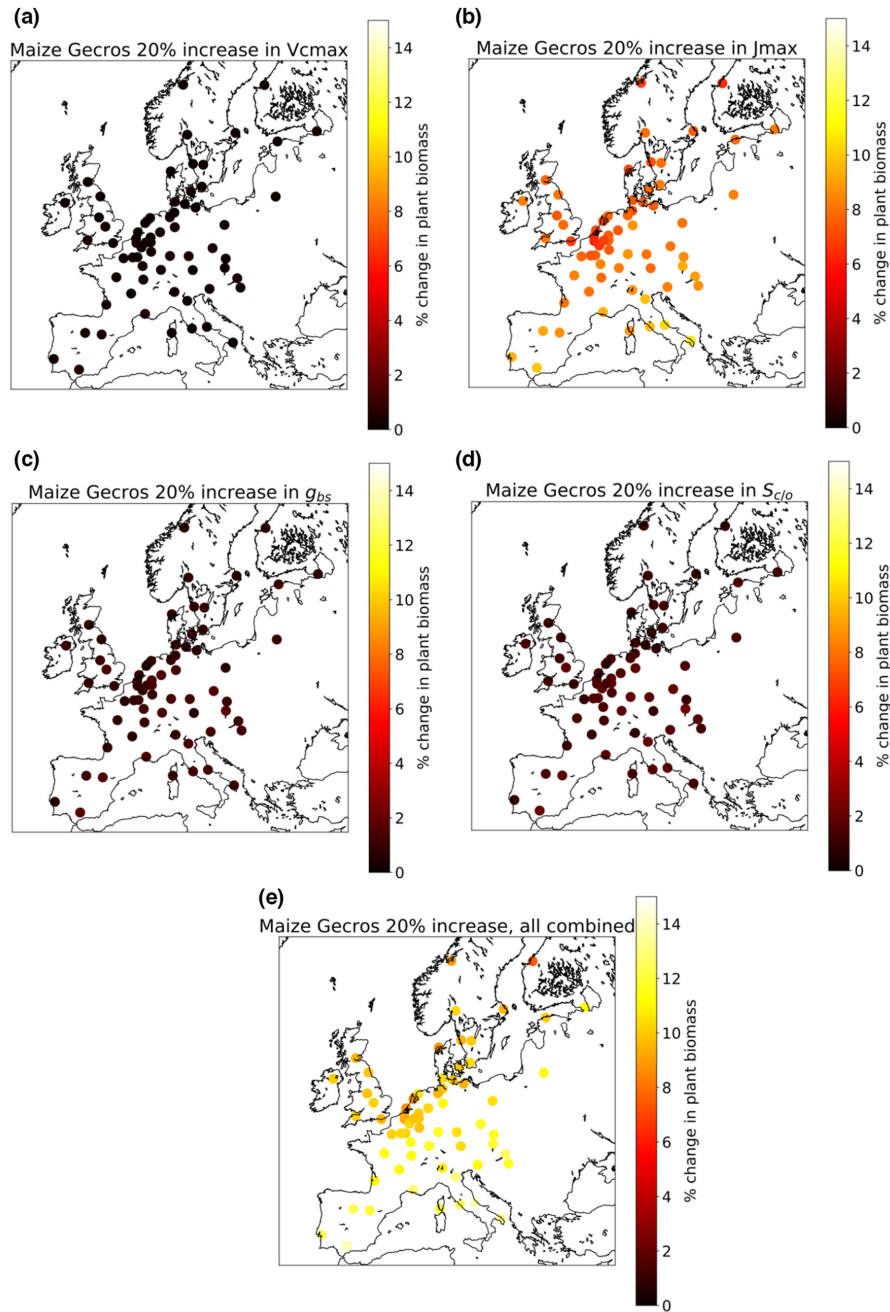
FIGURE 4 The geographical distribution of maize yield responses across Europe to increases or decreases (i.e. improvements) in photosynthetic parameters calculated by GECROS

everywhere in Europe, as does g_m (wheat, Figure 2c; potato Figure 3c). Increasing J_{max}, on the other hand, produces a large increase in total plant biomass everywhere in Europe (wheat, Figure 2b; potato, Figure 3b; and maize, Figure 4b), as does κ_{2LL} (wheat, Figure 2e; and potato Figure 3e). For the C3 crops improving $S_{c/o}$ by 20% produces a moderate increase in total plant biomass throughout Europe, while for maize the response to an increase in plant biomass is less (Figure 4d). Decreasing g_{bs} (maize only, Figure 4c) produces only a small increase in biomass with little variation throughout. The response to all parameters in combination (wheat, Figure 2f; potato, Figure 3f; and maize, Figure 4e) produces Europe-wide increases in biomass.

Despite the overall homogeneity of the responses and the consistency with the mean responses, there is variation in response. The responses of wheat to increases in J_{max} and κ_{2LL} are weaker in northeastern England, the Netherlands, northwestern and western Germany, the Baltic and southern France and Spain. Potato behaves similarly. The response of maize to an increase in J_{max} is also lower in northern Europe than in southern Europe.

4 | DISCUSSION

The results show that improving photosynthesis can improve crop yield as has already been shown in practice

(e.g. Simkin et al., 2015). It is clear, however, that not all aspects of photosynthesis are equivalent in terms of the extent to which they appear to limit assimilation and ε_c, and therefore how useful they will be as targets for improvement. These conclusions based on modelling need to be validated by measurements of field-grown plants.

We have simulated the effect on crop yield parameters by improving some basic parameters defining the operation of photosynthesis. We have done this for a narrow, erect-leaved monocot crop (wheat), a broad-leaved dicot crop (potato) and a C4 monocot (maize) and in the absence of limitation by water supply. The results show that improving some aspects of photosynthesis results in yield increases, while improving other aspects does not. The parameters that conspicuously improve yield (J_{max}, κ_{2LL} and $S_{c/o}$) positively affect light-use efficiency under non-light-saturating conditions and in addition both J_{max} and $S_{c/o}$ affect assimilation under light-saturated (or nearly so) conditions. The lack of any impact on yield from improving V_{cmax}, which is believed to be connected to light-saturated rates of photosynthesis, is telling. The limitation of a photosynthetic light-response curve by V_{cmax} would limit assimilation, but probably only at high irradiances. The fact that most leaves in a canopy are shaded by upper leaves contributed to the lack of the impact of increased V_{cmax} on yield. In addition, photosynthetic at high irradiances could also be limited by J_{max} as is implied by the beneficial effect on yield of improving the regeneration phase of the Calvin cycle, which results in an increase in J_{max}. Archontoulis et al. (2012) observed that points along an entire irradiance response curve under ambient and higher CO_2 mole fraction conditions are essentially electron transport determined. In the case of limitation by electron transport (another determinant of J_{max}), a transition from electron transport limitation to limitation by, e.g. Rubisco or triose phosphate utilisation, would be expected to be accompanied by a downregulation of electron transport. The occurrence of this downregulation can be measured via the kinetics of oxidised P700 reduction after a light–dark transition (Genty & Harbinson, 1996; Harbinson & Hedley, 1989; Harbinson & Yin, 2017; Laisk & Oja, 1994). At least under physiologically permissive conditions, the kinetic constraint on photosynthetic electron transport does not usually change in response to increasing irradiance, although there are some exceptions (Ott et al., 1999). These data imply that photosynthesis can be wholly electron transport or possibly co-limited by electron transport and metabolism. It would be useful to have data from field-grown crops where it ought to be possible to determine a transition from electron transport to a metabolic limitation by measuring the rate constant for P_{700}^+ reduction following a light–dark transition.

Improved J_{max}, κ_{2LL} and $S_{c/o}$, even if their beneficial effects were to be limited by V_{cmax} at high irradiances, would still result in improved photosynthetic light-use efficiency at subsaturating irradiances. Over the daily course of irradiance and within the canopy, photosynthesis will often be operating under nonsaturating irradiances, so improving light-use efficiency under non-light-saturating conditions will be beneficial to carbon gain and growth. Notably yield increases accompany improvements in photosynthesis via improvements in the regeneration phase of the Calvin cycle (which increase J_{max}) (Driever et al., 2017; Simkin et al., 2015), and accelerating relaxation of the qE component NPQ, which improves light-limited efficiency after a high to low light transition (which will increase light-use efficiency under light-limited conditions) (Kromdijk et al., 2016). Clearly what we have shown here is that within the world of the model, improvements in photosynthesis can improve yield. Even if the models still have shortcomings these appear not to be generally limiting their effectiveness at predicting yield; this is supported by the simulation results of Gu et al. (2014) and Yin and Struik (2017) for Asian countries and of Wu et al. (2019) for Australia.

The geographical variation of the yield increments resulting from fixed increases in photosynthetic parameters is important. They imply that a 'one size fits all' for yield improvement for Europe will not work. Given the geographical variation in agriculture even within European countries, this geographical dimension will not be a surprise, but it is still a matter that needs to be properly taken into account as we develop pan-European solutions to future-proof our crops. It is, however, reassuring that those photosynthetic properties that did have a significant effect on yield do still have a significant effect everywhere, it is just that the scale of the effect varies. On the other hand, those traits that have only a weak effect on average have only a weak effect everywhere, at least among sites for which we simulated. This implies that at least as far as photosynthesis and yield improvement go, Europe can focus on only a subset of all the possible photosynthetic properties that could produce a positive effect on this process.

Our photosynthesis submodels are still static and do not yet account for the effect that rapid fluctuations in environmental factors, such as irradiance, have on photosynthesis, and therefore on yield. We also must currently adopt a simple approach to dealing with canopy architecture while we would prefer an approach based on a more accurate canopy model, which allowed a more accurate simulation of radiation within the canopy under different solar angles and meteorological conditions. This would require combining a large-scale model such as GECROS with more detailed, fine-scale (both spatially

and temporally) simulations of light flecks in a canopy alongside (e.g. Burgess et al., 2021; Retkute et al., 2018) the photosynthetic response to these rapid fluctuations in irradiance and temperature (e.g. Kaiser et al., 2018; Morales et al., 2018). Such a model would tend to be a detailed simulation of the canopy and its interaction with its physical environment alongside a detailed leaf or plant level simulation of photosynthesis, and presumably more. This would be an exciting development and seems to be the way to go, but it would be computationally demanding if it were used to simulate the developing and mature crop canopy of a whole season and for multiple years and sites. Whatever the future holds, the results from our modelling exercise do confirm that better photosynthesis is likely to lead to better crop yields in Europe. This improvement is likely to apply across most of Western and Central Europe (the EU)—drought stress limitations only seemed to be a limitation in Spain and parts of France for wheat yields modelled by the APSIM model (Taylor et al., unpublished). Although initial results for Asian climatic conditions showed that improving photosynthesis could give a higher percentage of increase in productivity under moderate drought, compared with the increase projected for the case in the absence of drought (Yin & Struik, 2017), further modelling of drought limitation should be undertaken. Other local variations in yield responses also need to be better understood.

CONFLICT OF INTEREST
The authors have stated explicitly that there are no conflicts of interests in connection with this article.

DATA AVAILABILITY STATEMENT
Executables of GECROS for non-coomercial purposes can be obtained upon request from the corresponding author. The meteorlogical data used is the property of the EU's Joint Research Centre and can be obtained from them, but all other input data used in this work can be obtained from the corresponding author.

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