Annals of Applied Biology ISSN 0003-4746

RESEARCH ARTICLE

Crop production structure and stability under climate change in South America

R. Ferrero[1,2,3], M. Lima[2,3,4] & J.L. Gonzalez-Andujar[1,3]

1 Departamento Protección de Cultivos, Instituto de Agricultura Sostenible, Consejo Superior de Investigaciones Científicas (CSIC), Córdoba, Spain
2 Center of Applied Ecology & Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile
3 Laboratorio Internacional de Cambio Global, LINCG (CSIC-PUC), Santiago, Chile
4 Departamento de Ecología, Pontificia Universidad Católica de Chile, Santiago, Chile

Keywords
Crop management; food production; negative feedback; nonlinearity; regional dynamics models; time series.

Correspondence
Rosana Ferrero, Departamento Protección de Cultivos, Instituto de Agricultura Sostenible (IAS), Consejo Superior de Investigaciones Científicas (CSIC), Alameda del Obispo, s/n Apdo. 4084, 14080 Córdoba, Spain. Email: rferrero@ias.csic.es

Received: 7 May 2016; revised version accepted: 4 September 2017; published online: 27 November 2017.

doi:10.1111/aab.12402

Abstract

Southern South America is expected to play an increasingly important role in global food production, but climate change could seriously threaten it. Here we have analysed long-term historical data for major crops (rice, oats, barley, sunflower, soybean, sorghum, wheat, maize) at subnational scale to (a) look for common features among crop yield dynamics, evaluating their structure and implications for the persistence of that crop; (b) address complex crop responses to changes in environmental growing conditions; and (c) identify climate impact hotspots that are crucial for adaptation and mitigation. We have proposed a novel methodological approach based on dynamics systems in order to understand the processes behind annual crop yield fluctuations. We report the results of general patterns in the internal process (biophysical adjustments by rapid negative feedbacks) regulating crop production and analyse how it influences crop persistence and yield ceilings. The structure of a crop yield dynamic system defines its behaviour, but climate variations could displace it from yield equilibrium and affect its stability. Our findings suggest that weather conditions have a stronger impact on yield growth at high rather than at low yield levels (non-additive impacts). This allows agriculture management to be refined and applied more efficiently, weakening the relationship between crop productivity and climate change and predicting the response of crop production to yield-improvement strategies. We have identified those crops and regions which are most vulnerable to the current climate change trends in southern South American agroecosystems. Our results allow us to point to new ways to enhance self-regulatory success, maximising the efficiency of crop production and reducing climate impacts. We have discussed important implications for crop management and climate change mitigation in an area where agriculture plays a key role in its socioeconomic and ecologic dimensions.

Introduction

Global food demand is increasing rapidly. Ensuring food production in a growing population and the changing climate pose a major challenge to scientists, resource managers and policymakers (Alexandratos & Bruinsma, 2012; Porter *et al.,* 2014). Changes in temperature, precipitation and CO_2 emissions are expected to have net negative effects on global agriculture, particularly in developing countries (IPCC, 2014). Southern South America is expected to play an increasingly important role in global food production because of the region's ability to produce and export agricultural commodities, its potential of new arable land and its share of renewable water resources (Magrin *et al.,* 2014). However, the most relevant studies in the region are limited to a few crops in La Pampa (Magrin *et al.,* 2005 – wheat, maize, sunflower, soybean; Asseng *et al.,* 2013 – wheat; Verón *et al.,* 2015 – maize, wheat, soybean). No studies have so far evaluated the effects of climate change across a large series of crops and subregions in southern South America. Also, there are several examples of discordance between the results of crop yield studies in the region that makes it difficult to identify common patterns of vulnerability to climate change (e.g. for wheat, Verón *et al.* (2015) detected mainly a negative impact of temperature on crop yield, whereas Magrin *et al.* (2005) and Asseng *et al.* (2013) identified a positive effect of rainfall). Therefore the objectives of our research were to (a) look for common features among several crop yield dynamics evaluating their structure and implications for the persistence of that crop; (b) address complex crop responses to changes in growing conditions; (c) identify climate impact hotspots at subnational scale that are crucial for decision-making on adaptation and mitigation.

The structure of a dynamics system has a defining influence on its behaviour (Berryman, 1989). An increasingly common approach to studying crop yield dynamics is the use of statistical models to evaluate the response of yields to climate changes (Lobell & Field, 2007; Lobell *et al.,* 2011). These models can be applied extensively because they require low detailed input data, have a low uncertainty and are more suitable for larger spatio-temporal scales (Lobell & Burke, 2010; Shi *et al.,* 2013). However, the models usually make the implicit (and in an extreme case, unrealistic) assumption that crop yield dynamics is governed by the weather and independent of the yield level (i.e. the same quantity of yield is added in each unit of time) and then crop yield growth could continue indefinitely. This assumption could only be appropriate for modelling systems beyond the maximum potential crop yield, which is not usually the case for most crops and regions. We all know that the upper limit of crop production is set by the climate conditions and the genetic potential of the crop (e.g. Doorenbos & Kassam, 1979), and therefore we have to explicitly include it in our crop statistical models. It can be seen as a random walk process with a distribution that becomes wider with time (i.e. its variance is unbounded and there is no correlation in time; Royama, 1992). However, empirical evidence shows that historical crop yield dynamics has been fairly stable and fluctuates around a trend (or around its persistent state if there is no trend) but does not deviate or drift unboundedly away from it (Lin & Huybers, 2012; Grassini *et al.,* 2013). Recent reports have also indicated the necessity of recognising biophysical limits to crop yield in order to account crop yield growth and stagnation (Ray *et al.,* 2012; Grassini *et al.,* 2013). Individual physiology or height-structured competition for light affect the conversion of those resources into biomass (Purves & Pacala, 2008), so that crop yield growth rate is usually lower for high yield values, although traditional statistical models assume that it is constant. Here we propose that the best way to accommodate temporal variations in crop growth rates is with nonlinear growth models. Specifically, we propose the logistic model as the functional form for crop yield growth analysis because of its flexibility, realism, predictability and generality. Stable and stagnant crop yield changes could be the consequence of a negative feedback structure (due to biophysical internal processes), able to persist over time in a state of dynamics equilibrium with their environment (Ferrero *et al.,* 2014, 2017). Understanding and modelling how both feedback mechanisms and climate interact in shaping the dynamics of crop yield may be fundamental to our ability to predict crop response under climate change.

Climate and CO_2 emissions may have complex effects on crop yield rates. The reliability of our predictions and mechanistic understanding of crop yield dynamics are influenced by whether additive or non-additive approaches are made (see, e.g. Schlenker & Roberts, 2009). However, the interactive (non-additive) effects of climate and crop yield have usually been ignored, or are modelled with polynomial functions of climate, independent of yield level, which are very difficult to interpret (e.g. Schlenker & Roberts, 2009; Lobell & Burke, 2010; Lobell *et al.,* 2011). Again, we suggest that the response of the crop to climate variations may not be independent of its yield level because – for example – a crop usually does not respond in the same way to water availability at high yield (high biomass) as when it is at low yield levels (low biomass; e.g. the milestone publication of Doorenbos & Kassam (1979) and our recent study, Ferrero *et al.* (2014)). Generally, when the crop has a higher yield, it also has a greater water demand and, therefore, we over-estimate the response of the crop to climate change if we do not consider it, at least for high-yield systems. Recently, we used models with biologically interpretable parameters, that also take into account the nonlinear crop yield growth previously discussed, to understand hydric stress in maize throughout Spain (Ferrero *et al.,* 2014), and the effects of weed community diversity and climate on maize and soybean in a long-term experiment in Michigan, USA (Ferrero *et al.,* 2017). Here we consider whether general patterns exist for a more profound understanding of crop yield dynamics in order to develop wide-ranging strategies for coping with the impacts caused by climate change.

In this study, we have hypothesised the existence of biophysical processes (negative feedback structure) regulating crop yield fluctuations and the non-additive interactions between environmental factors and crop yield levels. We analysed eight strategic crops at subnational scale in southern South America: oats (*Avena sativa* L.), barley (*Hordeum vulgare* L.), sorghum (*Sorghum* spp.), rice

(*Oryza sativa* L.), wheat (*Triticum aestivum* L), maize (*Zea mays* L.), sunflower (*Helianthus annuus* L.) and soybean (*Glycine max* Merr.). More specifically, statistical models combining internal (feedback structure) and external (climate; CO_2) processes and long-term historical data (20–50 years) have been used in order to understand crop yield persistence and its role in determining crop yield responses to climate change impacts. We identified those crops and regions that are most vulnerable to the actual climate change trends in South American agro-ecosystems. Our study could have important implications for management of crops and climate change mitigation, especially, in an area where agriculture plays a key role in its socioeconomic and ecologic dimensions.

Materials and methods

Study site and focal crop yields

Historical yield data or the mass harvested per unit area (kg ha^{-1}) for Argentina (1969/70–2010/11), Uruguay (1960/61–2010/11), Chile (1979/80–2010/11) and Brazil (at least 19 years; see Fig. S1 in Appendix S1, Supporting Information, for details on regions) were obtained from their respective statistical yearbooks. We used Global Historical Climatology Network data on monthly temperature and rainfall (mean, minimum, maximum and extreme; Lawrimore *et al.*, 2011). For sites with missing data (Valparaiso, Santiago, Chillán, Valdivia), we obtained Chile's weather annuals in climatologic yearbooks.

Climate and CO_2-related variables

Climate-related variables in the crop growing season were considered to be determinant drivers of yield crop fluctuations. Here, we considered average temperature, the maximum and minimum temperature and the total rainfall for this period. In addition to modelling the general (average) effects of climate on crop yield, we included the effects of extreme temperature or precipitation events in the growing season, which may have disproportionately large impacts on final yields. The growing seasons selected for the different crops were rice (November–February), oats (March–December), barley (March–December), sunflower (October–February), maize (October–May), wheat (June–November), sorghum (November–April) and soybean (November–May). Additionally, also considered was the annual effect of carbon dioxide (CO_2), an important atmospheric gas that contributes to global warming. The country's data on the emissions of CO_2 (kt) were taken from the World Bank's World Development Indicators (World Bank, 2012) as a proxy of CO_2 in the atmosphere.

Diagnosis and statistical models of yield dynamics

To remove any trends on crop yield, we used detrending (i.e. rotating the series around the linear or quadratic trend). We defined the annual rate of yield increases as the first-differences of log-yield $R_t = Y_t - Y_{t-1}$, where Y_t is the detrended log-yield at time t (log transformation transforms absolute differences to relative differences and allows reduced heteroscedasticity) and Y_{t-1} is the same series with 1 year of delay (lags 1). We built a first model that included the effects of internal processes on R_t without any exogenous perturbation. In order to do that we used the generalised exponential form of the discrete logistic model (Ricker, 1954; pure *endogenous* model),

$$R_t = r_{\max} - \exp\left(a \cdot Y_{t-d} + c\right) \tag{1}$$

where Y represents the log-yield data at time t, d is number of time lags to be included in the model, $r_{\max}$ is a positive constant representing the maximum productive rate observed and c and a are parameters. We used the partial rate correlation function (PRCF; Royama, 1977) to determine how many time lags (d) should be included in the model (1).

Eqn 1 was modified to represent additive and non-additive crop responses to environmental perturbations (external processes; e.g. temperature effects). Additive perturbations were considered through the inclusion of the Z_t term,

$$R_t = r_{\max} - \exp\left(a \cdot Y_{t-d} + c\right) + b \cdot Z_{t-d'} \tag{2}$$

where Z_t is the environmental perturbations (e.g. precipitation), d' denotes the number of lags to be included in the model (with $d' = 0$ and 1) and b is a parameter. Environmental conditions exert additive perturbation effects on the annual rate of yield increases through changes in $r_{\max}$ (*vertical* effect, *sensu* Royama, 1992; Text S1 in Appendix S2). Both equilibrium point and the speed at which the system approaches equilibrium could be altered.

Changes in c (Eqn 1), involve the non-additive interactive effects of climate or CO_2 and crop yield levels (*lateral* effect, *sensu* Royama, 1992),

$$R_t = r_{\max} - \exp\left(a \cdot Y_{t-d} + c + b \cdot Z_{t-d'}\right) \tag{3}$$

Here the environmental perturbations affect the yield potential but not its stability.

Finally, environmental perturbations may have a non-additive influence on yield dynamics as the parameter a changes (Eqn 1; *nonlinear* effect, *sensu* Royama, 1992),

$$R_t = r_{\max} - \exp\left(\left(a + b \cdot Z_{t-d'}\right) \cdot Y_{t-d} + c\right) \tag{4}$$

In this last case, both the equilibrium point and the speed at which the system approaches equilibrium could change.

Model fitting and model selection

We fitted Eqns 1–4 using nonlinear least squares regressions with the *nls* library in the software *R* (R Development Core Team, 2011). In particular, the models were fitted by minimising the Akaike criterion (AIC; Sakamoto *et al.*, 1986), and maximising pseudo R^2 measures based on the residual deviance (Cameron & Windmeijer, 1996). Models were chosen on the basis of their goodness-of-fit, their ability to describe the correct dynamics and their appropriateness.

Results

Biophysical internal processes

Between 26% and 83% of the variance in annual rates of yield increase was explained by biophysical internal processes (i.e. first-order-negative feedback processes) in major crops and regions in South America (see pure *endogenous* model in Table S1 and Fig. S2 in Appendix S1). All crops presented a stabilising negative feedback structure and, therefore, self-regulation in their dynamics.

Additive and non-additive climate and CO_2 effects

Several models selected for evaluating climate change impacts on crop yield alterations between regions explained the additional 4%–33% of their variance (Fig. 1; Table S1 and Fig. S3 in Appendix S1). We found that the interaction between climate variables or CO_2 emission and crop yield level (non-additive effects) were more common than an independent perturbation of crop yield (additive effects; Table S1 in Appendix S1).

Several patterns emerge from these models. For some crops, such as maize, oat, barley and sunflower, annual crop growth rates were affected mainly by temperature (Fig. 1; Fig. S3 in Appendix S1). We found that oat yield dynamics was explained best by maximum temperature, with negative and non-additive effects in Paraná (Brazil) and Araucania (Chile) but with positive responses (additive and non-additive) in Uruguay (Fig. 1B). In southern Brazil (Rio Grande do Sul) and Uruguay, extreme temperature influenced annual barley yield growth rate additively, but further west in Chile (Araucania and Los Lagos; Fig. 1A) we found non-additive responses. For sunflower, non-additive effects of maximum temperature were also found in Uruguay and La Pampa (Argentina), but in the former it improved annual yield growth rates and in the latter its effect was negative. Minimum temperature affected sunflower yield variations through negative and non-additive responses in Entre Ríos (Argentina; Fig. S3 in Appendix S1). In Córdoba, Buenos Aires and Santa Fé (Argentina), we found that maize yield variability was explained best by negative impacts of high temperatures, and more so at high-yield years (non-additive, Fig. S3 in Appendix S1), whereas minimum temperatures had positive and additive effects on maize production in Uruguay.

For soybean, sorghum and wheat, the results were more variable (see Fig. S3 in Appendix S1). While in the central region of Argentina (Córdoba and Santa Fé) temperature variability was more important for soybean yield fluctuations, in the east of South America precipitation and CO_2 emissions were more important (in Paraná (Brazil) and Uruguay, respectively). Sorghum annual yield growth rate was negative and non-additively affected by maximum temperatures in central regions of Argentina (Córdoba, Entre Ríos, Santa Fé, Santiago del Estero and Buenos Aires) and positively by rainfall in Minas Gerais (Brazil). Finally, the influence of temperature on wheat yield growth was statistically significant and positive in Santa Fé (Argentina) and Paraná (Brazil), but negative in Buenos Aires (Argentina), Uruguay and Bío Bío (Chile). Also for wheat, we detected the effects of rainfall in Río Grande do Sul (Brazil) and CO_2 emissions in Córdoba (Argentina).

Finally, we determined that rainfall affected rice production through non-additive effects in Uruguay and Corrientes (Argentina), but in Maule and Bío Bío (Chile) minimum temperature was a better explanation of rice yield variability (Fig. S3 in Appendix S1).

Discussion

Crop yield dynamics is a key aspect for food security under climate change (Grassini *et al.*, 2013), mainly in South America where special emphasis is given to its role for global food production and environmental sustainability. Understanding crop yield interannual variability will enable us to improve it and to diminish the adverse impacts of agriculture for social and ecological systems. Here we analysed the effects of internal and external processes on the main crops (maize, soybean, wheat, rice, barley, oat, sunflower and sorghum) and producing countries (Argentine, Chile, south Brazil and Uruguay) of the region between 1960 and 2011. We found common features among crop yield dynamics due to growth constraints, complex crop responses to climate changes and hotspots that are crucial for adaptation and mitigation.

Biophysical internal processes have an influence on crop yield dynamics

We found that all crops studied across most regions of South America showed regulation by biophysical internal processes as the main drive of crop yield dynamics

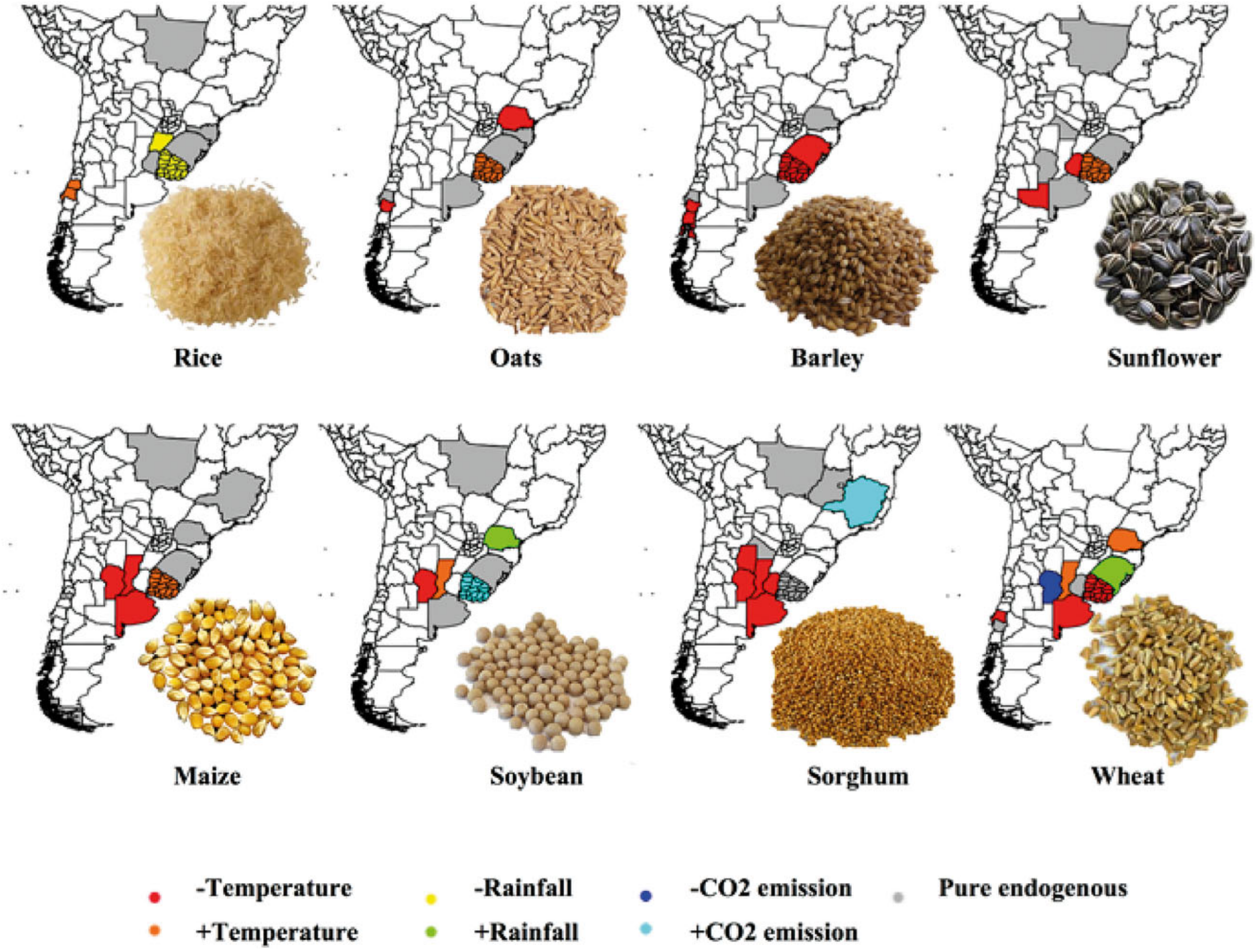

Figure 1 Annual crop yield growth rate responses to mean maximum temperature (MMXT, °C) for (A) barley in Los Lagos (Chile) with non-additive impacts and (B) oats in Uruguay with additive impacts. We divided each plot according to quartiles of MMXT (different colours), where shaded area shows confidence bands. See Table S1 in Appendix S1 for description of other models for temperature, precipitation and carbon dioxide emission effects on eight strategic crops in South America.

and its temporal persistence (Table S1 in Appendix S1). Our results suggest a general pattern of internal regulation on crop systems, which explained the essential features of the dynamics observed: high frequency, stable fluctuations and a dynamics equilibrium (its yield potential in the regions where the crop is produced). Regulation tends to produce stability by damping the effects of any changes in the environment (in other words, it does not follow a random walk). This is a non-trivial result for management purposes because such a regulatory mechanism may influence potential declines or recovery in crop yield. Our results are consistent with the recent evidence of stabilisation, stagnation and the hypothesis of a biophysical yield ceiling (Ray *et al.,* 2012; Grassini *et al.,* 2013). Nevertheless, unlike these studies, here we did not use threshold models, but we modelled internal limitations on annual crop yield growth rates that produce bounded variations and autocorrelation between time steps. Our findings suggest that regulation structure by biophysical limits could improve our understanding and prediction of climate change problems.

Environmental external processes have additive and non-additive impacts on crop yield dynamics

We assessed additive and non-additive crop responses to climate change in historical time series models and evaluated changes in the yield potential and its stability due to these perturbations (Fig. 1; Table S1 and Fig. S3 in Appendix S1). A novel aspect of the observed crop yield dynamics is the fact that non-additive climatic effects (the effect of the interaction between climate and crop yield level) are much more common than the additive ones (an independent effect of climate on crop yield level). Here we modelled explicitly the interactive (non-additive) effects of climate and crop yield, unlike previous studies that use polynomial regression or threshold levels – difficult to interpret – to account for nonlinear climate effects on crop yield (Schlenker & Roberts, 2009; Lobell *et al.*, 2011). Our results suggest that climate impacts are particularly harmful at high yield levels, when crops demand more nutrients but the availability of resources decreases or remains constant. As a result of non-additive climatic effects, small changes in a climate factor could exert big ones in the average yield but would not perturb the stability of equilibrium. This general finding on crop yield dynamics is crucial to crop yield forecasting and for management purposes, because ignoring it could lead to oversized predictions about mitigation tools under climate change by implying that these tools are equally effective at low and high crop yield levels. Finally, it is important to highlight that because all crops are basically systems defined at high yield levels, it is essential to model and predict the problems that generate non-additive climate effects.

Regional summaries: which crops in which geographic regions are most threatened

A few studies have explicitly compared climate impact for different regions or crops to identify areas at most risk (Porter *et al.*, 2014). Here we found that the effect of climate variability on crop yield was evident in several regions of southern South America and for most crops. Negative impacts of climate variability have been more common than positive ones. Also, we detected the great sensitivity of crop yields to extreme temperatures unlike most studies in the region, which highlight the role of rainfall (e.g. Magrin *et al.*, 2005; Asseng *et al.*, 2013) but in concordance with a recent study in the Pampas (Verón *et al.*, 2015) and with the global trend (Abrol & Ingram, 1996; Lobell & Field, 2007; Lobell *et al.*, 2012; IPCC, 2014; Fig. 2). Differences in the methodology used may explain this disagreement because – unlike our analysis – the first studies used crop simulation models that tended to over-estimate rainfall importance (Maltais-Landry & Lobell, 2012). Specifically, temperature was the only variable explaining oat, barley, sunflower and maize performance, mostly in a negative and non-additive way. These facts imply that warmer conditions mainly affected crops at high yield levels, probably due to low nutrient intake under high temperature levels (Abrol & Ingram, 1996) or by increased water stress (Lobell *et al.*, 2013), decreasing the yield equilibrium for most of the crops studied. However, positive temperature effects were mainly found in the south east of the region: Uruguay (oat, sunflower and maize), Santa Fé (soybean and wheat) and Paraná (soybean and wheat), where water does not appear to be a limiting factor (Magrin *et al.*, 2014). Specifically, positive and non-additive effects on temperature were the important factor for yield growth rate in oat, sunflower and maize in Uruguay, soybean in Paraná (Brazil), wheat in Córdoba (Argentina) and rice in Maule and Bío Bío (Chile). For example, it has been suggested that warming may prevent the stress of low minimum temperatures at high latitudes like in Chilean rice crops, because freezing may decrease the absorption of water and mineral nutrients (Yoshida, 1981; Zia *et al.*, 1994) or reduce plant growth and leaf elongation rates (Sowiński *et al.*, 2005). The existence of both patterns is not surprising, because the relationship between crop yield growth and temperature could be visualised as a hump-shaped curve. Crop yield growth is slow at the lower and upper ends of a given temperature range, and highest at some optimal point. The optimal temperature varies for each crop and depends on its physiology. Therefore, we might find both positive and negative outcomes under different temperature values.

In Corrientes (Argentina) and Uruguay, though rice is irrigated, rainfall was a major problem due to El Niño/Southern Oscillation (ENSO) events of high rainfall (see Magrin *et al.*, 2014). Here we detected that rainfall affected rice production through non-additive effects maybe because of lesser solar radiation in years of high rainfall, with more negative impacts in high-yield years. As these regions are important rice producers in South America, our results suggest that using climate forecasting to reduce production risks should consider non-additive consequences on rainfall regimes, due to ENSO events.

Elevated CO_2 is expected to have impacts on crop yield (Ainsworth *et al.*, 2002). Our results showed that CO_2 emission exhibited both positive and negative effects on soybean (Uruguay) and wheat (Córdoba, Argentina) crops, respectively, mostly through additive effects (Fig. 2). Positive responses of increased CO_2 emissions on grain yield are in agreement with previous studies, which postulated that the primary effect of plant response to rising atmospheric CO_2 is to increase yield (Ainsworth *et al.*, 2002). However, wheat responded negatively to CO_2, probably due to the interactions of CO_2 with high temperatures, water status or low nitrogen fertiliser availability (Lawlor & Mitchell, 2000). Consistent with previous research, C3 species such as wheat and soybean are expected to respond more strongly than C4 crops. Regional CO_2 effects are not often considered (but see McGrath & Lobell, 2013), but our results suggest that yield response to increased CO_2 will vary between regions due to interactions with other environmental variables. Further research should include these interactions in statistical models to fully understand potential impacts

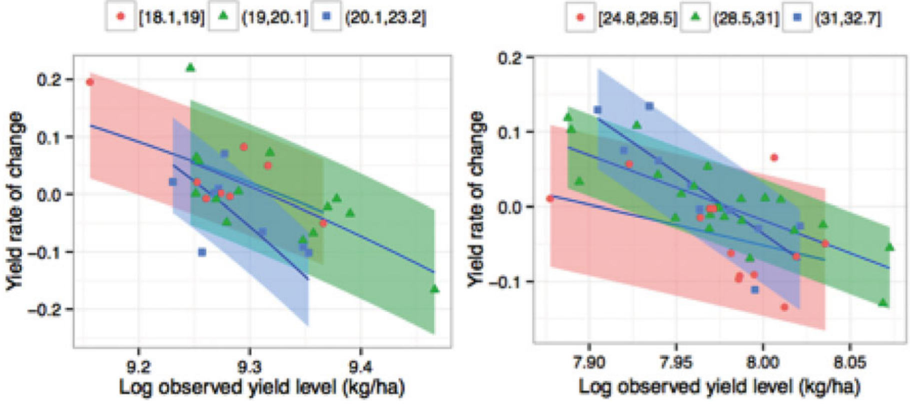

Figure 2 Estimated net impact of temperature, rainfall and CO_2 emission on eight major crop productions in South America in addition to internal processes (e.g. pure endogenous model). We report the most relevant external driver for each crop and region, as detected by the fitting of the models (see Table S1 in Appendix S1).

of CO_2 on food production. For example, the benefit for soybean would not be so promising, because it has been suggested that, under future climate change conditions, the interactive effects of elevated CO_2 and warmer temperatures are not likely to benefit soybean growth (McGrath & Lobell, 2013). As soybean and wheat are main crops in South America, our model could be the benchmark from which to evaluate future CO_2 changes and their interaction with climate-related variables.

Some caution should be exercised in interpreting these results. Here our models explain a high variability with respect to previous statistical models (e.g. Verón *et al.*, 2015; 30%–47%) probably because we considered particular temperature or precipitation events which could have pronounced effects on yield. For example, in specific locations, we accounted for more than 80% of the variability in a crop's yield. The variance percentages not explained by these statistical models could be due to technological factors, soil conditions and/or climate on a lower local scale than the regional one. Also, the accuracy of statistical models is dependent on the spatial scale (at more local scales, the role of precipitation may be more important than temperature; Porter *et al.*, 2014) and the reliability of input data (yield or weather measurements; e.g. Sadras *et al.*, 2014). We detected that crop yield dynamics were controlled by simple feedback structures, and therefore, only one feedback dominated its dynamics close to equilibrium (Berryman, 1999). However, this could change in the future given some external or internal factors, and it may be possible to find complex regulatory structures and alternative stable states if the climate keeps changing. Moreover, although our models have the advantage of the parameters having a direct biological interpretation, a parsimonious structure and more flexibility (Royama, 1992), nonlinear model forms often ensure, but not guarantee, proper extrapolation. This is particularly important for soybeans and wheat, where positive effects of recent climate variability in the region have been detected, but the results should be projected carefully because more complex dynamics can emerge and more warming might slow yield gains as in global wheat production (Asseng *et al.*, 2015). In addition, it should be noted that our study used CO_2 national levels to estimate the effect of elevated CO_2 on crop yields so that we could be underestimating this effect. Local measurements are needed in the future to achieve more accurate models on the effect of CO_2. Finally, while our study revealed new and interesting findings, follow-up studies should examine the interactions between different aspects of climate change to improve our adaptation options in agriculture.

Conclusions

We have shown the existence of general patterns for the major crop yield dynamics in South America based on the interactions between internal (biophysical limits by first-order-negative feedback) and external (climate and CO_2 emission) factors. These results show crop yield as a regulated process unlike a random walk as presented previously. Statistical models for crops need to account for the universal trade-off between yield growth rate and yield levels, and here we have proposed a flexible model with nonlinear functions and biological meaning that does not include artificial breakpoints. We have identified those crops and regions that are most vulnerable to climate change in South America. We have also recognised that distinguishing the effects of both additive and non-additive climate impacts will help us to identify the mechanisms that influence the response of agroecosystems to environmental change. We suggest that projections of crop yield models based on extension of historical trends of the past decades should be viewed with caution because we must consider the crop yield level (i.e. its status) in both the deceleration of its rate of increase (due to biophysical limits) and in its interaction with climate change (by non-additive responses). Our findings may be crucial to predicting the response of crop to yield-improvement strategies and may have important implications for management and adaptation measures for crop systems and climate change mitigation. Finally, we strongly suggest the importance of theoretical dynamic models based on biological knowledge for understanding the interaction between regulation structure and environmental factors in shaping the dynamics of crop yields. This allows us a deeper understanding of ecological processes than was possible with traditional approaches. The methods we develop are general and can be applied to a wide range of crops.

Acknowledgements

R. F. gratefully acknowledges receipt of a grant from the Fundación Carolina. J. L. G-A and R. F. were supported by FEDER (European Regional Development Funds) and the Spanish Ministry of Economy and Competitiveness funds (AGL2012-33736). R. F. and M. L. acknowledge financial support from Center of Applied Ecology and Sustainability (CAPES; CONICYT FB 0002-2014). The authors are grateful to Laboratorio Internacional en Cambio Global (LINCGlobal) for their support.

References

Abrol Y.P., Ingram K.T. (1996) Effects of higher day and night temperatures on growth and yields of some crop plants. In *Global Climate Change and Agricultural Production. Direct and Indirect Effects of Changing Hydrological, Pedological and Plant Physiological Processes*, pp. 124–140. Eds Fakhri Bazzaz and Wim Sombroek. Rome, Italy: Wiley and FAO, United Nations.

Ainsworth E.A., Davey P.A., Bernacchi C.J., Dermody O.C., Heaton E.A., Moore D.J., Morgan P.B., Naidu S.L., Yoo Ra H., Zhu X., Curtis P.S., Long S.P. (2002) A meta-analysis of elevated [CO_2] effects on soybean (*Glycine max*) physiology, growth and yield. *Global Change Biology*, **8**, 695–709.

Alexandratos N., Bruinsma J. (2012) World agriculture towards 2030/2050: the 2012 revision. *ESA Working Paper*, No. 12-03. Rome, Italy: Food and Agriculture Organization of the United Nations.

Asseng S., Travasso M.I., Ludwig F., Magrin G.O. (2013) Has climate change opened new opportunities for wheat cropping in Argentina? *Climatic Change*, **117**, 181–196.

Asseng S., Ewert F., Martre P., Rötter R.P., Lobell D.B., Cammarano D., Kimball B.A., Ottman M.J., Wall G.W., White J.W., Reynolds M.P., Alderman P.D., Prasad P.V.V., Aggarwal P.K., Anothai J., Basso B., Biernath C., Challinor A.J., De Sanctis G., Doltra J., Fereres E., Garcia-Vila M., Gayler S., Hoogenboom G., Hunt L.A., Izaurralde R.C., Jabloun M., Jones C.D., Kersebaum K.C., Koehler A-K., Müller C., Naresh Kumar S., Nendel C., O'Leary G., Olesen J.E., Palosuo T., Priesack E., Eyshi Rezaei E., Ruane A.C., Semenov M.A., Shcherbak I., Stöckle C., Stratonovitch P., Streck T., Supit I., Tao F., Thorburn P.J., Waha K., Wang E., Wallach D., Wolf J., Zhao Z., Zhu Y. (2015). Rising temperatures reduce global wheat production. *Nature Climate Change*, 5, 143–147.

Berryman A.A. (1989) The conceptual foundations of ecological dynamics. *Bulletin of the Ecological Society of America*, **70**, 230–236.

Berryman A.A. (1999) Principles of population dynamics and their application. Stanley Thornes (Publishers) Ltd., Cheltenham, United Kingdom. 243 pp.

Cameron A.C., Windmeijer F.A.G. (1996) R-squared measures for count data regression models with applications to health-care utilization. *Journal of Business & Economic Statistics*, **14**, 209–220.

Doorenbos J., Kassam A.H. (1979) Yield response to water. FAO Irrigation and Drainage, Paper 33. Rome, Italy: Food and Agriculture Organization of the United Nations.

Ferrero R., Lima M., Gonzalez-Andujar J. (2014) Spatio-temporal dynamics of maize yield water constraints under climate change in Spain. *PLoS One*, **9**, e98220.

Ferrero R., Lima M., Davis A.S., Gonzalez-Andujar J.L. (2017) Weed diversity affects soybean and maize yield in a long term experiment in Michigan, USA. *Frontiers in Plant Science*, **8**, 1–10. http://doi.org/10.3389/fpls.2017.00236

Grassini P.K., Eskridge M., Cassman K.G. (2013) Distinguishing between yield advances and yield plateaus in historical crop production trends. *Nature Communications*, **4**, 2918.

IPCC (2014) Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. In *Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Eds V.R. Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea and L.L. White. Cambridge, UK and New York, NY, USA: Cambridge University Press. 688 pp.

Lawlor D.W., Mitchell R.A.C. (2000) Crop ecosystem responses to climatic change: wheat. In *Climate Change and Global Crop Productivity*, pp. 57–80. Wallingford, UK: CAB International.

Lawrimore J.H., Menne M.J., Gleason B.E., Williams C.N., Wuertz D.B., Vose R.S., Rennie J. (2011) An overview of the global historical climatology network monthly mean temperature data set, version 3. *Journal of Geophysical Research*, **116**, D19121.

Lin M., Huybers P. (2012) Reckoning wheat yield trends. *Environmental Research Letters*, **7**, 024016.

Lobell D.B., Burke M.B. (2010) On the use of statistical models to predict crop yield responses to climate change. *Agricultural and Forest Meteorology*, **150**, 1443–1452.

Lobell D.B., Field C.B. (2007) Global scale climate–crop yield relationships and the impacts of recent warming. *Environmental Research Letters*, **2**, 014002.

Lobell D., Schlenker W., Costa-Roberts J. (2011) Climate trends and global crop production since 1980. *Science*, **333**, 616–620.

Lobell D.B., Sibley A., Ortiz-Monasterio J.I. (2012) Extreme heat effects on wheat senescence in India. *Nature Climate Change*, **2**, 186–189.

Lobell D.B., Hammer G.L., McLean G., Messina C., Roberts M.J., Schlenker W. (2013) The critical role of extreme heat for maize production in the United States. *Nature Climate Change*, **3**, 497–501.

Magrin G.O., Travasso M.I., Rodríguez G.R. (2005) Changes in climate and crop production during the 20th century in Argentina. *Climatic Change*, **72**, 229–249.

Magrin G.O., Marengo J.A., Boulanger J.-P., Buckeridge M.S., Castellanos E., Poveda G., Scarano F.R., Vicuña S. (2014) Central and South America. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 1499–1566. Eds V.R. Barros, C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea and L.L. White. Cambridge, UK and New York, NY, USA: Cambridge University Press.

Maltais-Landry G., Lobell D.B. (2012) Evaluating the contribution of weather to maize and wheat yield trends in 12 US counties. *Agronomy Journal*, **104**, 301–311.

McGrath J.M., Lobell D.B. (2013) Regional disparities in the CO_2 fertilization effect and implications for crop yields. *Environmental Research Letters*, **8**, 014054.

Porter J.R., Xie L., Challinor A.J., Cochrane K., Howden S.M., Iqbal M.M., Lobell D.B., Travasso M.I. (2014) Food security and food production systems. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 485–533. Eds C.B. Field, V.R. Barros, D.J. Dokken, K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea and L.L. White. Cambridge, UK and New York, NY, USA: Cambridge University Press.

Purves D., & Pacala S. (2008). Predictive models of forest dynamics. *Science*, **320**, 1452–1453.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: the R Foundation for Statistical Computing.

Ray D.K., Ramankutty N., Mueller N.D., West P.C., Foley J.A. (2012) Recent patterns of crop yield growth and stagnation. *Nature Communications*, **3**, 1293.

Ricker W.E. (1954) Stock and recruitment. *Journal of Fisheries Research Board of Canada*, **11**, 559–623.

Royama T. (1977) Population persistence and density dependence. *Ecological Monographs*, **47**, 1–35.

Royama T. (1992) *Analytical Population Dynamics*, pp. 371. London, UK, and New York, NY, USA: Springer/Chapman & Hall.

Sadras V.O., Grassini P., Costa R., Cohan L., Hall A.J. (2014) How reliable are crop production data? Case studies in USA and Argentina. *Food Security*, **6**, 447–459.

Sakamoto Y., Ishiguro M., Kitagawa G. (1986) *Akaike Information Criterion Statistics*. Dordrecht, The Netherlands: D. Reidel.

Schlenker W., Roberts M.J. (2009) Nonlinear temperature effects indicate severe damages to U.S. crop yields under climate change. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 15594–15598.

Shi W., Tao F., Zhang Z. (2013) A review on statistical models for identifying climate contributions to crop yields. *Journal of Geographical Sciences*, **23**, 567–576.

Sowiński P., Rudzińska-Langwald A., Adamczyk J., Kubica I., Fronk J. (2005) Recovery of maize seedling growth, development and photosynthetic efficiency after initial growth at low temperature. *Journal of Plant Physiology*, **162**, 67–80.

Verón S.R., de Abelleyra D., Lobell D.B. (2015) Impacts of precipitation and temperature on crop yields in the Pampas. *Climatic Change*, **130**, 235–245.

World Bank (2012) *World Development Indicators*. World Bank. URL http://data.worldbank.org/data-catalog/world-development-indicators/wdi-2012.

Yoshida S. (1981) *Fundamentals of Rice Crop Science*. Manila, Philippines: International Rice Research Institute.

Zia M.S., Salim M., Aslam M., Gill M.A., Rahmatullah (1994) Effect of low temperature of irrigation water on Rice growth and nutrient uptake. *Journal of Agronomy and Crop Science*, **173**, 22–31.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Diagnostic tools and optimal models by region in South America for all cereals crops.

Appendix S2. How changes in the parameters of equation (1) translate the conditional production curve $R_t = f(Y_{t-d}, Z)$ moving it vertically or laterally, and changing its relative shape (nonlinear).