

# New wheat breeding paradigms for a warming climate

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Plant breeding has been successful in adapting crops worldwide with one of the latest challenges being adaptation to warmer days and nights. Taking wheat as a case study, here we show current elite nurseries express a range of levels of heat adaptation. Generally, the higher the selection ratio for yield response under warming, the less stable the yield response across environments. Specifically, less than one-third of genotypes trialled adapted well to the 0.26 °C warming of the last decade, and the phenotypes were stable in only 26% of environments. With continued warming, selection ratio falls 8.5% and stability falls 8.7% for each 1 °C increase in local temperature. Overall, faced with more climate variability, breeders need to revisit their breeding strategies to integrate genetic diversity that confers climate resilience without penalties to productivity in favourable seasons.

A global challenge today is how to address a rising demand for crop-based food due to population growth and rising incomes, at the same time as climate change is likely to reduce global crop production<sup>1,2</sup>. Global wheat yield losses of 4–6% are predicted for each 1 °C increase in

(SSP) (Supplementary Fig. 1). We considered yield variations caused by environment ( $E$ ) and genotype–environment interaction for 3,652 lines across sites in their targeted mega-environment (ME), wheat areas having broadly similar abiotic and biotic constraints, cropping systems and purpose (Fig. 1a and Supplementary Fig. 2). The change in yield variation ( $\Delta Y$ ) for each genotype–site–year combination was computed, relative to the corresponding yield variation in the baseline period (1981–2010).

### Climate change across the trials

Projected climate across the trials exhibits three main features. First, increases in mean growing-season temperature advance crop development, resulting in shorter periods of growth and less yield. The consequence is a reduced time window for growth and often suboptimal canopy development to intercept light throughout the cycle. As a result, radiation intercepted decreases, first at a few sites with the onset of warming, then extending to nearly all sites when the mean temperature is warmed by 3 °C. Across trials the simulated intercepted radiation decreases almost linearly with the increase in temperature, approaching a 20% loss with 6 °C warming (Fig. 1b). Second, the risk of heat waves extends more frequently and significantly outside the present ranges experienced at many trial sites. The number of extreme degree days greater than 30 °C increases exponentially with the global increase in temperature, with occurrences rising at most trial sites (Fig. 1c); consequences can be disastrous depending on intensity and duration. Third, over 70% of trial sites receive less rainfall when warming exceeds 3 °C (Fig. 1d), reducing transpiration potential for carbon fixation and

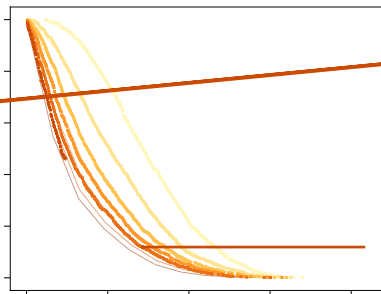
canopy cooling and risking photo-inhibition and accelerated senescence. Note that this decrease in rainfall can be partly ascribed to the shorter growth period, so it does not necessarily imply increased water stress across all trial sites.

### Genotypes exhibit diverse yield responses to warming

Regressing  $\Delta Y$  against temperature increase ( $\Delta T$ ) for all the genotypes revealed their specific responses to future warming, which are widely divergent whether for multiple genotypes in one environment (Fig. 2a) or one genotype across different trial sites (Fig. 2b). The fitted regression curve can be used to identify warm-adapted genotypes, that is, those with a yield change ( $\Delta Y$ ) value greater than zero. Because we allowed nonlinearity in the regression, many warm-adapted genotypes have a  $T_{point}$  beyond which the positive  $\Delta Y$  starts to go below zero, named as the warming threshold. Figure 2c arrays the estimated warming thresholds of all genotypes across stations. The warming threshold represents the maximum possible warming of the local temperature that the genotype yield response can withstand and so depends on the genotypic temperature–yield response and local climatic characteristics.

There was genetic diversity for response. Of the 3,652 genotypes studied, 96% exhibited a certain level of warming adaptation capacity in at least one station (Supplementary Table 3). In addition, many genotypes showed much greater adaptation capacity to the extent that the median of genotype warming thresholds is 5.2 °C. Lines in the nurseries are bred for specific traits in contrasting environments not





For all the nurseries and warming levels, estimated WA is inversely proportional to SE, as indicated by the inverse sigma-shaped curves (Fig. 3). The reciprocal relationship between WA and SE is intuitively understandable in that breeding for a locally adapted cultivar is much easier than breeding a cultivar with a wider adaptation. This relationship also shows the paradox between two major wheat breeding objectives—higher selection efficiency and wider stability—especially for pre-breeding programmes that develop germplasms to adapt to broad environments. Breeders can still expect varying combinations of WA and SE corresponding explicitly to areas under the curves (Extended Data Fig. 1). With climate warming, all curves shift towards the origin of the axes, suggesting both objectives would become more difficult to achieve. By using the centroid concept (Extended Data Fig. 1), we aggregated the possible SE and WA pairs into two unique indices ranging from 0 (lowest) to 1 (highest): selection efficiency index (SEI) and wide adaptation index (WAI) (equation (4)). We further compared the indices for different levels of warming (Fig. 3 insets).

Compared with the baseline of 1981–2010, wheat-growing-season temperature during 2011–2020 averaged across the trial sites increased by 0.26 °C (Supplementary Fig. 3). Estimated SEI and WAI to adapt wheat to this warming are 0.31 and 0.26, respectively, averaged across the six nurseries (Figs. 3 and 4). This means an average selection efficiency of 31% can be expected in selecting genotypes from current ones to cope with the present 0.26 °C warming, with potential stability expected at 26% of stations in the corresponding ME. The values clearly differ among nurseries (Extended Data Fig. 2), suggesting contrasting efficiency in developing warm-adapted varieties among nurseries, probably because nurseries have different breeding targets, germplasm pools and environmental diversities.

### Changes under future climate

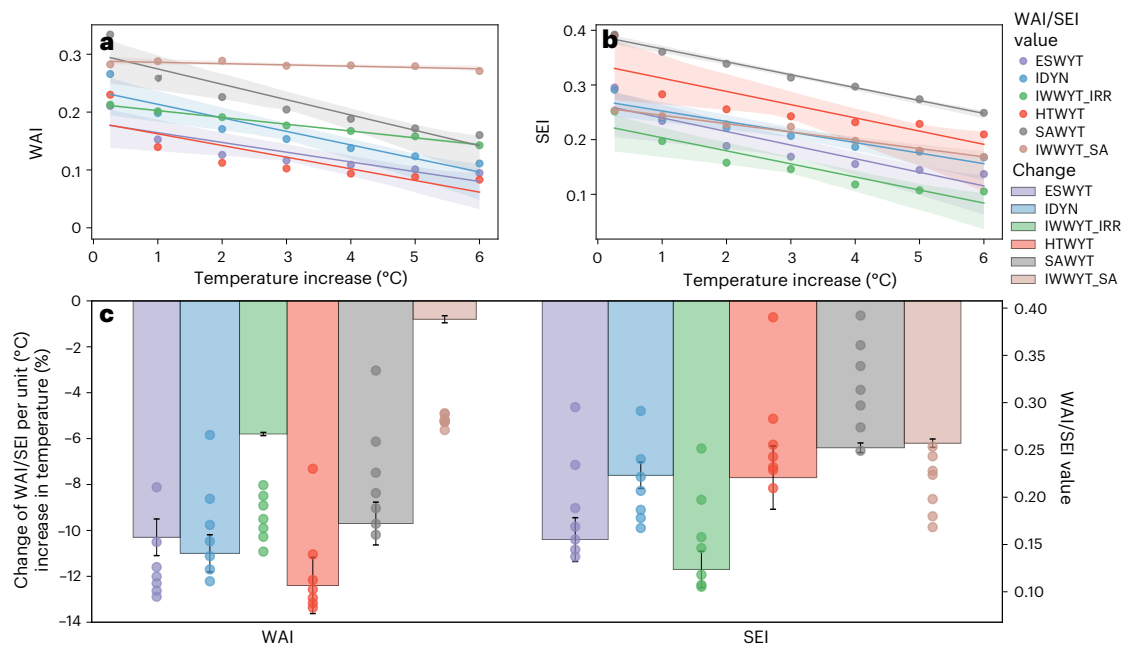
With continued warming, both SEI and WAI decline significantly ( $P < 0.05$ ) for all breeding programmes (Fig. 4a,b). For a 1 °C degree increase in local temperature, the mean SEI and WAI decrease by

8.5% and 8.7%, respectively (Fig. 4c). As these decreases explicitly indicate lower selection ratios and more instability under climate change, breeding warm-adapted genotypes will become more difficult in the future.

These declines indicate a need to refine present crossing and/or selection models. Studies among elite material show that many heat-adaptive traits<sup>13</sup> show significant genetic variation in CIMMYT wheat breeding pools. Physiological criteria are now considered in crossing elite by elite lines aiming for trait synergies and cumulative gene action for heat tolerance. Given the relatively narrow genetic basis of most modern crops, and especially wheat, access to alternative gene pools—including that in wild relatives—is essential to explicitly target adaptation to: warmer days and nights, unpredictable and more frequent heat waves and the possibility of dry spells that exacerbate heat stress. Currently, mainstream gene pools are not adequately characterized to enable complementary heat-adaptive traits to be purposefully hybridized. Furthermore, apparently broadly adapted germplasms are necessarily constrained to relatively small temperature ranges of present selection environments. This is particularly the case for the elite breeding programmes, such as ESWYT and IWWYT-IRR (Supplementary Table 2 provides nursery name), breeding high-yielding traits as the key objective in colder ME with less risk of warming and optimal management, such as irrigation.

### Roles of breeding target for climate-responsive traits

With the strong monotonic temperature trends and better understanding of the phenology control genes (that is, *PPD*, *VRN*), selecting cultivars with slower development rates (that is, growing-degree days) has been proposed to deal with climate change in some places. For example, an early sowing system combined slower-developing wheat genotypes can increase wheat yield across Australia under climate change<sup>14</sup>. To corroborate this strategy, we repeated the computation this time assuming an unchanged phenology for each genotype–environment



**Fig. 4 | Changes in WAI and SEI due to current and future warming.** **a–c**, Change in WAI (**a**), change in SEI (**b**) and rate of change in WAI and SEI (**c**) across the six nurseries. Each point in **a** and **b** indicates an estimated figure of WAI and SEI, respectively, whereas the lines denote the trends and shading represents the 95% confidence interval of the trends. In **c**, the height of bar represents the

estimated rate of change of WAI and SEI, estimated from the estimated figure of WAI and SEI for the seven warming levels (coloured points). The error bars show the 95% confidence interval of the estimated changing rate and bar width indicating the relative value of WAI and SEI for the current warming level of 2011–2020 (0.26 °C).

combination at different temperature profiles (Extended Data Figs. 3 and 4). The results confirmed the benefits of breeding for higher thermal time requirements because this strategy moderately offsets the reductions in SEI and WAI at a magnitude of 8.5% and 8.7% (Extended Data Fig. 5b), respectively. However, it is still challenging to select higher thermal time requirement genotypes because of higher risks related to large climate variability and extreme weather events, as indicated by the lower values of SEI and WAI at lower warming levels. In some spring wheat regions, earlier sowing increases the frost risk occurring at sensitive reproductive stages, for example.

One important factor omitted in the model is the effects of elevated CO<sub>2</sub> concentration on wheat adaptation. More photosynthesis, reduced stomata conductance and greater productivity are known as CO<sub>2</sub> fertilization effects. The short testing periods (mostly one year) for most genotypes in the trials means that this factor was not included in the regression by the model. The exact extent of elevated CO<sub>2</sub> effects (eCO<sub>2</sub>) on wheat yields are currently debated<sup>15</sup>. We therefore repeated the computation this time adding an arbitrary and fixed effect of CO<sub>2</sub> fertilization in the model. Not surprisingly, compared with the results where eCO<sub>2</sub> effects are not considered, estimated SEI and WAI for the present warming (0.26 °C) increases by 2–3 times, reaching a mean of 0.6 in SEI and 0.68 in WAI (Extended Data Fig. 4). However, the SEI and WAI still decrease with an increase in warming for most nurseries, but to a much lesser extent, –2.3% and –3.5% per 1 °C, respectively (Extended Data Fig. 5c). As stated, these simulations are simplistic and do not consider the fact that higher CO<sub>2</sub> cannot be expected to offset negative climate effects such as warmer nights, heat waves, delayed rain or rain causing anaerobic soil conditions.

## Discussion

Our results regarding the climate impacts on wheat breeding are probably too optimistic. This is partly because effects of weather extremes are probably underestimated. For example, we only included one extreme climate variable, EDD30, in the prediction model. The projected increase in extreme climate intensity and frequency is widespread in

global arable areas<sup>16</sup>, which may cause large yield damage and probably offset the yield benefits caused by rising CO<sub>2</sub><sup>17</sup>. These yield damages are not fully captured in our model, in part because the historical weather in most trial sites used to train the model had no clear trends in many extremes, such as short periods of very high temperatures and intense rainfall events. These forms of extreme weather are becoming more common and can be highly detrimental to crop yields, so is a priority topic for future studies<sup>18</sup>.

It is important to note that we selected a limited number of climate factors to avoid model overfitting. Furthermore, the random forest (RF) algorithm used to fit the yield-climate relationship and make the prediction has its limitations for prediction with future climate. Compared with traditional statistical approaches (for example, multiple linear regression), RF is able to handle interactions and nonlinear relationships among the variables due to its non-parametric and ensemble classification nature, giving higher prediction accuracy. However, its predictions for the future climate conditions are limited to the observed data range<sup>19</sup>. Repeating the prediction with multiple linear regressions in the model resulted in smaller values in both SEI and WAI under warming for all nurseries (Extended Data Fig. 5c), with less agreement in predicting historical yields (Supplementary Fig. 4). In addition, limitations in the trial data undermine the model's prediction ability. For some nurseries, trial sites are bias located in limited regions, such as HTWYT, which has most of its sites in India, which reduces the temperature (extreme high temperature) range. Most genotypes were tested for only one year, reducing the potential of confronting large range of climate environments, particularly extreme climate.

Despite possible underestimation, our results reveal three concrete lines of evidence of climate change impacts on wheat breeding, pointing to pre-emptive innovations in modern breeding methods. First, the fast change in SEI (–8.5%) and WAI (–8.7%) with the increase of local temperature suggests that current breeding methods are not fully capturing the diversity for heat-tolerant traits in present elite gene pools and keep raising the bar for heat tolerance. This can be accelerated by exploring genetic diversity in novel gene pools,

including the whole Triticeae tribe, which has been adapting for 25 million years to massively changing climates, versus a few thousand years for bread wheat, for example. With reduced climate resilience and slower cultivar development than the warming trends found in the world<sup>20,21</sup>, the need to increase genetic variability for climate adaptation is urgent, particularly in developing countries, where warming rate is fast and unprecedented and the breeding cycle is mostly longer than in developed countries<sup>22</sup>. CIMMYT has a pre-breeding programme that phenotypes land races and more exotic sources for climate resilience traits<sup>23</sup>. This has led to detection of heat-tolerant phenotypes without yield penalty in favourable conditions based on a haplotype with the largest impact coming from the wide D genome<sup>24</sup>. Once such haplotypes are identified, new breeding techniques such as gene editing can be contemplated and selection and crossing models refined. To achieve

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## Methods

Data from four spring wheat trials (ESWYT, IDYN, HTWYT and SAWYT) and two winter wheat trials (IWWYT-IRR and IRRYT-SA) in the International Wheat Improvement Network (IWIN) were used in the analysis (Supplementary Table 2). IWIN grows contemporaneous and well-performing germplasm under a range of environmental conditions, with the intention of distributing improved germplasm worldwide to the targeted mega-environments (ME) defined by CIMMYT (Supplementary Fig. 2). Each year, cooperators in the network receive a different set of selected germplasms from the coordinators—CIMMYT for spring wheat and ICARDA for winter wheat—and are requested to grow the trials using the best farming practices typical of the area around the test site. Most entries are planted for one or two years, with a few, including check lines, grown repeatedly over successive years or between trials. We conducted a quality control of the data with the method described in Xiong et al.<sup>36</sup> and selected the entries with complete records of grain yield and phenology for at least one site.

The six trials cover most wheat areas and have different breeding goals for specific environments. The Elite Spring Wheat Trial (ESWYT)<sup>37</sup>, the International Durum Yield Nursery (IDYN)<sup>38</sup> and the International Winter Wheat Yield Trial (IWWYT-IRR)<sup>39</sup> test, respectively, spring bread wheat germplasms, spring durum wheat and winter wheat, selecting for high-yielding germplasms under largely optimal environmental and management conditions. Three stress nurseries evaluate wheat germplasms developed for specific abiotic tolerance, the International High Temperature Wheat Yield Trial (HTWYT)<sup>40</sup> for terminal heat stress, the International Semi-Arid Wheat Yield Trial (SAWYT)<sup>41</sup> for drought in spring wheat and the International Winter Wheat Yield Trial Semi-Arid (IWWYT-SA)<sup>39</sup> for drought in winter wheat. Distribution of germplasm to the three stress nurseries is similar to the high-yielding nurseries, but crop management is different as the corresponding abiotic stress is applied, such as sowing later to exert heat stress during flowering or under rain-fed conditions to induce drought stress. From the datasets, we extracted the yield and phenology (sowing, heading and maturity dates) for each line, environment and year. Data points with at least two phenology records (sowing and maturity) and yield were kept. Any replicates among the data points were averaged for the line–location–year combination.

The trials did not record environmental variables, so we collected the historical and future climate data from publicly available databases. Historical daily weather data (1979–2021), including maximum (Tmx) and minimum temperatures (Tmn), incoming shortwave radiation (Rad), precipitation (Pr) and wind speed at 10 m above ground (Ws) were obtained from the AgERA5 dataset, a global reanalysis agrometeorological dataset developed by the European Centre for Medium-Range Weather Forecast (ECMWF) at 10 km × 10 km resolution<sup>42</sup>. ERA5 has been widely used in climate change research<sup>43</sup>, and its performance in capturing interactional trends in climate has been intensively evaluated at the global and regional levels<sup>44,45</sup>. For future weather data, we downloaded diagnostic output from Global Climate Models (GCM) in the Coupled Model Intercomparison Project Phase 6 database (CMIP6)<sup>46</sup>. We selected the climate variables for the period (1981–2100) generated by five GCMs (Supplementary Table 1), driven by three social-economical pathways (SSPs) (Supplementary Fig. 1) to consider a range of possible futures. The daily output from the five GCMs have been bias-corrected with an observational dataset in the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP)<sup>47</sup>. The AgERA5 and CMIP6 GCM grid cells containing nursery sites were selected to use for model forcing.

Six agrometeorological variables (Tmx, Tmn, Rad, Pr, Ws and EDD30) for three wheat-growing periods—vegetative, reproductive and grain

filling—were estimated and paired to all genotype–environment combinations under AgERA5 and projected climate. EDD30 is the accumulated daily Tmx (°) greater than 30 °C. Vegetative refers to the period from sowing to 300 growing-degree days (GDD) before heading, reproductive refers to the period from 300 GDD before heading to 100 GDD after heading, and grain filling is from 100 GDD after heading to harvest<sup>48</sup>. Crop phenology is important for estimating agrometeorological variables, but the records from many stations are incomplete, especially for variables related to heading, so we took a process-based crop modelling (CERES-Wheat) approach to estimate the missing phenology information. The detailed approach for filling in phenology gaps and evaluation of its performance is described in Xiong et al.<sup>36</sup>, including validation showing that it provides a reasonable prediction of heading for most trial environments with an  $R^2$  greater than 0.8. The same approach was used to predict the phenology for future climate in which the heading and maturity date were estimated for each genotype–environment combination by assuming sowing date did not change and was calculated as the median of the historical sowing date for each site.

We employed a standard quantitative genetic model<sup>49</sup> (equation (1)) to fit wheat yield ( $Y_{t,g,s,a}$ ) for genotype  $g$  across environment defined as site  $s$  and year  $a$  in nursery  $t$ .

$$Y_{t,g,s,a} = \mu_t + G_{t,g} + E_{t,s} + GE_{t,g,s} + \varepsilon \quad (1)$$

where  $\mu_t$  is the grand mean of the nursery,  $G_{t,g}$  is the deviation of genotype  $g$  from the genotypic mean,  $E_{t,s}$  is the corresponding deviation of site  $s$ ,  $GE_{t,g,s}$  is the interaction between environment and genotype and  $\varepsilon$  is an error term. As climate affects yield through changes in  $E$  and  $GE$ , we incorporated climate covariables into equation (2)

$$Y_{t,g,s,a} = \mu_t + G_{t,g} + E'_{t,s} + f_g(\mathbf{X}_{g,s,a}) + \varepsilon \quad (2)$$

in which  $\mathbf{X}_{g,s,a}$  is a vector of climate variables for genotype  $g$  in environment ( $s \times a$ ), consisting of six agrometeorological indices split into three growing periods.  $E'_{t,s}$  is environmental deviation caused by non-climate factors (that is, soil and management), equalling  $E_{t,s}$  minus deviations  $EC_{t,s}$  due to climate.  $EC_{t,s}$  was estimated based on mean maturity date of the site  $s$  based on a linear fit relationship between site yield and maturity date.

In equation (2), yield variations ( $Y_{t,g,s,a} - \mu_t - G_{t,g} - E'_{t,s}$ ) indicate the genotypic response to climate across environments, represented by  $f_g(\mathbf{X}_{g,s,a})$  and estimated by fitting the yield variation against the climate vector ( $\mathbf{X}_{g,s,a}$ ) with trial data. The Random Forest algorithm (RF)<sup>50</sup> was used for the fitting. RF is a non-parametric machine learning technique based on a special ensemble of classification and regression trees. Compared with traditional statistical approaches, RF does not assume a certain shape of response function, so complex interactions and nonlinear relationships among the variables can be handled. We also tested alternative methods such as linear regression (that is, locally estimated scatterplot smoothing) for the fitting and continued with the approach that resulted in the highest agreement between observed and modelled yields. The  $f_g(\mathbf{X}_{g,s,a})$  was applied on generated climates to estimate yield variations over scenario years  $a$  (1981–2100). Yield change ( $\Delta Y'_{g,s,a}$ ) is the difference between modelled yield variation in the year  $a$  (2011–2100, covering both past and future years under climate scenarios) and the mean of the corresponding baseline (1981–2010).

To examine yield effect of elevated CO<sub>2</sub> concentration (eCO<sub>2</sub>), we computed a yield promotion ( $\Delta Y'_a$ ) by multiplying an affecting ratio of eCO<sub>2</sub> ( $\partial_{r,a}$ ) to the mean of  $Y_{t,g,s,a}$  of the baseline (1981–2010), then compared the  $\Delta Y'_a$  with  $\Delta Y'_{g,s,a}$  to examine the net effects of climate change, genotype–environment interaction and eCO<sub>2</sub>. The  $\partial_{r,a}$  is a



nonlinear function of CO<sub>2</sub> concentration in future year  $a$  and scenario  $r$ , induced from experiments summarized by Amthor et al.<sup>51</sup> and Kimball<sup>52</sup>, in which the maximum yield enhancement ratio of 15% was assumed at the CO<sub>2</sub> concentration of around 800 μmol mol<sup>-1</sup> with yield benefits levelling off at higher concentrations.

Finally, we identified the adaptation capacity of genotypes across environments. For the 1,350 DY (90 years × 5 GCMs × 3 SSPs) for each genotype–station combination, we regressed DY against its corresponding DT by assuming a universal quadratic relationship. The genotype was considered to be warm-adapted in an environment if the relationship followed an inverse U shape. The temperature threshold is the temperature increase point beyond which yield change starts to drop below zero, as estimated from the fitted equation. Genotypes with DY that are always below zero in an environment are considered to not show warm adaptation, with the threshold set at 0 °C.

To assess how current breeding strategy performs in developing warming-adapted wheat under climate change, we examined two important criteria in breeding—selection ratio and adaptation stability. This assessment was simplified by estimating two corresponding vectors for each nursery for various warming levels, based on the obtained temperature threshold matrix  $A_{g,s}$  (equation (3)).

$$\mathbf{WA}_i = \sum_{j=1}^g (A_{i,j} \geq T) \times 1, \quad \mathbf{SE}_i = \sum (\mathbf{WA} \geq \mathbf{WA}_i) \text{ for } i = 1, 2, \dots, g \quad (3)$$

where, for a given warming level  $T$ , a  $g$  elements vector  $\mathbf{WA}$  was first generated to measure the wide adaptation, also considered as the environmental stability, of genotypes for the warming adaptation, represented by the number of stations where the genotype exhibits the warming adaptation ( $A_{g,s} \geq T$ ). Corresponding to each element of  $\mathbf{WA}$ , the selection efficiency (SE), namely how many genotypes can be selected with the stability equal to or greater than  $\mathbf{WA}$ , was then estimated. Each pair of ( $\mathbf{WA}$ ,  $\mathbf{SE}$ ) represents possible combinations of  $\mathbf{WA}$  and  $\mathbf{SE}$  in selecting warm-adapted cultivars from the current germplasms. These values can also be normalized among nurseries (WA%, SE%) by dividing  $\mathbf{WA}$  and  $\mathbf{SE}$  by the number of station ( $s$ ) and genotype ( $g$ ), respectively. Finally, one pair of indices of WAI and SEI, spanning from 0 to 1, were aggregated for each nursery and warming level (that is, 0.26 °C, the warming extent of 2011 to 2020 related to the baseline 1981–2010, 1 °C, 2 °C, 3 °C, 4 °C, 5 °C and 6 °C), by weight averaging all possible  $\mathbf{SE}$  and  $\mathbf{WA}$ , respectively, as function 4.

$$\text{WAI} = \frac{\sum_{i=1}^g \mathbf{WA}_i \times (\mathbf{SE}_i / \sum \mathbf{SE}_i), \text{SEI} = \frac{\sum_{i=1}^g \mathbf{SE}_i \times (\mathbf{WA}_i / \sum \mathbf{WA}_i)}{\sum \mathbf{WA}_i} \quad (4)$$

The WAI and SEI indicate the mean potential of the nursery for selecting warm-adapted cultivars to cope with a particular warming level.

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

The original IWIN nursery data are publicly available at <https://data.cimmyt.org>. The climate data for historical period (1980–2021) are from the European Centre for Medium-Range Weather Forecast (<https://www.ecmwf.int>)—AgERA5 gridded weather dataset. The projected climate data for 2015–2100 generated by five Global Climate Models are from the Inter-Sectoral Impact Model Intercomparison Project (<https://www.isimip.org>). The cleaned nursery data and corresponding climate and environmental variables prepared for this study are available at <https://doi.org/10.7910/DVN/3GAKGY> (ref. 53).

## Code availability

Data analysis scripts, including random forest (RF) yield and  $G \times E$  forecasting and plotting, were developed with Python v3.11.4 and deposited in Harvard Dataverse at <https://doi.org/10.7910/DVN/3GAKGY> (ref. 53). Requests for scripts for the analyses performed can be directed to W.X.

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**Author contributions**

W.X. and M.P.R. conceived the study. C.M., B.A., K.M., F.O. and Z.H. collected and processed the data. W.X. and J.C. analysed the data. W.X. and M.P.R. wrote the paper, and all contributed to the writing.

**Competing interests**

The authors declare no competing interests.

**Additional information**

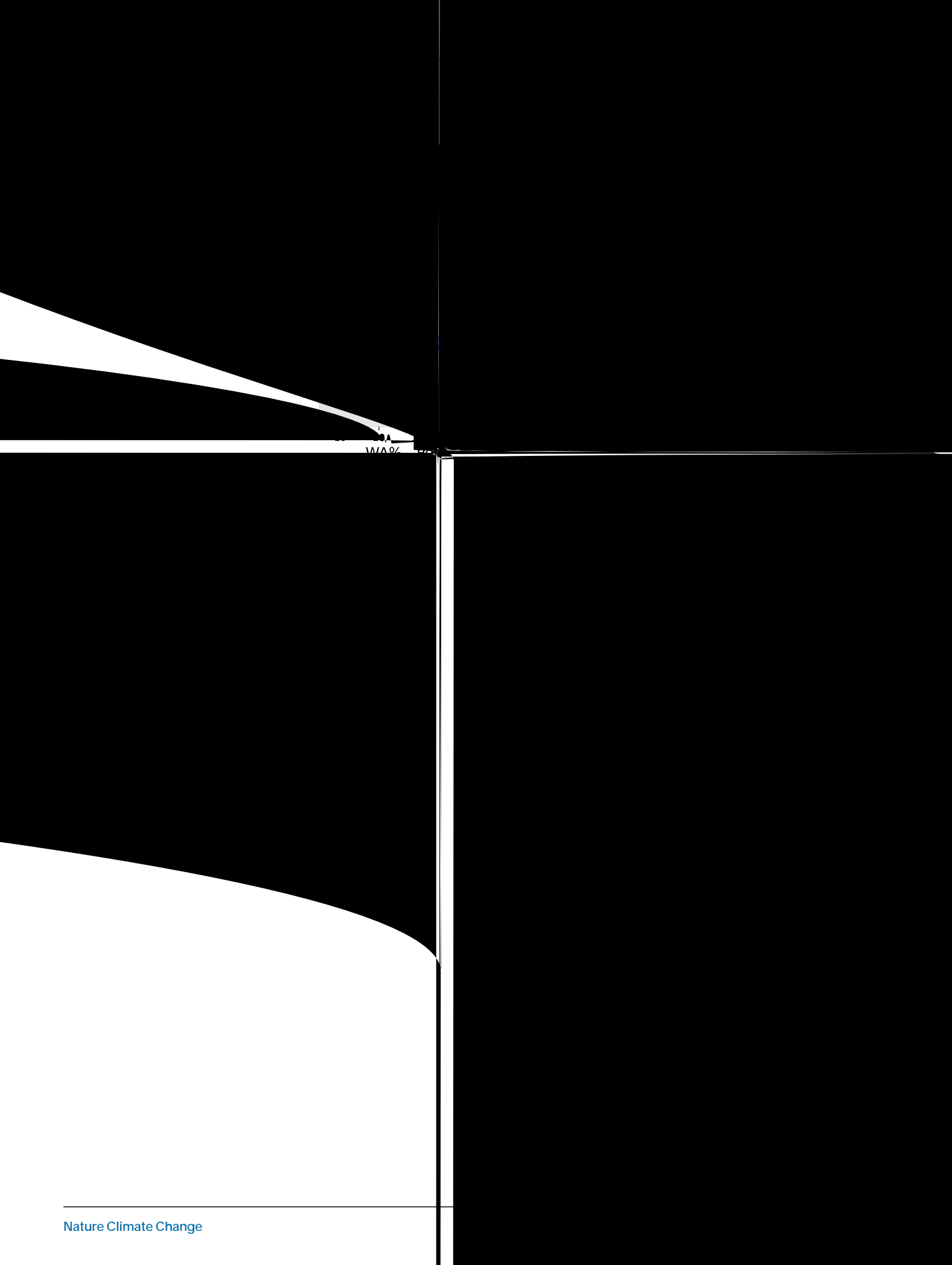
**Extended data** is available for this paper at <https://doi.org/10.1038/s41558-024-02069-0>.

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41558-024-02069-0>.

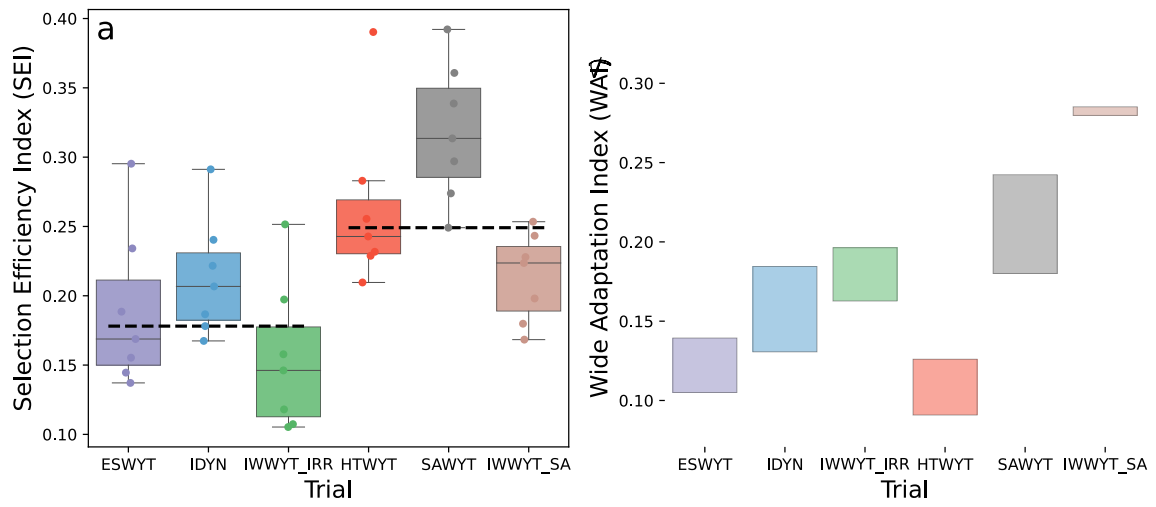
**Correspondence and requests for materials** should be addressed to Wei Xiong or Matthew P. Reynolds.

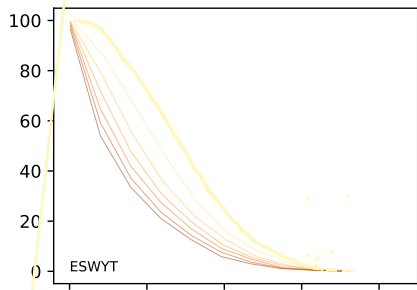
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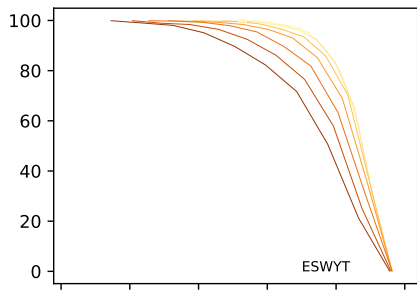
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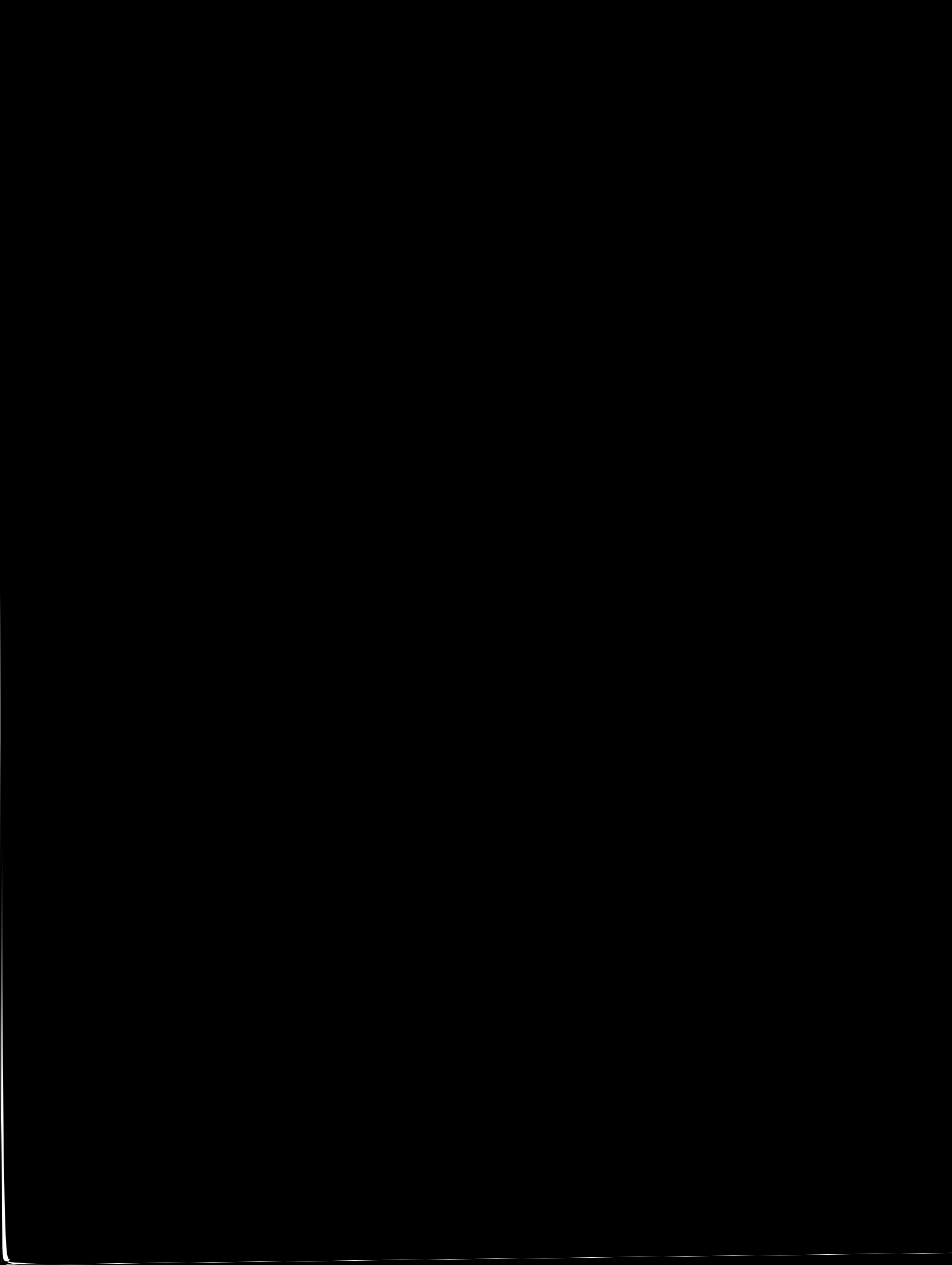


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# Report

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