

District specific, in silico evaluation of rice ideotypes improved for resistance/tolerance traits to biotic and abiotic stressors under climate change scenarios

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Abstract Using crop models as supporting tools for analyzing the interaction between genotype and environment represents an opportunity to identify priorities within breeding programs. This study represents the first attempt to use simulation models to define rice ideotypes improved for their resistance to biotic stressors (i.e., diseases); moreover, it extends approaches for evaluating the impact of changes in traits for tolerance to abiotic constraints (temperature shocks inducing sterility). The analysis—targeting the improvement of 34 varieties in six Italian rice districts—was focused on the impact of blast disease, and of pre-flowering cold- and heat-induced spikelet sterility. In silico ideotypes were tested at 5-km spatial resolution under current conditions and climate change scenarios centered on 2020, 2050, and 2085, derived according to the projections of two general circulation models–Hadley and NCAR–for two IPCC emission scenarios–A1B and B1. The study was performed using a dedicated simulation platform, i.e., ISIde, explicitly developed for ideotyping studies. The ideotypes improved for blast resistance obtained clear yield increases for all the combinations GCM×emission scenario×time horizon, i.e., 12.1 % average yield increase

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under current climate, although slightly decreasing for time windows approaching the end of the century and with a marked spatial heterogeneity in responses across districts. Concerning abiotic stressors, increasing tolerance to cold-induced sterility would lead to a substantial yield increase (+ 9.8 %) only for *Indica*-type varieties under current climate, whereas no increases are expected under future conditions and, in general, for *Japonica*-type varieties. Given the process-based logic behind the models used—supporting coherence of model responses under future scenarios—this study provides useful information for rice breeding programs to be realized in the medium-long term.

1 Introduction

The development of crop models has been driven since the end of the 1960s by two main objectives: increasing the efficiency of agricultural production systems to maximize yields while reducing costs, and supporting breeding programs via in silico analyses of the genotype×environment interaction (Donatelli and Confalonieri [2011](#page-13-0)). Both these goals are crucial to successfully facing the challenges deriving from the need for increasing the economic and environmental sustainability of agricultural systems. However, most modeling studies focused on the first one, and a large number of applications targeting the development of tools for optimizing management practices were developed. Instead, the use of crop models for designing plant ideotypes—second goal—is still in its infancy (Tardieu [2010\)](#page-14-0).

The development of process-based modeling frameworks integrating the available knowledge on the genotype×environment interaction —and on how such interaction is modulated by management practices—could effectively support breeding programs (Boote et al. [2001](#page-12-0)), which usually require 10 to 15 years and sizable resources to gain effective results, although marker-assisted breeding could reduce this time by 3-6 years (Alpuerto et al. [2009](#page-12-0)). Genetic improvement can be emulated via changes in the values of the model parameters describing specific morphological and physiological plant traits (Duncan et al. [1967](#page-13-0); Semenov and Stratonovitch [2013](#page-14-0); Confalonieri et al. [2013\)](#page-13-0). This allows one to develop in silico ideotypes that can be used (i) a priori, to identify the complex of genes on which breeders should focus (Herndl et al. [2007](#page-13-0)), or (ii) a posteriori, to efficiently test the performances of the modified genotypes under different agro-environmental contexts and over long-term periods (Hammer et al. [2002\)](#page-13-0). Interesting attempts have been made along these lines for different crops: Aggarwal et al. ([1997](#page-12-0)) used ORYZA1 to estimate the impact of changes in vegetative and reproductive rice traits in tropical environments. Raza et al. ([2013](#page-13-0)) used the crop model CropSyst to analyze the relationship of alfalfa cultivar traits with soil water dynamics to derive an ideotype for temperate, semi-arid conditions. Drewry et al. [\(2014\)](#page-13-0) successfully demonstrated how changes in canopy structural traits could allow to simultaneously improve productivity and water use efficiency in modern cultivar of soybean. The main limits in the use of crop models for this kind of studies lie in the absence of explicit algorithmic formalizations representing the genetics behind morphological and physiological traits, and thus in possible discrepancies between in silicoimproved varieties and their in vivo realizations (Hammer et al. [2002\)](#page-13-0). However, a model can be considered suitable to reproduce the behavior of a given genotype when it implements parameter-driven response functions reflecting the way the plant actually reacts to agro-environmental conditions (Tardieu [2003](#page-14-0)). Model parameters must have a biophysical meaning, and changes in their values should impact on multiple physiological processes, thus reproducing the feedback mechanisms of gene expression (Boote et al. [2001\)](#page-12-0). Finally,

a conservative definition of in silico ideotypes can be achieved only by changing parameter values within the range of their known genetic variability.

"Stressors" are defined as environmental factors assuming values—or evolving with dynamics—that prevent the plant to complete its cycle or achieve an acceptable yield. Despite the key role of biotic (e.g., diseases) and abiotic (e.g., lodging) stresses in determining actual crop production levels (e.g., Oerke [2006\)](#page-13-0), model-based ideotyping studies have completely ignored traits related to resistance to diseases and—except for drought and only few studies about heat stress (e.g., Singh et al. [2014](#page-14-0))—to tolerance to critical environmental conditions. A reason for this is the absence of specific algorithms for biotic and abiotic stressors in most of the available crop models (Donatelli and Confalonieri [2011\)](#page-13-0). The inclusion of these factors in in silico ideotyping studies could instead greatly support the design of medium and long-term breeding programs, since expected changes in climate (IPCC [2007\)](#page-13-0) would likely lead to shifts in breeding priorities, making the integrated, a priori evaluation of the performances of new cultivars a pre-requisite for defining effective adaptation strategies (Semenov and Stratonovitch [2013](#page-14-0)). Extreme events are expected to increase their frequency, undermining future global food security (Battisti and Naylor [2009\)](#page-12-0). Breeders should thus know which traits will be the key ones in the coming $15-25$ years to derive the most suitable varieties in this challenging context. As an example, increasing drought tolerance in wheat could appear as a priority under current climate in Europe whereas, according to future projections, heat stress would likely represent the major constraint to wheat production in this area (Semenov and Shewry [2011\)](#page-14-0).

Rice ($Oryza sativa$ L.) is the staple food for more than a half of the world population (FAOSTAT, <http://faostat.fao.org/>) and should be considered as a key crop in this context. Rice production is indeed heavily affected by biotic stressors, with blast (Magnaporthe oryzae B. Couch) being one of the most severe threats to rice yields in the main production districts worldwide. Each year, blast is indeed responsible for losses in the global rice production that ranges from 10 to 30 %. Farmers are thus forced to apply chemical treatments to prevent blast epidemics, increasing the economic cost and the environmental impact of rice-based cropping systems. The development of varieties resistant to *M. oryzae* is therefore the primary objective of any rice breeding program worldwide (Ballini et al. [2008\)](#page-12-0). Concerning abiotic factors affecting rice production, critical temperatures during panicle differentiation and flowering stage inducing spikelet sterility play a major role (Suh et al. [2010;](#page-14-0) Sanchez et al. [2014](#page-14-0)).

This study presents the results of the first in silico evaluation of the performances of ideotypes derived from the introgression of traits for resistance to biotic stressors in available rice genotypes. Moreover, ideotypes improved for tolerance to abiotic factors (temperature shocks inducing sterility) were also evaluated. Simulation results are analyzed in light of the different responses achieved in different production districts and under different climate scenarios.

2 Materials and methods

2.1 The study area

Italy is responsible for more than a half of the total European rice production, with 1,500,000 tons produced on 246,500 ha in 2011 (FAOSTAT, [http://faostat.fao.org/\)](http://faostat.fao.org/). Rice plays an important role in the country, because of economic, social, and cultural reasons, and it is

mainly grown under flooded conditions in six districts (Fig. S1, Online Resource 1) characterized by markedly heterogeneous conditions. The Lombardo-Piemontese is the widest, accounting for 90 % of the Italian rice cropped area (National Rice Authority, www.enterisi.it), followed by the Emiliano (9965 ha), Veneto (5992 ha), Oristanese (3524 ha), Sibari (565 ha), and Toscano districts (279 ha). Climate conditions are nearly continental in the northern districts (i.e., Lombardo-Piemontese and Veneto) becoming typical of lowland littoral areas while moving to the southern part of the country (i.e., Sibari and Oristanese districts). Southern areas are also characterized by heat waves and drier weather, especially during the growing period of rice (i.e., from May to September).

The high latitudes of the main three districts (around 45° N) expose the crop to cold air irruptions from the Alps that—when occurring between panicle initiation and heading—could induce spikelet sterility. The frequency of this event is about 1 every 4 years, and the intensity could lead to yield losses larger than 30 % for the most susceptible varieties. Concerning fungal diseases, they affect rice production regardless from the district; blast represents the most serious and widespread pathogen (Faivre-Rampant et al. [2011\)](#page-13-0), requiring the application of chemical treatments on more than 75 % of the Italian rice acreage.

2.2 Data used for the ideotyping experiment

Daily maximum and minimum air temperatures, global solar radiation, rainfall, wind speed, and reference evapotranspiration needed for the baseline climate were extracted from the MARS database [\(http://mars.jrc.ec.europa.eu/mars/Web-Tools\)](http://mars.jrc.ec.europa.eu/mars/Web-Tools) at 25-km×25-km spatial resolution. For the generation of climate change scenarios, the uncertainty related to the future economic, demographic, and technological development was handled by using the projections of two emission scenarios (A1B and B1; IPCC [2007\)](#page-13-0) as provided by two general circulation models (GCM): Hadley3 (UKMO-HadCM3, Gordon et al. [2000\)](#page-13-0) and NCAR (NCAR-CCSM3, Collins et al. [2004\)](#page-12-0). A1B is a conservative scenario, based on a balanced use of fossil and non-fossil energy resources, whereas for B1, the implementation of mitigation strategies to reduce carbon emissions is assumed. Climate change projections associated with these emission scenarios are thus considered to be, respectively, at the high and low range of current forecast (IPCC [2007](#page-13-0)). Four 20-year time horizons were considered: 1991–2010 (baseline), 2020–2040, 2050–2070, and 2085–2105. The generation of synthetic weather series was carried out using the CLIMAK weather generator (Confalonieri [2012\)](#page-13-0), which has proved its reliability under a variety of conditions, also in comparative studies (e.g., Acutis et al. [1998](#page-12-0)). For each combination emission scenario×GCM×time frame×MARS grid cell, monthly mean temperature and precipitation anomalies were applied to the CLIMAK parameters describing baseline rainfall and temperature patterns. In particular, CLIMAK parameters on which deltas were applied are monthly α and β of the gamma distribution for rainfall amount and the four coefficients (annual mean maximum and minimum temperatures for dry and rainy days) of the second-order Fourier series for temperature. Future climate change scenarios used to test the performance of rice ideotypes are described in Table S1, Online Resource 2. In agreement with Coppola and Giorgi ([2010](#page-13-0))—who assessed climate change projections provided by 19 GCMs over the Italian peninsula—the greatest temperature increase is realized under the A1B emission scenario, whereas the B1 leads to the lowest. GCMs also affected climate projections, with Hadley3 providing warmer scenarios than NCAR, in agreement with findings of Covey et al. [\(2003\)](#page-13-0). Projected rainfall varies across scenarios without displaying clear patterns; however, the combination GCM×emission

scenario Hadley-A1B leads to a "drier" climate during the rice growing season as compared to NCAR-B1. Spatial heterogeneity in climate change projections is expected, with northern districts showing greater temperature increase than the southern ones (e.g., +4.5 and +2.5 °C for the Lombardo-Piemontese and Oristanese districts, respectively, under the Hadley-A1B 2085 scenario).

Since most of the biophysical processes—e.g., crop growth and development, plantpathogen interaction, spikelet sterility, floodwater effect on vertical thermal profile—were simulated using an hourly time step, hourly weather data were estimated at runtime using generators implemented in the CLIMA software library ([http://agsys.cra-cin.it/tools/clima/](http://agsys.cra-cin.it/tools/clima/help/) [help/\)](http://agsys.cra-cin.it/tools/clima/help/).

Rice distribution maps—as well as sowing dates—were derived from an integrated analysis of available thematic cartography (European Corine Land Cover for the year 2006; [http://](http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-clc2006-100-m-version-12-2009) [www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-clc2006-100-m-version-12-](http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-clc2006-100-m-version-12-2009) [2009\)](http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-clc2006-100-m-version-12-2009) and remote sensing data. Ten years (2002–2011) of MODIS 8-Day composites images—MOD09A1 product of surface reflectance at 500-m spatial resolution—were processed in order to derive a rice distribution database. The processing method combines information on the status of vegetation and on the presence of floodwater to detect rice areas and derive information on rice development (Boschetti et al. [2009](#page-12-0)). Remote-sensed information—10 years median—were aggregated at $5-km \times 5-km$ spatial resolution, identified as elementary spatial unit for the simulations in light of (i) the spatial resolution of the different information layers and (ii) the need for finding a compromise between the level of detail to represent the spatial heterogeneity among and within rice districts and the computational cost of the simulations.

To account for the heterogeneity of rice varieties commonly grown in Italy (Russo [1994](#page-13-0)), 34 varieties were selected as the basis for the ideotyping study according to their representativeness in each of the six Italian rice districts. The criterion for the selection was a relative presence higher than 1 % in the district in at least 3 years during the period 2006–2010 (National Rice Authority, www.enterisi.it).

2.3 The simulation environment

2.3.1 The modeling solution

Simulations were performed using the WARM model (Confalonieri et al. [2009\)](#page-13-0), adopted since 2005 by the European Commission for rice monitoring and yield forecasting in Europe. In the configuration used in this study, crop growth and development are reproduced using an hourly time step, in both cases with a curvilinear response function to temperature. Floodwater effect on vertical thermal profile is simulated by using the TRIS micrometeorological model (Confalonieri et al. [2009\)](#page-13-0), based on the solution of the surface energy balance equation for each 10-cm canopy layer and for air-water interface, for the latter assuming the heat accumulation into the water as storage term. TRIS, coupled with a model for plant height, allows using temperature at the meristematic apex for the simulation of development and thermal shock around flowering, and mid-canopy temperature for photosynthesis. Biomass accumulation is simulated with a net-photosynthesis approach based on radiation use efficiency (RUE), the latter modulated by temperature, senescence, atmospheric $CO₂$ concentration, and lightsaturation of the enzymatic chains. For the latter, a quadratic function decreasing RUE for global solar radiation higher than 25 MJ m⁻² day⁻¹ is used (Choudhury [2001](#page-12-0)). Photosynthates

partitioning to the different plant organs, as well as translocation to grains during grain filling, are simulated using a set of beta and parabolic functions driven by development stage and by partitioning to leaves at emergence. Daily increase in leaf area index (LAI) is derived from leaf biomass rate and a development-driven specific leaf area, whereas leaf senescence is simulated by killing LAI units that reached a thermal time threshold. WARM parameters for crop growth and development are shown in Table S2, Online Resource 2.

Concerning the simulation of abiotic damages, the impact of cold-induced spikelet sterility is simulated by reducing the amount of assimilates daily partitioned to the grains according to the stress factor (Sterility_F, 0-1, unitless) shown in Eq. 1 (Confalonieri et al. [2009\)](#page-13-0):

$$
Sterility_F = \left\{ \sum_{i=d_{1.6}}^{d_{1.9}} \left\{ bellF_i \cdot \sum_{h=i}^{24} (T_{TC} - T_{i,h}) \right\} \right\} \quad 1.6 < DVS < 1.9 \cap T_{TC} > T_{i,h} \quad (1)
$$
\n
$$
elsewhere
$$

where $d_{1.6}$ and $d_{1.9}$ are the days corresponding to panicle initiation and heading, respectively, with 1.6 and 1.9 being the values assumed in those stages by a development stage numerical code (DVS; 0, sowing; 1, emergence; 2, flowering; 3, physiological maturity; 4, harvestable) obtained by standardizing the cumulated thermal time; T_{TC} (°C) is the threshold temperature inducing sterility; $T_{i,h}$ is the temperature of day i at hour h; bellF_i—representing the different susceptibility in the period between panicle initiation and heading—is derived from a normal distribution function (Eq. 2):

$$
bellF_i = \frac{\delta}{\gamma\sqrt{2\pi}} \cdot \exp\left[\frac{(DVS_i - 1.8)^2}{2\gamma^2}\right]
$$
 (2)

where DVS_i is the DVS of the day i; γ and δ are the empirical coefficients set, respectively, to 0.1 and 0.25. The threshold temperature was set, in this study, to 12 and 13 °C for current Japonica-type and *Indica-type* varieties, respectively. The impact of heat-induced spikelet sterility is simulated using the same approach but with $(T_{i,h}-T_{TH})$ used instead of $(T_{TC}-T_{i,h})$ in Eq. 1, being T_{TH} (°C) the threshold temperature for heat-induced sterility (i.e., 35 °C for Japonica-type and 35.5 °C for *Indica*-type varieties).

From panicle initiation to heading, photosynthates daily partitioned to panicles are reduced as a function of the integral of SterilityF. From flowering to the end of grain filling phase, the value of *Sterility_F* cumulated till heading (*DVS* 1.9) is used.

The simulation of blast impact on rice growth was carried out by using the set of models of the Diseases software library ([http://www.cassandralab.com/components/\)](http://www.cassandralab.com/components/), implementing approaches for the simulation of (i) the phases of infection, latency, infectiousness, sporulation, spores dispersal, and (ii) the impact on plants.

The whole epidemic development is simulated as a function of agro-environmental variables—e.g., leaf wetness, air relative humidity, air temperature—and variety resistance. The models implemented in the library were successfully evaluated for blast against a large set of data from field experiments in northern Italy (Bregaglio et al. [2013\)](#page-12-0). Parameters describing the specific responses of *M. oryzae* to environmental conditions are given in Table S3, Online Resource 2. According to Bastiaans [\(1991\)](#page-12-0), the impact of blast epidemic on the crop is simulated by considering the reduction of green leaf area and the decrease in the photosynthetic activity of remaining green leaf tissues. The first coupling point between the disease and the crop model is represented by the dynamic removal of the fraction of diseased leaf area

using a compartmental susceptible-exposed-infected-removed model (Bregaglio and Donatelli [2015;](#page-12-0) [http://www.cassandralab.com/components/\)](http://www.cassandralab.com/components/). This allows to take into account the reduction in the amount of light absorbed because of the lesions. A second coupling point concerns the decrease in the photosynthetic rate in the remaining green leaf area via a linear function relating disease severity and rice radiation use efficiency (Bingham and Topp [2009](#page-12-0)).

The WARM modeling solution was here implemented in a dedicated platform (ISIde; In Silico Ideotyping platform), based on the BioMA architecture (Donatelli and Rizzoli [2008](#page-13-0)), specifically developed for district-specific ideotyping studies and targeting breeders as final users. ISIde is currently available for the six rice districts in Italy, although its software architecture allows its extension to other contexts or crops. The complete documentation of all the models and software components implemented in the modeling solution is available at [http://www.cassandralab.com/components.](http://www.cassandralab.com/components)

2.3.2 Parameterization of the solution for current genotypes

Adapting the modeling solution to the 34 selected varieties required the definition of the values of parameters describing morphological and physiological plant features, and of those involved with the simulation of biotic and abiotic stressors.

Five phenological groups were identified by applying the k-means clustering method (Dulli et al. [2009\)](#page-13-0) to the length (days) of the vegetative and reproductive phases reported for each variety by the National Rice Authority ([www.enterisi.it\)](http://www.enterisi.it/). This agency indeed carried out extensive field trials in different sites and seasons to provide a detailed description of morphological and phenological characteristics of the main Italian rice cultivars. Starting from available parameter sets for Italian *Indica*- and *Japonica*-type varieties obtained by calibrating model parameters using data from field experiments (Confalonieri et al. [2009](#page-13-0)), new parameter sets were thus developed by combining information on the ecotypes with those derived from the cycle length clusters (Table S2, Online Resource 2).

Parameters involved with blast resistance (Table S4, Online Resource 2) were derived by screening the databases and reports of both the National Rice Authority [\(www.enterisi.it\)](http://www.enterisi.it/) and the Regional Agency for Agricultural and Forest Services ([www.ersaf.lombardia.it\)](http://www.ersaf.lombardia.it/). These agencies performed extensive multi-site and multi-year trials from 2000 to 2011 where the resistance of each cultivar to fungal pathogens was determined. These data were analyzed and integrated with information coming from interviews to a panel of Italian experts in rice diseases. This led to identify three blast resistance levels (low, moderate, intermediate), in agreement with Faivre-Rampant et al. [\(2011](#page-13-0)), who defined Italian rice varieties as having a low to intermediate resistance to leaf blast after extensive analyses performed under greenhouse conditions. The resistance levels were then translated into parameter values by increasing the length of the latency period and by reducing the infectiousness duration and the infection/ sporulation efficiencies in case of higher resistance (Table S3, Online Resource 2).

Temperature thresholds applied on hourly basis for cold- and heat-induced spikelet sterility for *Japonica*- and *Indica*-type varieties (12 and 13 °C, 35 and 35.5 °C, respectively; Table S4, Online Resource 2) were retrieved from literature (Andaya and Mackill [2003;](#page-12-0) Dreni et al. [2012](#page-13-0); Sanchez et al. [2014](#page-14-0)) and consultation with local experts. This allowed to account for peculiarities of Italian rice cultivars, selected in recent decades to cope with the conditions explored in the main Italian rice district, considered extreme for rice because of the proximity to the Alps (Russo [1994](#page-13-0); Confalonieri et al. [2005](#page-13-0)). Information available did not allow to further discriminate among threshold values within each group of varieties.

2.3.3 Definition of the new ideotypes

The evaluation of the impact of potential improvement for resistance/tolerance level was carried out by changing values of model parameters representing these traits within the range of their known genetic variability. Ideotypes were thus created by assigning to resistance/tolerance parameters the values defined for resistant/tolerant varieties; this was considered as the level of improvement potentially achievable. Assumptions concern the absence of relationships between the traits involved with the processes analyzed and those related with other plant characteristics (e.g., Singh et al. [2012](#page-14-0) for resistance to pathogens). Resistant varieties—used as sources of effective resistance/ tolerance traits—are often traditional genotypes selected after long adaptation to the specific Italian agro-climatic context (Faivre-Rampant et al. [2011](#page-13-0); Russo [1994](#page-13-0)). For instance, the variety Gigante Vercelli, released in 1946 and has not been cultivated for decades, was already selected as a donor of blast resistance in breeding programs because of the resistance to main Italian strains of the pathogen (Roumen et al. [1997](#page-13-0); Faivre-Rampant et al. [2011\)](#page-13-0). It presents an intermediate resistance to blast disease. This value was thus used to set blast resistance parameters for the improved ideotypes. The temperature threshold below which cold sterility occurs was reduced—for the ideotypes—by 0.5 °C for *Japonica*-type and by 1 °C for *Indica*-type varieties. This led to set a lowest temperature threshold of 11.5 \degree C, which reflects the response of the cold tolerant varieties currently grown in the Italian district. The smaller magnitude of the improvement simulated for *Japonica*-type varieties is in line with their better adaptation to temperate conditions (Russo [1994;](#page-13-0) Suh et al. [2010](#page-14-0)). They present indeed slightly lower thermal requirements for both growth and development (Sanchez et al. [2014](#page-14-0)), and a lower threshold triggering sterility damages compared to Indica-type varieties (temperature thresholds applied on hourly basis are 12 versus 13 \degree C, Table S4, Online Resource 2). The opposite criterion was followed for the quantification of the possible genetic improvement for heat-induced sterility (increase in threshold temperature for heat-induced spikelet sterility was 0.5 °C for *Indica*-type and 1 °C for *Japonica*-type varieties), since *Indica*-type varieties are generally more suited to tropical environments (Sanchez et al. [2014\)](#page-14-0). A higher variability is reported for tolerance to heat stress in rice (Matsui et al. [2001](#page-13-0)), but Italian rice varieties have not been selected for this traits since they are rarely exposed to this damage.

The information available on the potential incidence of the different damages led to evaluate the ideotypes for tolerance to cold-induced sterility in the districts Lombardo-Piemontese, Veneto, Emiliano, and Toscano. For the same districts and in the Oristanese one, ideotypes were defined for blast resistance. Improvement involved with the tolerance to heat-induced sterility was instead tested for the districts Oristanese and Sibari.

For each climate scenario and elementary spatial unit, simulations were run twice for each variety: the first using the parameterizations for the current genotype and the second reproducing the behavior of the corresponding improved ideotype. Three production levels were considered: blast-, cold sterility-, and heat sterility-limited. For each production level, the percentage yield increase $(\Delta_{v}, \%)$ was quantified.

The total number of simulations was 19,910,400, given by the combination of 34 rice varieties, three production levels, two general circulation models, two emission scenarios, four time horizons, 20 years for each time horizons, two genotypes simulated—one for the current variety and one for the corresponding ideotype—and by 305 elementary simulations units.

3 Results and discussion

The high spatial resolution used to perform the simulations allowed an in-depth analysis of the performances of improved ideotypes. Figure 1 presents sample results for the main Italian rice district for (a) an ideotype derived by increasing blast resistance of the variety Volano (Hadley-A1B projections) and for (b) an ideotype derived by increasing the tolerance to cold-induced sterility for Thaibonnet (NCAR-B1). The largest increases for the blast resistance-improved ideotypes were achieved in the central-western part of the district when the current climate was considered, whereas they were achieved in north-western areas while moving forward the time horizon (Fig. 1a). In general, the eastern part of the district appears to be less affected by possible breeding programs in the long term (2085 time horizon). Figure 1b shows that a marked heterogeneity in the yield increase extent was simulated. The general north-south gradient is due to the colder climate in the northern part of the district, whereas the pattern characterized by a high level of granularity is—to a large extent—driven by differences in management practices. The use of different sowing dates, indeed, leads to shifts in crop phenology and, thus, in the time windows when the crop is susceptible, i.e., from panicle initiation to heading. Although benefits decrease while moving forward the climate projection because of the raising temperature, spot areas markedly affected can be observed for the 2085 time horizon. The reason is the shortening of the crop cycle due to the higher temperatures, which exposes the crop to the damage in an earlier moment during the season, when the frequency of cold air irruptions is higher.

Average yield increase for an ideotype derived by improving cv. Volano for resistance to blast disease

Average yield increase for an ideotype derived by improving cv. Thaibonnet for tolerance to cold-induced sterility

Fig. 1 Percentage yield increase in the Lombardo-Piemontese district due to the increased a resistance to blast disease for the variety Volano and b tolerance to cold-induced sterility for the variety Thaibonnet. For these sample results, the Hadley-A1B and the NCAR-B1 climate change scenarios were used, respectively, for blast and sterility. Simulations were performed at 5-km×5-km spatial resolution. For both examples, a marked spatial heterogeneity was observed, and a decrease of the yield increase extent while proceeding along the time horizons

The mean percentage yield increase achieved with the ideotypes improved for resistance/ tolerance traits compared to the 34 varieties they derive from are shown in Fig. 2 and Fig. [3](#page-10-0) for each combination general circulation model×time horizon×emission scenario. No results are presented and discussed for Sibari since the only stressor potentially present in the district heat-induced sterility—never affected the crop, regardless of the climate scenario.

In general, improving genotypes for their resistance to M. oryzae led to remarkable potential yield increases for all the varieties, regardless of the district and the time horizon (Fig. 2). The average yield increase was 11.87 %, with a small variability among districts and climate scenarios (coefficient of variation=11.6 %). However, future climate projections revealed that the extent of increases could experience a modest decline in some of the districts

Fig. 2 Yield increases due to the improvement of the 34 most representative Italian rice varieties for resistance to blast (average value of the 20-year period). White bars refer to results achieved under current climate, black and gray bars to the Hadley-A1B and NCAR-A1B realizations, respectively, striped and checkered bars to the Hadley-B1 and NCAR-B1 projections. Relevant benefits from possible breeding activities are expected for resistance to blast, regardless of the district and climate scenario

Fig. 3 Yield increases deriving from improving tolerance to pre-flowering cold-induced spikelet sterility in the Indica-type varieties studied (average values of the years in which the damage occurs). Results refer to yield increases achieved under: the current climate (white bars), the Hadley-A1B and NCAR-A1B climate scenarios (black and gray bars, respectively), and the Hadley-B1 and NCAR-B1 projections (striped and checkered bars). Under the conditions explored, a marked decrease of the impact of cold-induced spikelet sterility is expected

(Toscano and Veneto). The climate scenarios derived from the NCAR general circulation model and the B1 emission scenario led to the largest yield increases in most of the combinations district×time horizon, whereas the lowest were usually achieved with the combination Hadley \times A1B. This is explained by considering the thermal requirements of the pathogen (Table S3, Online Resources 2) and the temperature increases in the climate change projections. Under the conditions explored, indeed, the climate generated using the A1B emission scenario and the Hadley circulation model is characterized by large increases in temperature, in turn generating conditions less favorable for the pathogen, with temperatures during the crop cycle frequently exceeding the optimum for the pathogen. The differences in yield increase among districts—coefficient of variations ranging from 11 to 16 % according to the time horizon considered—were due to the different suitability of the climate conditions to blast epidemics. The Toscano district presented the highest yield increases, because of the large number of rice varieties with a low resistance to blast.

This study was carried out without considering the evolutionary potential of the pathogen that could rapidly develop new races more adapted to changing climate conditions (Chakraborty [2013\)](#page-12-0)—since no quantitative information is available on this issue.

Concerning ideotypes improved for the tolerance to cold-induced spikelet sterility (Fig. [3](#page-10-0)), Indica-type genotypes achieved larger yield increases with respect to Japonica-type ones in all the districts and for all the combinations general circulation model×emission scenario. For Japonica-type varieties, indeed, the increased tolerance did not lead to relevant benefits, especially under climate change scenarios (data not shown). However—even for *Indica* ideotypes—yield increases are comparable to those simulated for blast resistance-improved ideotypes only under current climate conditions. In effect, simulations performed using future climate projections revealed that their performances are expected to become increasingly similar to those of the current varieties, in turn raising doubts about the usefulness of breeding programs focusing on this trait in the medium/long term. The heterogeneity in the responses across districts was decidedly more pronounced compared to that discussed for the ideotypes improved for blast resistance: coefficients of variation calculated on the yield increases range from 30 to 87 % for the 2020 and 2050 time horizons, respectively. However, a large part of this variability is due to the low impact of cold-induced sterility on the yields simulated in the Emiliano district because of its warmer climate.

Contrarily to yield losses caused by blast, cold-induced sterility is driven by events—i.e., cold air irruptions during the period between panicle initiation and heading—that do not occur during all seasons and, even when they occur, present a different intensity. Under current climate, the frequency of these events is about 1 out of 5 years. Lowering the threshold temperature inducing the damage created a marked reduction of the average number of events under future climate projections, although with differences among general circulation models and emission scenarios.

The model did not simulate impacts of heat-induced sterility—for both current varieties and improved ideotypes—in the two districts potentially interested by this phenomenon (Sibari and Oristanese), regardless of the climate scenario and time horizon considered. This clearly indicates that rice in Italy would not be affected by this phenomenon even under conditions warmer than the current ones. Despite A1B already provides high-impact scenarios, further studies might involve the use of more severe emission scenarios (e.g., RCP 8.5, IPCC [2013](#page-13-0)) to test the performance of improved ideotypes under a wider range of climate conditions.

4 Conclusions

The development of new varieties better adapted to future climate is one of the most effective strategies to alleviate the impact of climate change on agriculture and related food security issues. In this context, identifying key traits is crucial since relatively few breeding cycle are exploitable in the forthcoming decades (Lobell et al. [2012\)](#page-13-0).

We performed here for the first time an in silico ideotyping study targeting the improvement of current genotypes for resistance traits to biotic stressors at district level. Traits related with tolerance to abiotic constraints were also evaluated. The analysis was carried out for rice in Italy by varying parameters referred to resistance/tolerance traits according to their known variability among Italian rice varieties. This allowed to define ideotypes accounting for the level of improvement potentially achievable for these traits. Simulations were performed under current climate conditions and using future climate projections, to provide indications able to properly cope with the time resources needed by breeding programs. Our results clearly demonstrate that—under the conditions explored—breeders should focus on increasing resistance to blast disease, since *M. oryzae* appears as the main factor limiting rice productions in Italy regardless of the district and the climate scenario. On the other hand, increasing tolerance to pre-flowering cold shocks inducing spikelet sterility would lead to sizeable benefits only for Indica-type cultivars under current climate conditions in three out of six districts (Lombardo-Piemontese, Veneto, Toscano), whereas no relevant yield increases are expected after 2020, despite the general circulation model and emission scenario. The effect of increasing $CO₂$ on photosynthetic rate and changes in phenological development were explicitly considered, thus providing a comprehensive evaluation of ideotypes. Despite the assumptions behind the study—i.e., (i) absence of interactions between resistance/tolerance traits and others, (ii) no adaptation strategies considered (e.g., alternative sowing date), and (iii) lack of pathogen potential evolution in response to long-term climate variations and increased host resistance—we demonstrated the usefulness of simulation models as tools for supporting breeding programs via the a priori evaluation of the suitability of different ideotypes for specific conditions (i.e., the districts).

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