Decline in climate resilience of European wheat

Helena Kahiluoto[a,1], Janne Kaseva[b], Jan Balek[c,d], Jørgen E. Olesen[e], Margarita Ruiz-Ramos[f], Anne Gobin[g], Kurt Christian Kersebaum[h], Jozef Takáč[i], Francoise Ruget[j], Roberto Ferrise[k], Pavol Bezak[i], Gemma Capellades[l], Camilla Dibari[k], Hanna Mäkinen[a], Claas Nendel[h], Domenico Ventrella[m], Alfredo Rodríguez[f,n], Marco Bindi[k], and Mirek Trnka[c,d]

[a]Sustainability Science, LUT University, 53851 Lappeenranta, Finland; [b]Natural Resources Institute Finland, 31600 Jokioinen, Finland; [c]Global Change Research Institute, Academy of Sciences of the Czech Republic, 60300 Brno, Czech Republic; [d]Institute of Agriculture Systems and Bioclimatology, Mendel University in Brno, 61300 Brno, Czech Republic; [e]Department of Agroecology, Aarhus University, 8830 Tjele, Denmark; [f]Centro de Estudios e Investigación para la Gestión de Riesgos Agrarios y Medioambientales, Universidad Politécnica de Madrid, 28040 Madrid, Spain; [g]Flemish Institute for Technological Research, 2400 Mol, Belgium; [h]Leibniz Centre for Agricultural Landscape Research, 15374 Müncheberg, Germany; [i]National Agricultural and Food Centre, Soil Science and Conservation Research Institute, 827 13 Bratislava, Slovakia; [j]Mediterranean Environment and Modelling of Agroecosystems (EMMAH), Institut National de la Recherche Agronomique (INRA), Avignon Université, 84914 Avignon, France; [k]Department of Agri-food Production and Environmental Sciences, University of Florence, 50144 Florence, Italy; [l]Fundació Mas Badia, Grupo para la Evaluación de Nuevas Variedades de Cultivos Extensivos en España, 17134 La Tallada d'Empordà, Spain; [m]Centro di Ricerca Agricoltura e Ambiente, Consiglio per la Ricerca in Agricoltura e l'Analisi dell'Economia Agraria, Sede di Bari, 70125 Bari, Italy; and [n]Department of Economic Analysis, University of Castilla-La Mancha, 45071 Toledo, Spain

Food security relies on the resilience of staple food crops to climatic variability and extremes, but the climate resilience of European wheat is unknown. A diversity of responses to disturbance is considered a key determinant of resilience. The capacity of a sole crop genotype to perform well under climatic variability is limited; therefore, a set of cultivars with diverse responses to weather conditions critical to crop yield is required. Here, we show a decline in the response diversity of wheat in farmers' fields in most European countries after 2002–2009 based on 101,000 cultivar yield observations. Similar responses to weather were identified in cultivar trials among central European countries and southern European countries. A response diversity hotspot appeared in the trials in Slovakia, while response diversity "deserts" were identified in Czechia and Germany and for durum wheat in southern Europe. Positive responses to abundant precipitation were lacking. This assessment suggests that current breeding programs and cultivar selection practices do not sufficiently prepare for climatic uncertainty and variability. Consequently, the demand for climate resilience of staple food crops such as wheat must be better articulated. Assessments and communication of response diversity enable collective learning across supply chains. Increased awareness could foster governance of resilience through research and breeding programs, incentives, and regulation.

wheat | cultivar | Europe | climate resilience | response diversity

Food security relies on the resilience of staple food crops to climatic variability. Climate change increases the uncertainty regarding local weather (1) and intensifies weather variability and extremes (2, 3). Reductions in wheat yield in global and temperate areas (4, 5) and an increase in yield variability are projected even with moderate warming (6). While food availability is endangered in the long term (4, 5), yield variability induces price volatility and speculation (7). Price volatility in the globally integrated food market threatens the stability of access to food by the poor, who spend a great proportion of their income on staple foods (7) also in Europe. Food insecurity enhances political instability and migration (8), which aggravate national and regional food security concerns. Consequently, food security (9) is an important goal of both national emergency supply strategies and the Common Agricultural Policy of the European Union (10). While the impact of trade on food availability is negligible in Europe, which produces one-fifth of world's wheat (11), the region is more prone to instability than net exporters of food or countries in chronic states of food stress (12). Wheat is the leading source of plant protein in the human diet (11) and the most important staple food crop in Europe, but climate resilience of European wheat is unknown.

Resilience refers to the capacity to maintain core functions of, for example, food supply chains, under disturbance, and ability to adapt to change (13), while climate resilience specifically buffers against climate-related uncertainty and variability (14). A diversity of responses to disturbance is considered a key determinant of resilience (15, 16). "Response diversity" implies diversity within a function in response to change or variability critical to the function (16), for example diversity within the wheat yield supply in response to climatic events that are critical to the yield. Not any diversity of cultivars ("type diversity") is effective, but the diversity in the responses to critical weather events can effectively enhance climate resilience (17). Resilience is an important complement to the currently dominant goal of crop improvement (i.e., yield potential), which remains important. Response diversity provides the actors and governance of crop supply chains with a practical tool to assess and enhance the climate resilience of crops and thus food security.

Climatic variability and extremes are responsible for one-third of the global variability in crop yields (6). Climatic variability

Significance

Food security under climate change depends on the yield performance of staple food crops. We found a decline in the climate resilience of European wheat in most countries during the last 5 to 15 y, depending on the country. The yield responses of all the cultivars to different weather events were relatively similar within northern and central Europe, within southern European countries, and specifically regarding durum wheat. We also found serious Europe-wide gaps in wheat resilience, especially regarding yield performance under abundant rain. Climate resilience is currently not receiving the attention it deserves by breeders, seed and wheat traders, and farmers. Consequently, the results provide insights into the required learning tools, economic incentives, and role of public actors.

explains 31–51% of the variability in wheat yield in western Europe and 23–66% of the wheat yield variability in eastern Europe, while in southern Europe climatic variability is responsible for 15–45% of the yield variability in Italy and Greece and more than 75% in southern Spain (6). Consequently, the dominant approach of adapting crops to climate change by tailoring the genotypes to the most likely long-term change remains insufficient. The climate resilience (14) of crops has become critical to stabilizing food supply (1, 17, 18) and avoiding price spikes (19, 20), especially for rain-fed European wheat (21). The climate resilience of crop yield performance has a strong genetic basis, but the phenotypic outcome exhibits an interplay with the environment. The capacity of a single crop genotype to maintain a good yield performance under climatic variability and extremes is limited; therefore, a set of cultivars with diverse responses to critical weather conditions is required to promote the climate resilience of crops.

Seed traders and farmers manage the climate resilience of crops annually by selecting sets of cultivars for sale and cultivation, while breeders contribute to the resilience in the long term by providing the diversity in responses among cultivars. We previously demonstrated a decline in the diversity of barley responses to weather despite an increase in the number of cultivars over the last decade in the main cultivation area in Finland (17). Here, we quantified the response diversity of wheat in nine European countries. We identified the variation in response diversity on farmers' fields (Fig. 1) and demonstrated the relation to climate resilience (Fig. 2). We further revealed the variation of weather responses among countries (Fig. 3) and among weather patterns in trials (*SI Appendix*, Fig. S1). We used yield and weather data from cultivar trials from 1991 to 2014 at 636 locations for 991 cultivars of winter wheat, spring wheat, and durum wheat in nine countries, as well as their cultivation areas in eight countries. First, we determined the responses of wheat yield to weather by identifying the agroclimatic variables critical to yield (step 1) (17), estimating the cultivar yield responses to the variables (step 2) (17), and grouping the weather variables based on the responses using principal component analysis (PCA, for R^2 values see *SI Appendix*, Tables S1 and S2) (step 3)

Fig. 2. Increase in the climate resilience of European wheat with increasing response diversity. The main figure shows the decrease in the variation in the percentage yield response to the weather patterns (agroclimatic PCs) critical to yield due to the increase in the number of weather response clusters considered. All of the cultivar yield data were utilized ($n = 100,985$). The box shows how combining cultivars from different clusters increases the yield stability under weather variability. The three exemplary cultivars (dark, yellow and green heads) represent clusters 1, 3 and 5, respectively, from Caslav, Czechia and were selected based on the largest number of observations and similar average yields ($n = 78$). If the cultivation area was evenly divided among the three cultivars from 2001 to 2007 in comparison with the cultivation of only the cultivar with the highest total yield (Apache), a 2% loss in total yield appeared, but the SD among the years declined by 16–32%. The relative size of the heads refers to the relative annual yields of the three cultivars.

(18). Second, we estimated the response diversity by clustering the cultivars based on the component scores (step 4) (18) and assessed the annual diversity indices for the clusters (response diversity) and individual cultivars (type diversity) in farmers' fields and trials by country (step 5) (17).

Materials and Methods

Data. Long-term data series of cultivar trials between latitudes 37.21° and 61.34° and longitudes −6.02° and 26.24° in nine countries across Europe (Finland, Denmark, Germany, Belgium, Czechia, France, Slovakia, Italy, and Spain) were used. In some countries (Fig. 1), the period was limited by data availability. The trials had a randomized complete block design or an incomplete block design with two to four replicates, and their management was similar to farmer practices. The cultivars in the experiments differed over time, but standard reference cultivars were used over long periods and across several countries. Cultivars with at least 20 yield observations were included in the assessment. The total number of clustered cultivars (minimum number of observations was 20) was 36 for Finland, 90 for Italy, 113 for Belgium, 139 for France, 140 for Germany, 169 for Czechia, 186 for Spain, 188 for Slovakia, and 265 for Denmark. Annual grain yield (kilograms per hectare) was used as the response variable. The entire cultivar yield data set comprised 100,985 observations.

Step 1: Identifying Agroclimatic Variables Critical to Wheat Yield. The agroclimatic variables that were potentially critical to yield (*SI Appendix*, Table S1) were selected based on responses reported in the literature (5, 22, 23). Data on these agroclimatic variables during crop phenological stages (24) were obtained from the stations closest to the cultivar trial sites. Missing data on sowing, heading, or maturity dates were estimated based on the corresponding dates for all of the cultivars from the same site and year. If a sowing date was missing, then it was assumed that the sowing dates of all cultivars did not differ (unless stated otherwise in the metadata). If no sowing date was available for a given site and year, then all data were discarded from further analysis. If the heading and maturity dates were missing, then the missing values were estimated using correlation analysis
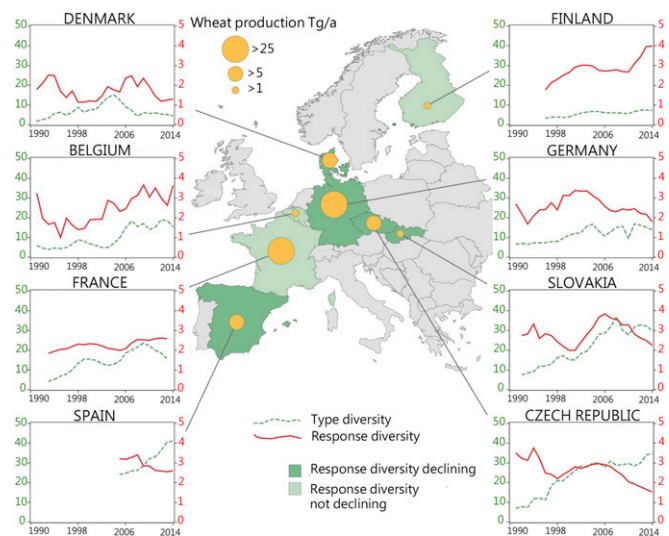

Fig. 1. Decline in climate resilience of wheat on farmers' fields after 2002–2009 in most European countries. The long-term trends of the diversity of the responses to critical weather patterns (response diversity), illustrating the climate resilience and the diversity of cultivars (type diversity). True diversities are shown representing the exponential of the Shannon index [exp(H)] (36, 37). All of the cultivar yield data were utilized ($n = 100,985$).
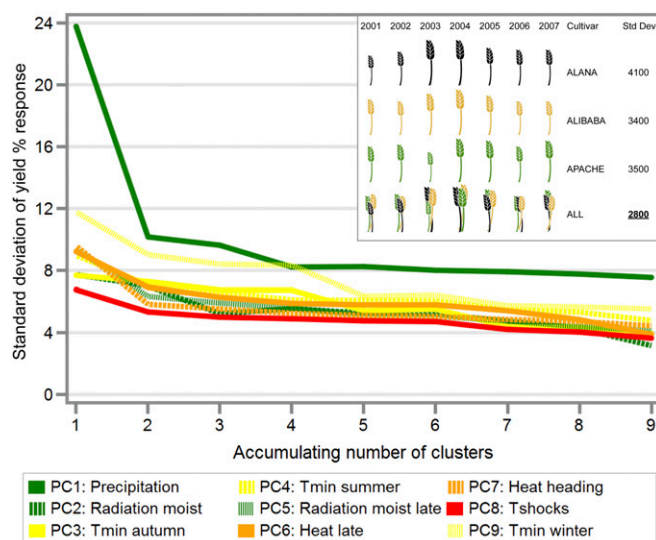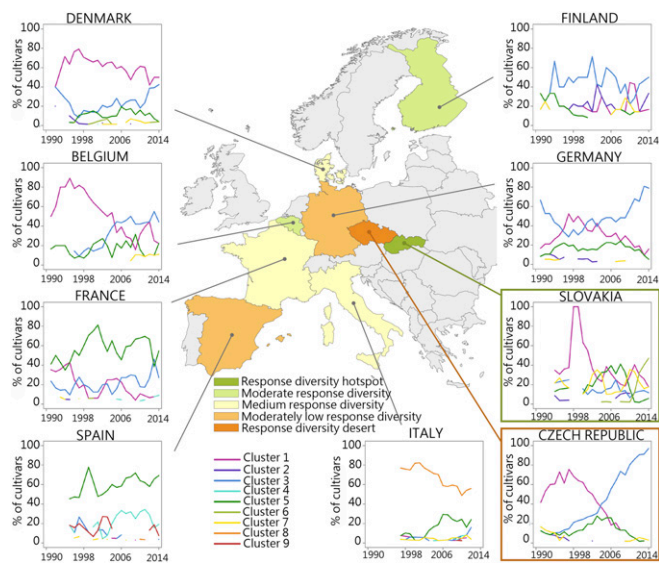
Kahiluoto et al.

Fig. 3. Climate resilience hotspots and deserts of European wheat. The country charts show the percentages of cultivars in each weather response cluster with different responses to weather patterns (agroclimatic PCs) critical to yield in cultivar trials. The colored (green to orange) areas on the map illustrate the response diversity classes based on the proportion of the dominant cluster (>90 to <50%), the number of other simultaneously important clusters (0–4), and the trends. All of the cultivar yield data were utilized ($n = 100,985$).

with overlapping data for the cultivars from the same site across the other seasons. If no overlapping data or limited (five or fewer) data pairs were available, then the heading and/or maturity dates were estimated using the thermal time above 5 °C obtained for the given cultivar from nearby sites and preceding/subsequent seasons. The analysis described below in more detail was based on a previously suggested procedure (25, 26).

Step 2: Estimating Cultivar Yield Responses to the Agroclimatic Variables. The observations for each agroclimatic variable were classified into three categories because the relations between grain yield and the agroclimatic variables were nonlinear in most cases. Some variables were also strongly correlated, leading to multicollinearity in the regression analysis. The random effects of country, site, and year were known to contain most of the variation and thus had to be taken into account. The 40th and 60th percentiles of the distributions of the agroclimatic variables were used to form categories of low, moderate, and high values for each variable. For example, the grain yield observations were divided into groups based on the number of rainy days experienced from sowing to maturity: fewer than 56, between 56 and 68, and above 68. The interaction of these categories with the grain yield of each of the 991 cultivars was analyzed using the following mixed model:

$$y_{ijklmn} = \mu + \text{cultivar}_i + \text{category}_j + \text{cultivar} \times \text{category}_{ij} + \text{treated}_k + \text{country}_l$$
$$+ \text{site}_m + \text{year}_n + \text{treated} \times \text{country} \times \text{site} \times \text{year}(\text{category})_{jklmn} + \varepsilon_{ijklmn},$$

where y_{ijklm} is the observed yield (annual yield), μ is the intercept, cultivar_i is the average yield level of the ith cultivar, category_j is the average yield level at the jth level of the categorized environment, $\text{cultivar} \times \text{category}_{ij}$ is the cultivar-by-environment interaction, and treated_k refers to the use of pesticides. All of the above effects are fixed in the model. Country_l, site_m, year_n, and the interaction of $\text{treated} \times \text{country} \times \text{site} \times \text{year} (\text{category})_{jklmn}$ are random effects of the lth country, mth experimental site, and nth year within the jth category.

For each cultivar and agroclimatic variable, the relative difference in yield between the extreme categories (high–low) was calculated. The relative difference was used to balance the differences between the yield levels of cultivars, although using the simple difference led to similar results. These data consisted of the grain yield responses of 991 cultivars to 43 agroclimatic variables. For example, the relative difference of the estimated yields of each cultivar that experienced fewer than 56 rainy days from sowing to maturity and the estimated yields of each cultivar that experienced more than 68

rainy days from sowing to maturity was calculated. Consequently, a positive grain yield response implied a positive effect of numerous rainy days.

Step 3: Grouping the Responses to the Agroclimatic Variables Using PCA. PCA was used to identify a simplified structure that best explained the variance in the data on the yield responses of the cultivars to agroclimatic variables. We also established the agroclimatic variables that behaved in similar ways. The first PC (i.e., agroclimatic factor) always accounts for most of the variability, and the last PC accounts for the least variability; therefore, only a few PCs are needed to contain most of the information. PCs with eigenvalues above one were retained, and the last PC was deleted based on interpretation and cross validation (27, 28). Nine PCs explained 70% of the total variation (varied from 15 to 5%). An orthogonal varimax rotation was used to achieve a more meaningful and interpretable solution. An oblique promax rotation was also tested but was found unnecessary based on relatively low correlations between PCs. The sampling adequacy, tested with the Kaiser–Melkin–Olkin (KMO) measure, was middling, with a KMO value of 0.77 (29).

We excluded 149 cultivars that were missing more than one-third of the yield response observations to the 43 agroclimatic variables to reduce the number of imputations and thus to improve reliability. A small number of cultivars ($n = 17$) were excluded as outliers because their score for one of the significant PCs was more than six SDs beyond the sample mean score (30). Multiple imputations (MI) with 100 replicates for missing data (10%) were used to obtain the PC scores, which were used to further analyze each cultivar. A multivariate normal approach via the Markov chain Monte Carlo method was used for the MI. The effects of the imputations on the PCA structure were studied by basing the PCA on a correlation matrix without imputations and were found to be negligible. Therefore, the imputations were retained in the data, and the PC scores calculated using the regression method were used in further analyses (31). PC scores were left unstandardized to give less weight to a possible noise element and decrease the sensitivity of the clustering results to the number of PCs retained (32). The effects of standardization and the use of truncated Mahalanobis distances were also examined but were found less interpretative.

Step 4: Clustering Cultivars Based on the Agroclimatic PC Scores. We clustered the cultivars based on their yield responses to agroclimatic variables (step 2). Clustering was based on the PC scores, calculated as a byproduct of PCA (step 3). The cultivars were clustered with Ward's (33) method, which starts with n clusters of size one and continues until all of the observations are included in one cluster. The squared Euclidean distances between data points were used. The number of clusters (nine) was selected based on the dendrogram, the pseudo t^2 criterion, and the variation in R^2 values (34). PC loadings (obtained in step 3) were used to weight the average yield responses to the agroclimatic variables (18). The PC loadings were squared and divided by the eigenvalue of each PC. Therefore, $\sum_{i=1}^{n} w_i = 1$, where n is the number of agroclimatic variables and component loadings. The weighted means and SEs were calculated according to the following equation:

$$\bar{x} = \frac{\sum_{i=1}^{n} w_i x_i}{\sum_{i=1}^{n} w_i}, \; SE = \sqrt{\frac{\sum_{i=1}^{n} w_i (x_i - \bar{x})^2}{n}},$$

where w_i is the weight and x_i is the average yield response to the ith agroclimatic variable.

The connection between the interannual stability of the yield and response diversity was investigated by calculating the relationship between the variation in the yield response to each of the nine PCs and the accumulated number of clusters. The pooled SDs, which are weighted averages of the SDs for several clusters, were calculated for the number of accumulated clusters from one to nine based on the dendrogram. For example, when eight clusters were compared with nine, only one of the former clusters was divided, and all others remained unchanged. The pooled SD was calculated as follows:

$$SD_{pooled} = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2 + \dots + (n_k - 1)s_k^2}{n_1 + n_2 + \dots + n_k - k}}, k = 1, \dots, 9,$$

where s is the SD of the kth cluster and n is the number of cultivars of the kth cluster.

Step 5: Assessing Response Diversity. The annual Shannon diversity index (H), which reflects the richness and evenness (35) of the distribution (36), was calculated for the cultivated area of cultivars (cultivar diversity) and for the clusters (response diversity) in every country, because the weather extremes relative to the phenological stages of wheat appear nationally rather than

Kahiluoto et al.

throughout Europe. The statistics on the national cultivation areas for cultivars in Finland, Denmark, Belgium, France, Germany, Czechia, and Spain apart from Andalusia during the period from 1991 to 2014 were utilized. In addition, the annual response diversities were calculated based on the relative number of cultivars in each cluster in the trials by country. A Shannon index equal to zero indicates that only one cultivar (or cluster) was cultivated in the country; the Shannon index increases as the number of cultivars or clusters (richness) and/or the evenness of the distribution of hectares or trials among them increases. The Shannon index gives an equal weight to each observation and is comparable among cases with different compositions (35, 36). The Shannon index was calculated according to the following equation:

$$H_i = -\sum_{k=1}^{K} \frac{w_{ik}}{W_i} ln \frac{w_{ik}}{W_i}, i = 1, \ldots, n,$$

where n refers to the number of countries, $k = 1, \ldots, K$ refers to the number of clusters; w_{ik} is the area cultivated by cluster k in country i; W_i represents the total area cultivated in country i; and w_{ik}/w_i is the proportion of area cultivated by cluster k. Indices were interpreted based on the exponent of the Shannon index, which is the true diversity (i.e., the effective number of cultivars or response clusters). On this scale, a community with a true diversity four times larger than that of another community is four times as diverse as the other community (37).

All statistical analyses applied the procedures MIXED, FACTOR, MI, SCORE, DISTANCE, and CLUSTER in SAS (version 9.4; SAS Institute Inc.).

Results and Discussion

Temporal Development of Response Diversity in Farmers' Fields. We found that the diversity of yield responses to weather patterns that are critical to yield (i.e., the proxy for the climate resilience of crops) is declining in farmers' wheat fields in most European countries. A rapid remedy is not expected because the trend of response diversity in the cultivar trials was not much better. In farmers' fields, the overall diversity of responses to weather began to decline in the first decade of the millennium (country-level P values <0.001 if not specified), with the sharpest decline occurring in Czechia since 2002 (Fig. 1). The decline in Germany began in 2003, in Spain in 2005 or earlier (data not available), in Slovakia in 2006, and in Denmark in 2009 ($P = 0.023$), leading to the lowest response diversity among the countries. The response diversity also showed a continuous declining trend from 1991 to 2014 in Czechia. This development may have contributed to the stagnation and increased variability in wheat yields in most of Europe during the same period, which has been mainly attributed to climate change (38–40). The only country with a recent increase in response diversity was Finland, which also exhibited the greatest response diversity (Fig. 1) and no observed increase in yield variability (40) despite the lowest number of cultivars (*Materials and Methods*) among the countries. Through the entire period from 1991 to 2014, the response diversity slightly increased in Finland, Belgium, and France ($P < 0.001$), but since 2006 Belgium was characterized by sharp variations and no increase ($P = 0.35$), and there was no clear evidence of an increase after 2008 in France ($P = 0.13$).

The diversity of crops in response to weather represents climate resilience, as confirmed by our data on the relation between the accumulated number of weather response clusters of cultivars and the interannual yield variability, as shown in Fig. 2. The decline in yield variance due to response diversity depended on cultivar, location, and year. Even if the response diversity of wheat generally declined, the diversity of wheat cultivars grown (i.e., type diversity) tended to slightly increase in the farmers' fields in most countries (Fig. 1). For the R^2 values associated with the weather patterns (PCs) see *SI Appendix*, Fig. S1, and for the critical agroclimatic variables see *SI Appendix*, Table S2.

Temporal Development of Response Diversity in Cultivar Trials. We identified a general declining trend in the response diversity of wheat cultivars not only in the farmers' fields but also in the cultivar trials. The decline was smaller and less consistent in the

trials than that in farmland, indicating an unexploited potential to draw upon the cultivars tested in the countries. The yield responses of the nine weather response clusters of cultivars identified (*SI Appendix*, Table S1) to the nine critical weather patterns determined as the agroclimatic principal components (PCs) (*SI Appendix*, Table S2) varied from +12 to −56% (*SI Appendix*, Fig. S1). The total number of weather response clusters of wheat cultivars in European trials increased until 1999, remained constant until 2004, and thereafter gradually declined. The total number of cultivars increased until 2001 and began to decline in 2009. As exceptions to this trend, the low number of cultivars in Finland has remained constant, and the strong increase with mainly United Kingdom-originating cultivars in Denmark abruptly and sharply declined from 80 cultivars in 2000 to ∼25 mainly Danish cultivars in 2014. The sharp decline in Denmark was promoted by wheat yield losses due to an exceptionally warm winter of 2007 with late incidents of frost (41). This event led to replacement of the foreign cultivars with local ones, likely contributing to the decline in response diversity.

Temporal Development of Weather Response Clusters. In the available sets of cultivars in northern and central Europe, a shift toward yield stability and benefit from late high solar radiation and less penalty from late heat and precipitation (cluster 3 replacing clusters 1 and 5) occurred as a response from breeders to the increased average temperatures during the late growing seasons of the 2000s (40). In contrast, in southern countries after 2000, a cluster that suffers from high minimum temperatures in summer, early drought, and heat at heading (cluster 5) more than the previously dominant clusters took over, aggravating the risk to yield loss (42). This development cannot be explained as a response of cultivar selection to climate change but may rather represent unintentional adverse side effects to selection for other traits. The response to rain appears to be a sneaking risk for the entire continent: No single wheat cultivar cluster responded positively to abundant precipitation (*SI Appendix*, Fig. S1). Wheat yield is generally sensitive to even a few days of exposure to water logging (43) and to wet weather that favors diseases and thus results in low yield (41). The yields of individual cultivars under scarce precipitation were even doubled compared with those under abundant precipitation (PC1 in *SI Appendix*, Fig. S1). These empirical findings are in line with simulations that suggested that heat stress rather than drought sensitivity is the limiting factor to the adaptation of wheat to climate change in Europe (42).

Resilience Deserts and Hotspots. We found a low diversity of weather response clusters—a response diversity "desert"—in trials of Czechia; smaller deserts were detected in Germany and Spain, and a durum wheat desert was found in Italy (Fig. 3 and *SI Appendix*, Fig. S1), which is the main durum producer in the world and is where most (1.6 million ha) of European durum wheat is cultivated. A single cluster (cluster 8) with all 44 durum wheat cultivars with >20 observations (apart from three durum cultivars in cluster 7 and one cultivar in cluster 3) dominated Italy. Durum suffers from heat at heading and high winter temperatures because cold temperatures are required for vernalization in the Italian durum germplasm (44). There is also an alarming similarity among northern and central European countries (apart from Slovakia), as well as among the southern European countries, in the development of the dominant weather response clusters of wheat cultivars (Fig. 3).

A response diversity hotspot was found in Slovakian cultivar trials, including one promising unique cluster (cluster 6) and a cluster currently nearly unique (cluster 7) to Slovakia.

In particular, the members of the currently most common cluster 6 benefited from high radiation, avoidance of drought, and warm autumn and winter, and a single cultivar in cluster 7 benefitted from above-average precipitation. All these characteristics

represent positive responses to weather patterns, which European clusters generally suffered from or did not respond to (*SI Appendix*, Fig. S1). This and other observed complementarities could be exploited to enhance resilience through cultivation and breeding. However, the properties of the cultivars that were adapted to different conditions, such as day length, maritime versus continental conditions, and length of the growing season, limit their utilization across Europe.

Possible Causes of Decline and Differences in Response Diversity. Repeated selection for few desirable characteristics from a continuously homogenizing and declining cultivar or genetic pool could be the reason for the observed decline in response diversity. While no genetic erosion in terms of loss of alleles was observed for wheat before the 1990s (45, 46), such a decline in alleles was found for durum after that period (47) and such a decline cannot be excluded for wheat in general. An activity called "face-lifting" of cultivars by breeders was identified as the cause of the decline in response diversity of Finnish barley in the main cultivation areas (17, 48). The homogenization of the genetic pool could be a consequence of a lack of incentives for breeders to introduce divergent material with uncertain benefits. The observed decline in response diversity coincides with an increasing dominance of crop improvement by private breeders, which accelerated in Europe around 2000. Increased competition and demand for cost efficiency increases the pressure for a shortened breeding cycle, irrespective of technology developments, and may contribute to the greater similarity among new cultivars launched in the market (48, 49). Periods of cultivar import from surrounding countries varied with a focus on local breeding in Belgium and led to a high diversity in weather responses. Conversely, a turn to mainly local cultivar selection in Denmark narrowed the response diversity and thus reduced the climate resilience of this export-oriented agricultural country.

The obvious explanation for the alarming decline and gaps in response diversity in European wheat is the absence of the explicit perspective of resilience to intensifying climatic variability and extremes in the wheat value chain. The prioritization of the yield potential of individual cultivars under current or projected average long-term climatic conditions, with a focus on harvest index and disease resistance (39), may have been influenced by early climate projections that did not consider uncertainty and variability. Since crop responses are nonlinear and exhibit thresholds in yield and quality (50) and the climatic variability is increasing (2), the benefit of response diversity will be even greater than that suggested by past yield data. An enhancement of response diversity through increased awareness of the significance of diversity in weather responses within the available set of cultivars is therefore of primary importance for wheat production and food security.

Enhancing Climate Resilience of European Wheat Through Response Diversity. There appears to be greater cultivar diversity in the trials at the European (*SI Appendix*, Fig. S1) than at the country level, but the substantial differences in conditions aggravate the direct utilization of cultivars across Europe. Funding for targeted research and an economic incentive to companies to utilize more cultivars from the European list of approved cultivars might diversify the cultivars used in national trials. Specific parts of wheat genome were also shown responsible, for example, for temperature response (51), which can be used in breeding a wheat cultivar portfolio with sufficient response diversity for Europe. Yield losses due to weather are currently not recorded in cultivar trials, which creates a tendency to not learn from the diversity of responses to weather variability. An option for immediate improvement thus is to document yield losses due to extreme weather events, and perhaps include them in a separate analysis.

The costs to breed a selection of genuinely different cultivars are likely higher than the costs to breed a homogenous selection. A broader selection also poses additional costs to traders even if indirect benefits through lower risks and reduced contract area requirements may also follow. For farmers, several cultivars do not necessarily cause additional costs but may even temporally equalize work demand. The benefits from response diversity may be greatest to the weakest actors in the wheat supply chain, such as farmers (yield stability) and disadvantaged consumers (price stability), while the public actor in charge of food security might benefit most. The development in response diversity of wheat appeared, indeed, less alarming in countries with traditions in private–public breeding partnerships such as Finland and Belgium, while in Germany, with low response diversity, private breeders have dominated for more than a century.

Farmers' demand could act as the incentive to breeders to diversify weather responses among wheat cultivars, but farmers currently focus on yield potential and quality. There is, however, no inherent trade-off between yield potential and diversity in weather responses. Yield stability is a complementary breeding goal in addition to yield potential and the average yield in the long term. While the example given here (Fig. 2) is mainly illustrative, in Finnish regions with high barley cultivar diversity where yield variations among years were low, also the average yield was greater than that in the regions with low cultivar diversities (52). Risk aversion varies among farmers, but the notable share (46%) of yield-independent subsidies in farm income in Europe (10) acts as a disincentive to innovations for yield security. For instance, the subsidies in Czechia are lower than in most European Union countries, and most of the farmland is rented, which creates a notable cost relative to the subsidies. Consequently, the demand by farmers for drought-resistant cultivars is clearly articulated in that country. Therefore, a cultivar portfolio with diversity in responses to weather could be a prerequisite for subsidies or loss compensation to farmers, and for a reduced price of an insurance.

The main challenge for enhancing the diversity in crop responses to weather events and thus the climate resilience lies in the required shift of the perspective to cover this aspect. The actors in wheat supply chains must shift the focus from individual cultivars and yield potential in good conditions to a portfolio of cultivars to include complementary responses to critical weather events. The lack of awareness and experience of the diversity approach keeps the focus on individual cultivars, which have a more limited yield stability potential than a portfolio of cultivars with diverse responses. The shift in perspectives toward resilience could be achieved through simple tools to demonstrate and communicate the diversity in cultivar responses between breeders, farmers, and traders (48), good examples rewarded by recognition (53), and "learning-by-doing" facilitated by the economic incentives or, likely most effectively, regulation. Initiating a dialogue within wheat value chains, for example by national emergency supply agencies, involving also research and policy makers, could help enhance the resilience of wheat supply chains and food systems (54). Diversity in responses provides a practical means to enhance robustness under weather variability and adapt to the uncertainty in climate change through portfolios of not only cultivars but also crops (18) and even marketing channels (17).

Conclusions

This assessment suggests that current breeding programs and cultivar selection practices do not sufficiently prepare for climatic uncertainty and variability. Human feedback to coupled social–ecological systems, such as agriculture and food systems, depends on institutional arrangements. Strong institutions can assist farmers and managers in breeding and seed trading companies to shift crop-yield-related tipping points induced by intensifying climate variability and price volatility and thus protect

the stability (55) of the European wheat, as well as other staple food crops around the world.

The national action plans and the Common Agricultural Policy of the European Union are instrumental to removing the current disincentives and introducing new incentives and regulation for diversity in crop responses to climatic uncertainties. However, regulation needs to imply sufficient flexibility to allow adaptive management and continuous collective learning. The European Commission might include effective diversification through assessment and management of response diversity in its toolkit of risk management measures for the use by the member states to support viable farm income and resilience to enhance food security (56).

Research is needed to advance the understanding of the genetic basis to yield and quality response to weather (51). Furthermore, the costs of the portfolio approach and benefits to security need to be quantified for communication of the value added and targeting the economic incentives in the value chain. The institutions should primarily facilitate overcoming the perceived uncertainty in costs and benefits before sufficient experiences are gathered for the transition (57) toward resilient cultivar choices. The approach of response diversity can be applied to counteract the observed decline of the resilience in food systems (12) under social–ecological volatility and uncertainty.

1. Rötter RP, et al. (2013) Modelling shifts in agroclimate and crop cultivar response under climate change. *Ecol Evol* 3:4197–4214.
2. Coumou D, Rahmstorf S (2012) A decade of weather extremes. *Nat Clim Chang* 2:491–496.
3. Trnka M, et al. (2014) Adverse weather conditions for European wheat production will become more frequent with climate change. *Nat Clim Chang* 4:637–643.
4. Challinor AJ, et al. (2014) A meta-analysis of crop yield under climate change and adaptation. *Nat Clim Chang* 4:287–291.
5. Asseng F, et al. (2015) Rising temperatures reduce global wheat production. *Nat Clim Chang* 5:143–147.
6. Ray DK, Gerber JS, MacDonald GK, West PC (2015) Climate variation explains a third of global crop yield variability. *Nat Commun* 6:5989.
7. Tadesse G, Algieri B, Kalkuhl M, von Braun J (2014) Drivers and triggers of international food price spikes and volatility. *Food Policy* 47:117–128.
8. Maxwell D (2012) Food security and its implications for political stability: A humanitarian perspective. FAO High Level Expert Forum on Addressing Food Insecurity in Protracted Crises (FAO, Rome).
9. FAO (1996) Rome Declaration on World Food Security (FAO, Rome).
10. European Commission (2017) The future of food and farming. Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions, 29.11.2017 COM 713, final (Commission of the European Communities, Brussels).
11. Food and Agricultural Organization of the United Nations (FAO) (2017) FAOSTAT. Available at www.fao.org/faostat/en/#data. Accessed February 7, 2017.
12. Suweis S, Carr JA, Maritan A, Rinaldo A, D'Odorico P (2015) Resilience and reactivity of global food security. *Proc Natl Acad Sci USA* 112:6902–6907.
13. Stone J, Rahimifard S (2018) Resilience in agri-food supply chains: A critical analysis of the literature and synthesis of a novel framework. *Supply Chain Manag* 23:207–238.
14. Carpenter S, Walker B, Anderies M, Abel N (2001) From metaphor to measurement: Resilience of what to what? *Ecosystems* 4:765–781.
15. Folke C, et al. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. *Annu Rev Ecol Evol Sci* 35:557–581.
16. Elmqvist, et al. (2003) Response diversity and ecosystem resilience. *Front Ecol Environ* 1:488–494.
17. Kahiluoto H, et al. (2014) Cultivating resilience by empirically revealing response diversity. *Glob Environ Change* 25:186–193.
18. Mäkinen H, Kaseva J, Virkajärvi P, Kahiluoto H (2015) Managing resilience of forage crops to climate change through response diversity. *Field Crops Res* 183:23–30.
19. Hajkowicz S, et al. (2012) Food price volatility and hunger alleviation–Can Cannes work? *Agric Food Secur* 1:8.
20. Galtier F (2013) Managing food price instability: Critical assessment of the dominant doctrine. *Glob Food Secur* 2:72–81.
21. Portmann FT, Siebert S, Döll P (2010) MIRCA2000–Global monthly irrigated and rainfed crop areas around the year 2000: A new high-resolution data set for agricultural and hydrological modeling. *Global Biogeochem Cycles* 24:GB1011.
22. Porter JR, Gawith M (1999) Temperatures and the growth and development of wheat: A review. *Eur J Agron* 10:23–36.
23. Trnka, et al. (2011) Agroclimatic conditions in Europe under climate change. *Glob Change Biol* 17:2298–2318.
24. Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. *Weed Res* 14:415–421.
25. Hakala K, et al. (2012) Sensitivity of barley varieties to weather in Finland. *J Agric Sci* 150:145–160.
26. Mäkinen H, Kaseva J, Virkajärvi P, Kahiluoto H (2017) Shifts in combinations of soil and climate deserve attention. *Agric Meteorol* 234–235:236–246.
27. Kourti T, MacGregor JF (1995) Process analysis, monitoring and diagnosis, using multivariate projection methods. *Chemom Intell Lab Syst* 28:3–21.
28. Kourti T, MacGregor JF (1996) Multivariate SPC methods for process and product monitoring. *J Qual Technol* 28:409–428.
29. Kaiser HF (1970) A second generation Little Jiffy. *Psychometrika* 35:401–415.
30. Wang D, et al. (2009) Comparison of methods for correcting population stratification in a genome-wide association study of rheumatoid arthritis: Principal-component analysis versus multidimensional scaling. *BMC Proc* 3:S109.
31. DiStefano C, et al. (2009) Understanding and using factor scores. *PARE* 14:1–11.
32. Mimmack GM, Mason SJ, Galpin JS (2001) Choice of distance matrices in cluster analysis: Defining regions. *J Clim* 14:2790–279.
33. Ward JH (1963) Hierarchical grouping to optimize an objective function. *J Am Stat Assoc* 58:236–244.
34. Yeo D, Truxillo C (2005) *Applied Clustering Techniques Course Notes* (SAS Institute Inc., Cary, NC).
35. Mulder CPH, et al. (2004) Species evenness and productivity in experimental plant communities. *Oikos* 107:50–63.
36. Shannon CE, Weaver W (1949) *The Mathematical Theory of Communication* (University of Illinois, Urbana, IL).
37. Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
38. Brisson N, et al. (2010) Why are wheat yields stagnating in Europe? A comprehensive analysis for France. *Field Crops Res* 119:201–212.
39. Lin M, Huybers P (2012) Reckoning wheat yield trends. *Environ Res Lett* 7:1–6.
40. Peltonen-Sainio P, Jauhiainen L, Hakala K (2009) Are there indications of climate change induced increases in variability of major field crops in the northernmost European conditions? *Agric Food Sci* 18:206–222.
41. Kristensen K, Schelde K, Olesen JE (2011) Winter wheat yield response to climate variability in Denmark. *J Agric Sci* 149:33–47.
42. Semenov MA, Shewry PR (2011) Modelling predicts that heat stress, not drought, will increase vulnerability of wheat in Europe. *Sci Rep* 1:66.
43. Malik AI, Colmer TD, Lambers H, Setter TL, Schortemeyer M (2002) Short-term waterlogging has long-term effects on the growth and physiology of wheat. *New Phytol* 153:225–236.
44. Motzo R, Giunta FG (2007) The effect of breeding on the phenology of Italian durum wheats: From landraces to modern cultivars. *Eur J Agron* 26:462–470.
45. van de Wouw M, Kik C, van Hintum T, van Treuren R (2010) Genetic erosion in crops: Concept, research results and challenges. *Plant Genet Resour* 8:1–15.
46. van de Wouw M, van Hintum T, Kik C, van Treuren R, Visser B (2010) Genetic diversity trends in twentieth century crop cultivars: A meta analysis. *Theor Appl Genet* 120:1241–1252.
47. Hekrar F, et al. (2016) Genetic diversity reduction in improved durum wheat cultivars of Morocco as revealed by microsatellite markers. *Sci Agric* 73:134–141.
48. Paavola S, Himanen SJ, Kahiluoto H, Miettinen R (2016) Making sense of resilience in barley breeding: Converting the concept of response diversity into a tool of reflection and decision-making. *Climate Change Adaptation and Food Supply Chain Management*, eds Paloviita A, Järvelä M (Routledge, Abingdon, UK), pp 43–54.
49. Tripp R (2002) Can the public sector meet the challenge of private research? Commentary on "Falcon and Fowler" and "Pingali and Traxler". *Food Policy* 27:239–246.
50. Porter JR, Semenov MA (2005) Crop responses to climatic variation. *Philos Trans R Soc Lond B Biol Sci* 360:2021–2035.
51. Juhász A, et al.; International Wheat Genome Sequencing Consortium (2018) Genome mapping of seed-borne allergens and immunoresponsive proteins in wheat. *Sci Adv* 4:r8602.
52. Himanen SJ, et al. (2013) Cultivar diversity has great potential to increase yield of feed barley. *Agron Sustain Dev* 33:519–530.
53. Moran D, Lucas A, Barnes A (2013) Mitigation win-win. *Nat Clim Chang* 3:611–613.
54. Himanen SJ, Rikkonen P, Kahiluoto H (2016) Codesigning a resilient food system. *Ecol Soc* 21:41.
55. Horan RD, Fenichel EP, Drury KLS, Lodge DM (2011) Managing ecological thresholds in coupled environmental-human systems. *Proc Natl Acad Sci USA* 108:7333–7338.
56. European Commission (2018) EU budget: The common agricultural policy beyond 2020. Fact sheet. CAP-Memo 18–3974 (Commission of the European Communities, Brussels).
57. Boona WPC, Moorsa EHM, Meijer AJ (2014) Exploring dynamics and strategies of niche protection. *Res Policy* 43:792–803.