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META-ANALYSIS

Cultivar mixtures increase crop yields and temporal yield stability globally. A meta-analysis

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Abstract

Cultivar mixtures have been proposed as a way to increase diversity and thereby improve plant production, but our understanding of the effects of mixing cultivars on crop diseases and resource-use efficiency remains fragmentary. We performed a meta-analysis to assess the effects of cultivar mixtures on crop yield, yield stability, resource-use efficiency, and disease severity compared with monocultures of twelve major crops. We found that, overall, mixing of cultivars increased crop yield by 3.82%. Yield gains from mixing cultivars were highest in rice (+16.1%), followed by maize (+8.5%), and were lowest in barley (+0.9%) and sorghum (no increase). Temporal yield stability increased with the number of cultivars in the mixtures. Overall, mixing cultivars increased crop biomass, leaf area index, photosynthetic rate, and Water-use efficiency by 5.1, 7.2, 8.5 and 4.3%, respectively, and decreased disease incidence by 24.1%. Cultivar mixtures were more effective in mitigating diseases and increasing yields in studies performed at lower latitudes, higher mean annual temperatures, and higher mean annual precipitation. Our study complements and adds to previous research, indicating that cultivar mixtures reduce crop losses to disease and enhance resource-use efficiency compared with monocultures globally. We conclude that the targeted use of cultivar mixtures with appropriate management practices can reduce resource and pesticide inputs while maintaining high yields, thereby promoting sustainable and productive agriculture.

Keywords Cultivar mixture · Disease severity · Resourced-use efficiency · Yield and yield stability

1 Introduction

The dominant model of agricultural intensification has been based on agrochemical inputs, large-scale monocultures, and landscape homogenization. Although this approach has produced large amounts of food to feed a growing world population, it has also put enormous pressure on natural resources and the environment (Folberth et al. 2020; Tamburino et al. 2020; Tscharntke et al. 2021), thereby endangering the basis on which agricultural productivity is built. Ensuring food security while maintaining healthy, sustainable ecosystems that can adapt quickly to changing environments is one of the most pressing challenges for agriculture (Hunter et al. 2017).

The use of cultivar mixtures refers to the simultaneous cultivation of at least two cultivars of the same species in the same field (Beillouin et al. 2021) to promote more complementary and efficient use of limited resources such as light, water, and nutrients (Kathju et al. 2003; Kaut et al. 2009; Wang et al. 2016; Grifths and York 2020; Beillouin

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et al. 2021; Schmid and Schöb 2022). This complementarity can reduce competition and allow crops to shift the allocation of resources from competition to grain yield (Wuest et al. 2021), thus enhancing crop yield. In addition, mixtures of cultivars with different resistance genes can increase the complexity and heterogeneity of host resistance, thereby reducing disease outbreaks (Borg et al. 2018; Yang et al. 2019) and thereby the need for pesticide application (Zhu et al. 2000). Cultivar mixtures may provide additional ecological services, such as weed suppression, reduced abundance of pests and increased availability of crop pollinators (Tooker and Frank 2012; Chateil et al. 2013; Barot et al. 2017).

Cultivar mixtures may be a more accessible option for large, mechanized farms than intercropping (mixing of different crop species), as cultivar mixtures provide increased diversity without requiring extensive changes in agronomic practices. Previous meta meta-analyses have shown that cultivar mixtures increased yield by 2.2–3.5% and improve yield stability in some crops and environments (Borg et al. 2018; Reiss and Drinkwater 2018). A major meta-analysis of the effects of cultivar mixtures (Reiss and Drinkwater 2018) did not included rice, a major staple crop on which much research on cultivar mixtures has been conducted. There has been no comprehensive analysis of the effects of mixed sowing on resource efficiency and disease severity for different crops at the global level. In addition, the use of the coefficient of variation (CV) to assess temporal and spatial relative stability in most published studies has been questioned because of the scale-dependence of the CV (Döring and Reckling 2018; Knapp and van der Heijden 2018), and alternative methods have been developed.

We conducted a global meta-analysis of cultivar mixtures vs. monocultures from 103 studies, comparing cultivar mixtures to their component monocultures to determine the effect of cultivar mixing on crop yield, leaf area index (LAI), net photosynthetic rate (Pn), water use efficiency (WUE), disease index (DI), and area under the disease-progress curve (AUDPC). Finally, we analyzed the relationships among environmental factors and the number of mixture components on yield and LAI, Pn, WUE, DI, and AUDPC.

2 Materials and methods

2.1 Data search and collection

We searched the Web of Science (http://apps.webofknowledge.com/) and the China National Knowledge Infrastructure (CNKI, http://www.cnki.net/) for relevant peer-reviewed journal articles, using the terms ‘crop OR variety OR cultivar AND mix OR mixture OR diversity OR intercrop OR blend OR multi-’. We used the following criteria to select publications for our review: (1) the experiment must be a mixed culture of a single species, excluding intercropping of different species; (2) experiment must be conducted in the field (greenhouse and laboratory experiments were excluded); (3) The research must include at least one of the following parameters: yield, Leaf area index (LAI), Net photosynthetic rates (Pn), Water use efficiency (WUE), Disease index (DI) and Area under the disease progress curve (AUDPC; see Supplementary Text 1); (4) the study must report the actual value for all treatments or the ratio of cultivar mixtures compared to component monocultures. When different publications included the same data, we included only the most complete dataset. In addition, we also included datasets from other meta-analysis studies on intraspecific mixed-species diversity (Kiaer et al. 2009; Huang et al. 2012; Reiss and Drinkwater 2018). Compared with previous meta-analysis studies, we have expanded the search article database by including CNKI as well and added more recent literature. We did not include results in which only average yields over treatments, sites or years were presented, because this would preclude calculation of variability, which is central to our analyses. We also included a larger set of response variables than previous meta-analyses, such as biomass, harvest index, grain protein content, LAI, Pn, WUE, DI and AUDPC. The final dataset on cultivar mixtures contained 103 publications (Supplementary Information).

For each selected study, raw data were collected directly from tables and text, including study site (longitude and latitude), mean annual temperature (MAT) and mean annual precipitation (MAP), initial soil properties (include SOC, pH, soil clay content) and mixture composition. While certain indicators, such as the number of days above a specific temperature or without rain and crop growing degree days, have a significant impact on crop growth and production traits, the majority of published studies with field experiments do not provide such detailed information. This limitation hinders a comprehensive meta-analysis, leading us to choose widely used metrics, such as annual average temperature and annual average precipitation in our study. While we acknowledge the limitation of this approach, these parameters have been commonly employed in various meta-analyses and offer a reasonable representation of climate conditions influencing crop performance.

We also categorized the plant traits used to construct mixtures from the component cultivars as either disease or physical or both (Reiss and Drinkwater 2018). Physical characteristics on which creation of mixtures was based included breeding history, heading date, height, lodging susceptibility, growth habit, maturity group, phenotype, and yield potential. Anywhere the authors noted the disease response of a cultivar, such as susceptibility or resistance, we categorized the mixtures as having a disease basis. If the data appeared in the form of a graph, then GetData software (https://getdata-graph-digitizer.software.informer.com/) was used to obtain the values. If the latitude and longitude of the test site were not provided, we used the Baidu map (https://map.baidu.com/) to determine latitude and longitude coordinates based on the location of the nearest city or the experimental station where the study was conducted. In a few cases where only a large geographical area was described in the publication, coordinates were not estimated. The experiments used in the meta-analysis included a wide range of locations across the globe (Fig. S1). If the MAT, MAP and initial soil properties of the test site were not provided, we extracted them for the approximate study locations from the World Clim-global climate data (https://worldclim.org/data/worldclim21.html) and the Harmonized World Soil Database (https://www.fao.org/soils-portal/data-hub/soil-maps-and-databases/harmonized-world-soil-database-v12/en/).

Temporal yield stability was calculated from any study completed over multiple years, while spatial stability was calculated from any study conducted at multiple locations. The coefficient of variation (CV) is frequently used as an index of yield variability, but it may not be appropriate if there is a systematic dependence of the variance (σ^2) on the mean yield (μ) following Taylor's power law. We therefore calculated the POLAR (POwer LAw Residuals) stability index (Döring et al. 2015), which removed the dependence of variance on mean yield. A higher CV or POLAR value indicated higher yield variability and lower yield stability. If there were multiple treatments at one site, we separated these treatments for stability calculations so that additional treatments do not appear to increase variability at a site.

2.2 Meta-analysis

A meta-analysis was used to analyze the responses of crop yield in mixed cropping using MetaWin 2.1. The effect size (lnR) was used (Hedges et al. 1999):

$$\mathrm{lnR} = \ln(\mathrm{X_m}/\mathrm{X_c})$$

where X_m and X_c denote actual and theoretical values for grain yield in mixed stands, respectively.

$$X_c = \sum\nolimits_i^t p_i u_i$$

Where p_i is the proportion of each of the t components in cultivar mixtures, and u_i is the cultivar monocultures yield.

As standard deviations were rarely available in the selected literature, a nonparametric weighting analysis was adopted to include as many studies as possible. The weighting factor for each effect size was calculated according to Pittelkow et al. (2015).

$$W_k = \frac{n_c \times n_m}{n_c + n_m}$$

Where W_k indicates the weight of k effect size, n_c and n_m represent field replicates of cultivar monocultures and mixtures groups, respectively. Mean effect sizes were estimated according to van Kessel et al. (2013):

$$\overline{lnR} = \frac{\sum(lnR_k \times w_k)}{\sum(w_k)}$$

Mean effect sizes and 95% confidence intervals (CI) on the estimated effect size were generated using the bootstrapping test (4999 iterations). If the 95% confidence interval values for the effect size of a variable did not overlap zero, then the treatment effects on the variable studied were considered statistically significant. The means of the categorical variables were considered significantly different if their 95% CIs did not overlap. To ease interpretation, the results for the analyses on lnR were back-transformed and reported as percentage change.

$$E = \left(e^{LnR} - 1\right) \times 100\%$$

We evaluated the presence of publication bias using graphical representations known as funnel plots. Funnel plots are scatter plots with the effect size on the horizontal axis and the standard error on the vertical axis. These plots are commonly employed in meta-analysis to visually assess the distribution of study results. We used the "metafor" package to assess asymmetry in funnel plots based on Egger's regression test in R Version 4.2.2. (Viechtbauer 2010). If the p-value of Egger's regression was more than 0.05 and the funnel plot was symmetric, we concluded that that there was no significant publication bias (Liu et al. 2023). In addition, we used the "stats" package in R for the correlation analysis. Principal component analysis was performed using CANOCO 4.5. To further quantify the relative importance of climate conditions, crop type, and initial soil properties, a random-forest approach was used by using the "rfPermute" packages in R.

3 Results

3.1 The effect of cultivar mixtures on yield and yield stability

The overall effect size of cultivar mixtures (2–9, but mostly <5 cultivars) on yield (grain for cereals, seed for legumes, sucrose for sugar beets) ranged from −0.58 to +0.87, with the mean effect size of 0.038. There was no significant publication bias for yield in our paper according to Egger's regression (Fig. S2). Of the 2539 comparisons in the dataset, 65% (1657) showed higher yield in mixed sowing (Fig. 1a). All crops, except sorghum, had significant increases in yield (Fig. 1e; Table S2). Wheat, with the largest number of comparisons (1,439), had an average 4.07% yield increase in cultivar mixtures. Rice had the largest yield increase (16.14%) (Fig. 1).

The effect size of cultivar mixtures on aboveground biomass was 0.050 (CI: 0.037, 0.063), and 78% had higher biomass in mixed sowing than monocultures in the dataset (Fig. 1b). Cultivar mixing significantly increased the Harvest Index (ratio of grain yield to aboveground biomass) by 0.025 (CI: 0.007, 0.045), and 60% of the comparisons showed a higher Harvest Index in mixed sowing than in monoculture (Fig. 1c). The effect size of cultivar mixtures on grain protein concentration was 0.005 (CI: 0.0003, 0.010), and 60% of the comparisons showed higher grain protein content in mixed sowing than monocultures (Fig. 1d).

Temporal ($R^2 = 0.013$, $P = 0.001$) and spatial CV ($R^2 = 0.021$, $P = 0.006$) decreased with an increase in the number of cultivars in the mixtures (Fig. 2a, c). Temporal POLAR decreased with increasing the number of cultivars in the mixtures, however, spatial POLAR did not (Fig. 2b, d).

3.2 Cultivar mixing and measures of resource utilization efficiency

Cultivar mixing increased Pn, LAI and WUE, by 8.48% (confidence interval, CI: [5.80, 11.64]), 7.22%, CI: [5.49, 9.07], and 4.30%, CI: [1.17, 7.30]), over monocultures, respectively (Fig. 3a). WUE, LAI and Pn were higher in mixtures than in monocultures (Fig. 3), and yield increased with each of these variables ($P < 0.001$; Fig. 3b-d, Table 1). Biomass increased with LAI ($P < 0.001$; Table 1) but decreased with WUE ($P = 0.001$; Table 1). Harvest Index increased with WUE ($P < 0.001$; Table 1). There was no significant publication bias for Pn, LAI and WUE in our paper according to Egger's regression (Fig. S2).

3.3 The effect of cultivar mixing on measures of plant disease

Plant disease was 24.14% (DI; CI: [–28.81, –19.56]) to 13.93% (AUDPC; CI: [–17.74, –9.93]) lower in mixtures than in monocultures (Fig. 4a). There was a negative relationship between the change in yield and DI ($P = 0.003$;

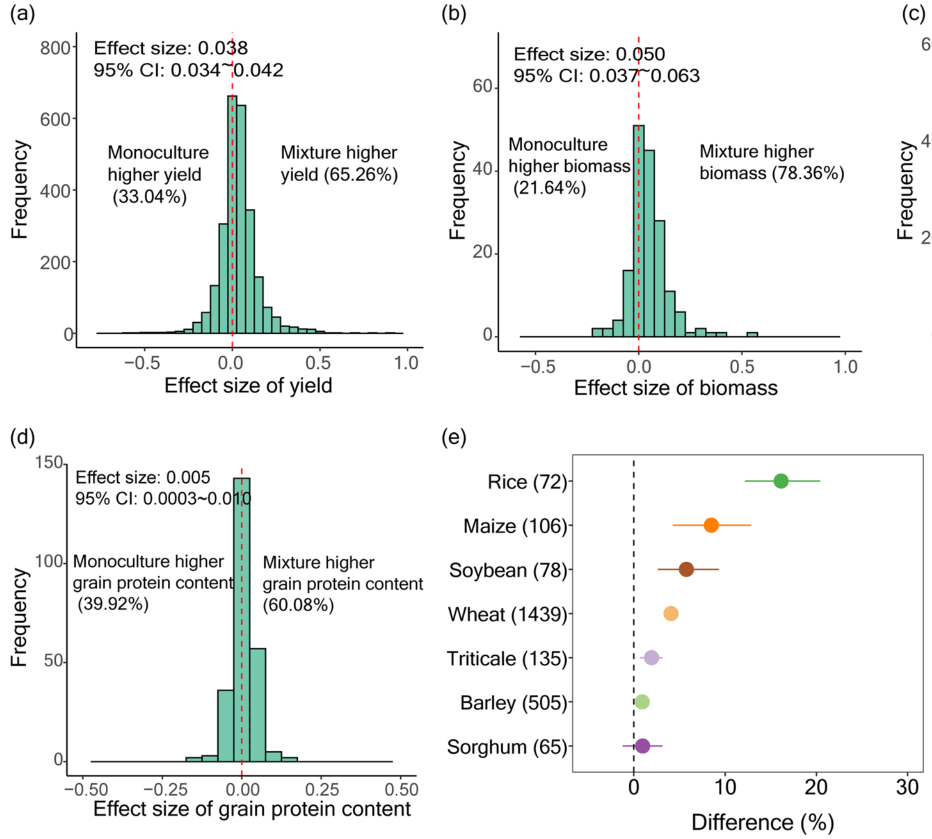

Fig. 1 Effect sizes of cultivar mixtures vs. monocultures on (**a**) yield, (**b**) biomass, (**c**) harvest index, and (**d**) grain protein content. (**e**) Difference in yield between mixtures and monocultures for major crops on which there were 4 or more published studies, ranked by mean effect. Values are mean effect sizes and error bars show the 95% CI. The number of observations for each category is shown in parentheses. The mean effect sizes were considered significant if the 95% CI does not include zero. For details see Tables S1 and 2.

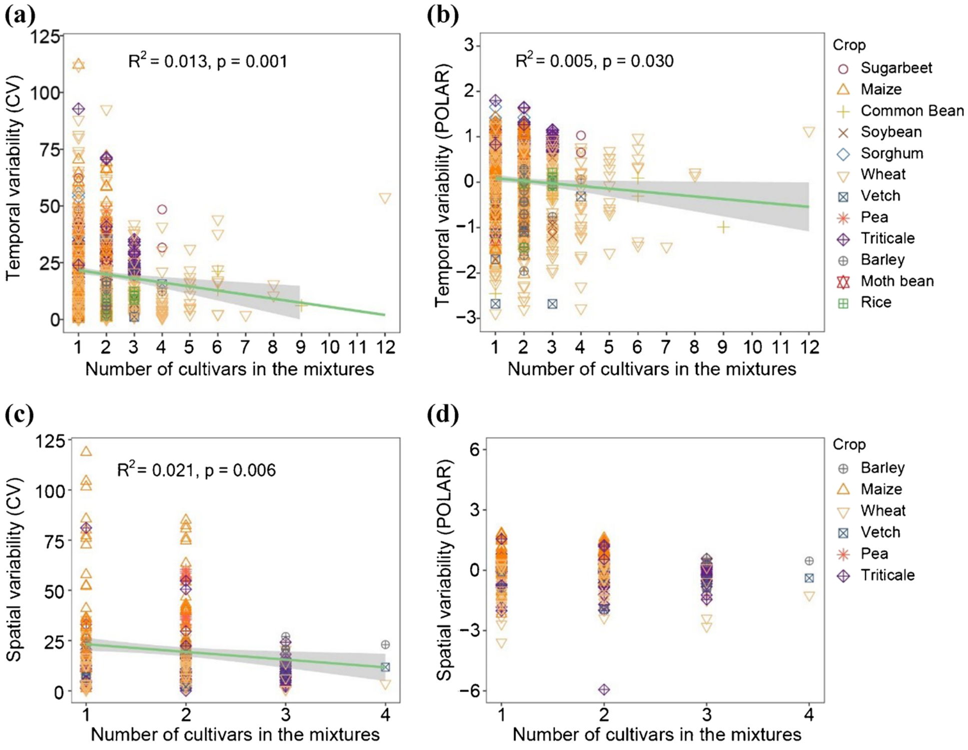

Fig. 2 | Yield variability versus number of cultivars in mixtures (1 = monoculture). **a**, **c** Relationships between the number of cultivars in the mixtures and the relative variability (based on coefficient of variation [CV]) across years (**a**) and sites (**c**). **b**, **d** Relationships between the number of cultivars in the mixtures and the relative variability (based on the POLAR value) across years (**b**) and sites (**d**). A higher CV or POLAR value indicated higher yield variability and lower yield stability. Moth bean (*Vigna aconitifolia* (Jacq.) Marechal), also known as matki or dew beans, are a type of legume native to India.

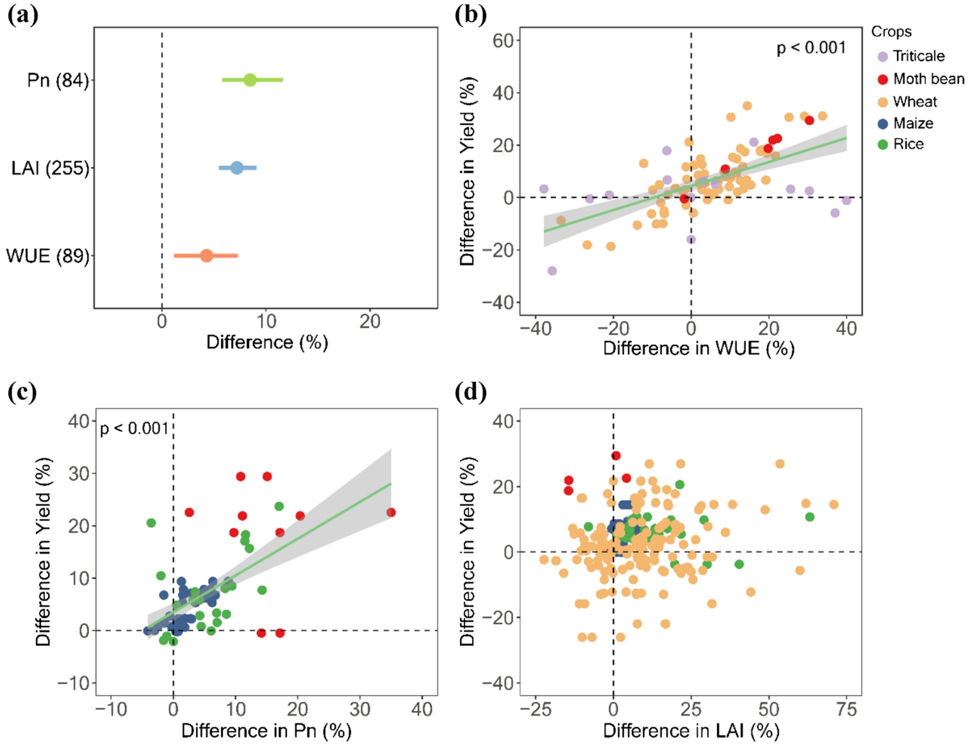

Fig. 3 Comparison in net photosynthesis rate (Pn), leaf area index (LAI) and water use efficiency (WUE) in cultivar mixtures and monocultures. (**a**) Difference in WUE, Pn, and LAI between mixtures and monocultures. Values are mean effect sizes and error bars show the 95% CI. The number of observations for each category is shown in parentheses. The mean effect sizes are considered significant if the 95% CI does not include zero. (**b**)–(**d**) Relationships between the difference between mixtures and monocultures in yield and in WUE (**b**), Pn (**c**), and LAI (**d**). For more detail see Table S3.

Table 1 Relationships between yield, biomass, and harvest index and net photosynthesis rate (Pn), leaf area index (LAI), and water use efficiency (WUE).

	Yield		Biomass		Harvest index	
	Regression coefficient	*P*-value	Regression coefficient	*P*-value	Regression coefficient	*P*-value
WUE	0.459	<0.001	–0.292	0.001	0.345	<0.001
Pn	0.671	<0.001	0.018	0.858	0.137	0.129
LAI	0.072	0.077	0.544	<0.001	0.058	0.640

Fig. 4c). Cultivar mixing reduced the DI of rice blast by 51.99%, the DI and AUDPC of wheat powdery mildew by 10.85% and 7.13%, and the DI and AUDPC of wheat rust by 32.28% and 29.87%, respectively (Fig. 4). There was no significant publication bias for DI and AUDPC in our paper according to Egger's regression (Fig. S2).

3.4 Effects of climate and soil variables on the relationship between number of cultivars in mixture and yield

Latitude, mean annual temperature (MAT), and mean annual precipitation (MAP) were the most influential variables modifying the effect sizes of cultivar mixing on yield (Fig. 5b). The effect size of cultivar mixing on yield was positively correlated with MAT and MAP, but negatively correlated with latitude (Fig. 5a). Overall, the effect of cultivar mixtures on yield correlated more with climatic factors than crop type and soil variables.

4 Discussion

4.1 Cultivar mixing improves yield and yield stability

It is widely recognized that species and genetic diversity generally contribute to ecosystem functioning, and primary production and total plant biomass generally increase with increasing diversity (Schmid and Schöb 2022). The use of crop species mixtures (intercropping) in mechanized agriculture is still limited due to the challenges in sowing, managing and harvesting more than one crop in the field. While not as diverse as intercrops, cultivar mixtures represent a more accessible and easily implemented way to reduce agricultural intensification under mechanized production.

Our results show that, compared with cultivar monocultures, crop yield was increased overall by 3.82% in cultivar mixtures (Fig. 1a), and rice showed the largest increases

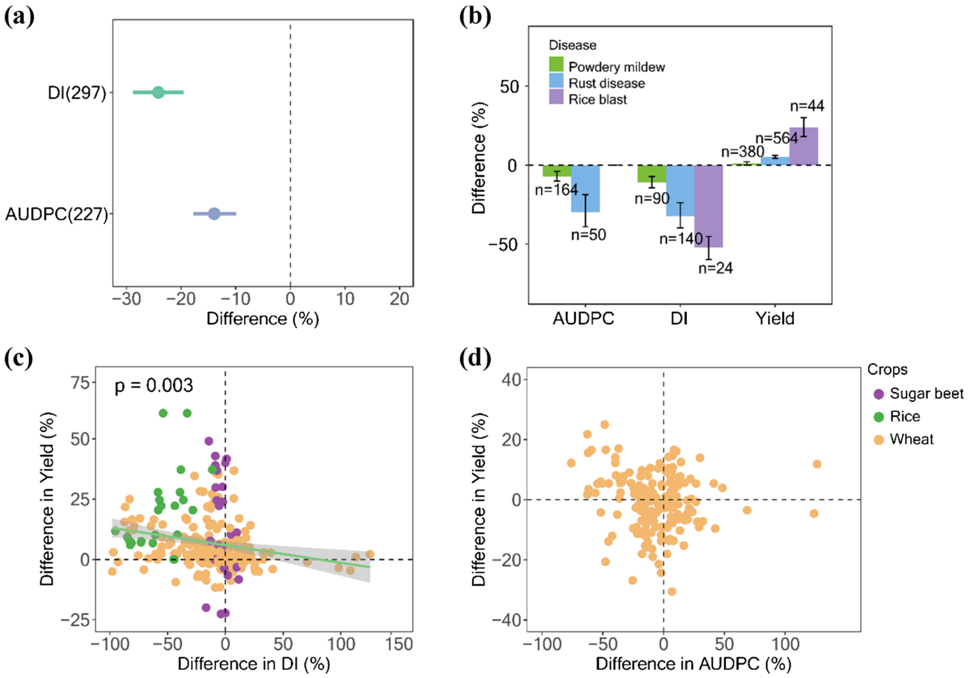

Fig. 4 Comparison of disease index (DI) and area under the disease-progress curve (AUDPC) for cultivar mixtures and monocultures. (**a**) Difference in DI and AUDPC between mixtures and monocultures. The number of observations for each category is shown in parentheses. (**b**) Differences in DI, AUDPC and yield between cultivar mixtures and monocultures associated with powdery mildew, rust disease and rice blast. Values are mean effect sizes and error bars show the 95% CI. The mean effect sizes were considered significant if the 95% CI does not include zero. (**c**, **d**). Relationships between differences in yield and in DI and AUDPC. For details see Tables S4, 5.

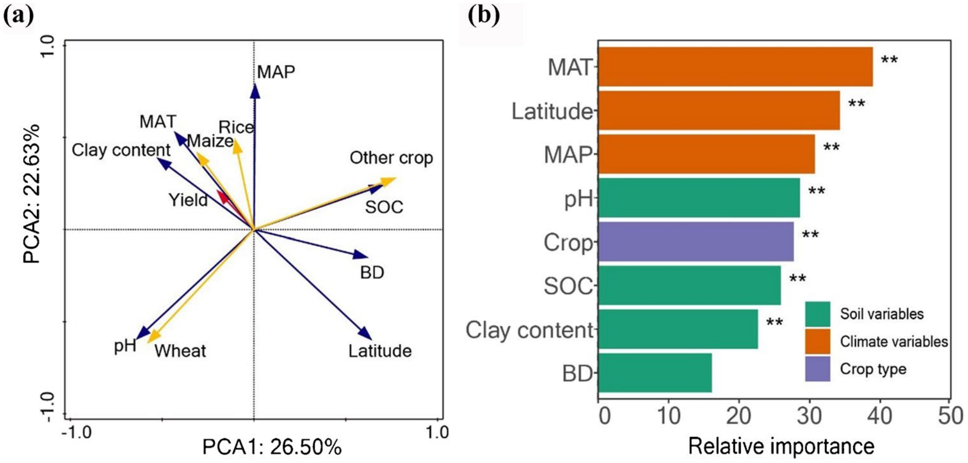

Fig. 5 Principal component analysis and variable importance in accounting for the effects of cultivar mixtures on crop yield. (**a**) Principal component analysis of the relationships between factors and increases in yield resulting from mixing. (**b**) Importance of factors affecting the increase in yield from cultivar mixing. Variables include latitude (the absolute value, measuring the distance from the equator), mean annual precipitation (MAP), mean annual temperature (MAT), initial soil organic carbon (SOC), soil pH (pH), soil clay content (Clay content), bulk density (BD), and crop (divided into wheat, maize, rice and other crops).

in yield among the major crops, 16.14% (Fig. 1e). Rice is susceptible to rice blast disease, which often causes large yield losses, and cultivar mixtures show reduced incidence. When highly disease-susceptible tall rice cultivars were interspersed among several rows of dwarf disease-resistant hybrids, the yield increased by 89%, and blast severity reduced by 94% compared to monoculture (Zhu et al. 2000). Additionally, tall rice cultivars are prone to lodging, especially under the high-input conditions. Rice cultivar mixing can decrease lodging in tall rice plants and enhance their capacity to absorb nitrogen (Finckh 2008; Zhu et al. 2000).

A recent study showed that increased crop species diversity promoted biomass production, and to a lesser extent, yield, and the difference was due to a reduction in reproductive allocation (harvest index) in crop mixtures (Chen et al. 2021). In our study, mixing cultivars increased both aboveground biomass of crops by 5.11% and their harvest index by 2.54% (Fig. 1b, c). This could be because the ecological niche differences within mixtures of cultivars of a single crop species are smaller than that of interspecific cropping (Wuest et al. 2021).

Ninety percent of the cultivar mixture experiments have been performed on cereal crops. Wheat is the most widely studied in China (Cai et al. 2019; Kong et al. 2022), Argentina (Sarandon and Sarandon 1995a, b), Italy (Lazzaro et al. 2018), France (Mille and Jouan 1997), Canada (Pridham et al. 2007), and the United States (Jackson and Wennig 1997; Mundt 2002). Wheat cultivar mixtures had a 4.07% greater yield than monocultures in our study (Fig. 1e). In maize, one of the world's three major staple crops, the increase in yield due to mixed sowing was primarily associated with differences between the mixed cultivars in height, morphology, and growth period, which promote canopy light interception and thereby population yield. Barot et al. (2017) suggested that crops or cultivars with high tillering, such as most wheat cultivars, could benefit more from mixtures of cultivars than crops that tiller less or not at all, such as maize. However, our study found that the effect of maize cultivar mixtures on yield was higher than that of wheat and barley, which may be due to its high morphological plasticity (Wang et al. 2017a, b; Hu et al. 2019). Cultivation of wheat, maize and rice are highly mechanized, and mixed sowing of cultivars is compatible with current machinery, so mixing of rice and wheat should be relatively easy to implement. Our results suggest that use of cultivar mixtures could increase yields considerably across the globe (Table S6). Cultivars currently used in mixtures have been bred for monoculture performance (Wuest et al. 2021), so even greater benefits are likely if varieties could be bred for high mixture performance in the future.

Extreme climatic conditions, pests and diseases pose enormous challenges to food production (Lobell et al. 2008; Prieto et al. 2015; Ray et al. 2015; Chaloner et al. 2021), and increasing genetic diversity in agricultural systems can be an effective strategy to address these issues (Prieto et al. 2015; Reiss and Drinkwater 2018). Cultivar mixtures can improve crop yield stability through sampling effects (populations with more genotypes are more likely to contain the best performing genotype in any given environment) and complementarity effects (the complementarity of different genotypes in resource use or pathogen susceptibility) (Turnbull et al. 2016; Barot et al. 2017).

The coefficient of variation (CV) has been used extensively to quantify relative yield stability (Tilman et al. 2006;

Schrama et al. 2018). Our study found that, when measured with the CV, the temporal (R^2=0.013, P = 0.001) and spatial stability (R^2=0.021, P = 0.006) of yield increased with the number of cultivars in mixture (Fig. 2a, c). Further, as expected from the known scale-dependence of the CV (Döring and Reckling 2018), temporal (R^2 = 0.027, P < 0.001) and spatial (R^2 = 0.068, P < 0.001) relative stability increased with average yield (Fig. S3). Thus, the reduced yield variability in cultivar mixtures was probably at least partly related to increased mean yield. A similar negative relationship has been shown in two further studies (Döring et al. 2015; Knapp and van der Heijden 2018). We employed POLAR stability (Döring et al. 2015) to remove scale-dependence of the stability measure. Our analysis found that the positive effects of cultivar mixtures on temporal yield stability (R^2 = 0.005, P = 0.030) are robust and are not driven solely by differences in the level of mean yield (Fig. 2b). This means that cultivar mixture did indeed increase temporal, although not spatial, yield stability. Temporal yield stability is critical for farmers to reduce inputs and cope with climate change.

4.2 Cultivar mixtures show improved resource-use efficiency

Modern agriculture is characterized by high inputs (fertilizers, pesticides). Although this has resulted in high production, it has also led to increased production costs, waste of resources, and extensive environmental pollution (Knapp and van der Heijden 2018; Li et al. 2020). Any functional differences that allow for complementary resource use among varieties could increase the uptake of resources such as water, mineral nutrients, and light, and this could explain why mixtures of varieties are generally more productive than monocultures of the same varieties (Kathju et al. 2003; Kaut et al. 2009; Tilman 2020). Recently, the relationship between intraspecific diversity and water use efficiency (Fang et al. 2014; Adu-Gyamfi et al. 2015) and net photosynthetic rate (Kathju et al. 2003; Li et al. 2019) have come into focus. Our study found that increases in yield due to cultivar mixing were associated with increased light-use efficiency (Fig. 3c) and water-use efficiency (Fig. 3b). Cultivar mixing had stronger effects on LAI and Pn than WUE (Fig. 3a). Light interception, leaf area index, and leaf photosynthetic capacity significantly affect canopy photosynthesis (Peng and Krieg 1991; Yao et al. 2016). Cultivar mixtures improve canopy aeration and stomatal conductance and reduce leaf resistance to the diffusion of water vapor (Kathju et al. 2003), thus increasing Pn by 8.48% (Fig. 3a), and thereby crop yield (Fig. 3c). Furthermore, cultivar mixtures with different plant heights and maturity form a slightly uneven canopy (Javad 2011), which could increase sunlit leaf area. In addition, mixed cropping can delay leaf senescence, increase LAI by 7.22% (Fig. 3a) and improve light interception rate (Board et al. 1992; Kaut et al. 2009), thereby promoting an increase of aboveground biomass (Table 1). Greater biomass means greater C-deposition into the soil, thereby improving soil quality (Barot et al. 2017) and contributing to carbon sequestration.

Agricultural production is the largest consumer of water globally, using 70% of the world's freshwater resources to irrigate 25% of the world's croplands (FAO 2020a). The Food and Agricultural Organization (FAO) forecasts a more than 50% increase in irrigated food production by 2050, which will require a 10% increase in water extracted for agriculture, provided water productivity improves (FAO 2020b), thus it is important to improve crop WUE. Multi-species intercropping can increase absorption of water by root systems because of spatial and temporal differences among the intercropped species (Liang et al. 2020; Zhang et al. 2021a, 2021b). This can also be the case, although probably to a lesser extent, for cultivar mixtures (Newton et al. 2012; Fang et al. 2014; Adu-Gyamfi et al. 2015; Wang et al. 2016). In the present study, mixing cultivars increased WUE by 4.3% (Fig. 3a). The advantages of cultivar mixtures may be strongest under conditions of drought (Fang et al. 2014; Wang et al. 2016; Reiss and Drinkwater 2018), because of the increased adaptability of mixtures to unpredictable environmental variation (Brooker et al. 2015; Döring et al. 2015).

4.3 Cultivar mixtures reduce disease severity

Diseases are a major cause of yield loss, and losses due to plant diseases caused by pathogenic microorganisms have been estimated at 13% to 22% annually in the world's important food crops—wheat, corn, soybean, potato, and rice (Savary et al. 2019; Wang et al. 2021). Pesticides have made a significant contribution to food security, but their widespread use not only promotes pesticide resistance in crops, but also has a negative impact on ecosystems and human health, threatening global food security and food safety (Beketov et al. 2013; Tang et al. 2021). Control of plant diseases in agricultural ecosystems through ecological methods is attracting increased attention (Huang et al. 2012; Zeller et al. 2012; Borg et al. 2018; Yang et al. 2019; Kristoffersen et al. 2020). Our results showed that AUDPC was reduced by 13.93% and DI was reduced by 24.14% when the varieties with different resistances were mixed (Fig. 4). Wheat powdery mildew, wheat rust disease (including leaf rust, stripe rust, stem rust) and rice blast are the three most studied crop diseases in cultivar mixtures. It is estimated that the global annual wheat yield loss caused by wheat rust pathogens is about 5.42% (Savary et al.

2019). Our study found that, compared with monocultures, wheat cultivar mixtures with rust-resistant varieties and rust-susceptible varieties reduced wheat rust AUDPC by 29.87% and DI by 32.28% and increased yield by 5.15% (Fig. 4b). Wheat powdery mildew causes a global wheat yield loss of 1.07% (Savary et al. 2019). Our study found that compared with monocultures, wheat cultivar mixtures with powdery mildew resistant and susceptible varieties reduced wheat powdery mildew AUDPC by 7.13% and DI by 10.85% and increased yield by 1.09% (Fig. 4b). Rice is one of the most important food crops in the world, and rice blast causes a global rice yield loss of 4.33% (Savary et al. 2019), threatening global food security (Shahriar et al. 2020). Rice cultivar mixtures reduced rice blast DI by 51.99% (Fig. 4b). Our study found that compared with monoculture, rice cultivar mixtures with rice blast resistant and susceptible varieties showed a 23.80% increase in yield (Fig. 4b). Mixed sowing can make a major contribution to the control of crop diseases, reducing yield loss and pesticide use.

The adoption of mixed cropping practices will influence plant breeding strategies for disease resistance. Each crop is susceptible to several diseases which are caused by pathogens. Developing single cultivars with resistance to multiple pathogens is challenging due to defense costs. Thus, breeding different cultivars, each with specific resistance traits, and then mixing them in the field to get a population-level defense effect, is more promising. In addition, we need simple and pragmatic approaches capable of capitalizing on the advantages derived from heightened genetic diversity within a field. Forst et al. (2019) provided a detailed introduction to designing mixtures based on general mixing ability and specific mixing ability. The prospect of crop genetic improvement targeted at mixed cropping systems presents a promising avenue to enhance sustainability and productivity in agriculture (Zeller et al. 2012).

We categorized the type of characteristics used to construct mixtures from the component cultivars as disease resistance or physical characteristics, or both. Our results show that mixtures based on physical characteristics achieved higher yield benefits than those based on disease resistance. One should be cautious in generalizing this conclusion, as some of the increases in yield in mixtures based on physical characteristics may be due to reductions in disease. Therefore, the yield benefits obtained based on physical traits and disease resistance traits cannot not be directly comparable in this study. Mixtures chosen on the basis of both disease resistance and physical characteristics achieved higher yield benefits than those based on only one of these traits (Fig. S4). These mixtures exhibit greater functional trait diversity, providing a broader range of functional traits and consequently yielding greater benefits in terms of increased and stabilized production (Reiss and Drinkwater 2018).

Previous meta-analyses have demonstrated that mixing components and field management have important effects on yield (Borg et al. 2018; Reiss and Drinkwater 2018). Those studies have shown that (1) the relative yield of mixtures with more varieties and more functional trait diversity was higher; (2) cultivar mixtures increase yield most under low-pesticide and low-fertilizer inputs. Our study found that environmental variables (especially climatic variables) had more important influences on the effect size of cultivar mixtures on yield than did crop species identity. The yield effect increased with increasing MAT and MAP and decreased with increasing latitude (Fig. 5). Thus, cultivar mixtures showed greater yield increases in at lower latitudes (Reiss and Drinkwater 2018). There are numerous other possible explanations for this, such as relationships between environmental conditions and biodiversity effects, increased disease and insect pest pressure in the tropics, differences in agricultural practices or the crops themselves, e.g. rice, with its high mixture effect, is grown at lower latitudes (Fig. 5). While the explanation for differences in the effects of cultivar mixtures in different agricultural systems awaits further research, our results show that cultivar mixtures increase yields across a wide range of crops and farming systems.

4.4 Quality and acceptability of cultivar mixture products

The reluctance of farmers to grow cultivar mixtures in developed regions is largely due to the demands of major purchasers of grain for uniformity in yield components and composition. For example, large breweries want a consistent material composition of barley to produce consumer products that are the same across places and years (Newton et al. 2009). The same applies to wheat production for baking. Even though the products from cultivar mixtures are likely to be of equal or higher quality than the more standardized products from cultivar monocultures (Newton et al. 2009), the increased variation in composition may present a challenge to producers and consumers.

In some sectors, different cultivars are often mixed in storage silos during the harvesting period, with no meticulous control over the proportions (Barot et al. 2017). The objective is generally to achieve minimal thresholds for specific important characteristics (protein content, specific weight, etc.). This is compatible with the use of cultivar mixtures (Barot et al. 2017). In addition, research has shown that quality (e.g. protein, including gluten) and its stability is higher in mixtures (Horner et al. 1975a, 1975b; Swanston et al. 2005; Vlachostergios et al. 2011). Hence, cultivar mixtures should be acceptable in most cases.

5 Conclusions

We performed an analysis of the effects of cultivar mixing on 12 crops, including rice, and found that mixing cultivars enhanced crop yield by 3.82% overall. Additionally, we examined yield stability, using measures with and without scale dependence, and found cultivar mixtures increased temporal yield stability. This suggests that mixtures of varieties of a single crop offering the potential to increase diversity and thereby improve productivity and sustainability. Cultivar mixtures increased crop biomass, leaf area index, photosynthetic rate, and water use efficiency by 5.1, 7.2, 8.5 and 4.3%, respectively), and decreased disease incidence (by 24.1%), thereby increasing crop yield. Mixed sowing can make a significant contribution to enhancing resource utilization efficiency, controlling crop diseases, reducing yield loss, and minimizing pesticide use, confirming its benefits for the sustainable development of agriculture. The effect of cultivar mixing on yield varies significantly depending on climate conditions and soil properties. Cultivar mixtures were more effective in mitigating diseases and increasing yields at lower latitudes, higher mean annual temperatures, and higher mean annual precipitation. It is likely that that the development of methods for targeted breeding of varieties for high mixture performance can result in further increases yield and yield stability of varietal mixtures.

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Data availability The datasets generated and analyzed during the current study are available from the sources cited and, if necessary, from the corresponding author on request.

Code availability The codes for analysis during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interest We declare that we have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethics approval Not applicable

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