



Crop cultivar mixtures stabilize productivity, partly via facilitation, when conditions are less benign

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ABSTRACT

Context of problem: Crop cultivar mixtures can increase and stabilize productivity; however, their effects on year-to-year temporal stability are positive in some cases, and neutral or negative in others. This inconsistency is not understood, in part because the mechanisms underlying the effects of diversity on stability are not clear, and in part because we do not understand the role of the abiotic environment on the functioning of crop mixtures.

Objective of research question: To test whether maize cultivar mixtures increase maize productivity and temporal yield stability compared to monocultures, in benign vs. less benign conditions, our objective was to explore the role of facilitation in the overall effect of crop diversity.

Methods: We performed two field experiments comparing mixtures of up to eight cultivars to monocultures over five years at Zhangye with irrigated conditions and with higher organic matter, total nitrogen, available phosphorus and available potassium, and over four years at Lishu with rainfed conditions without irrigation, and with lower soil fertility. Water supply at Zhangye was 18.5% higher than at Lishu and the water supply at Lishu was dependent on precipitation with greater year-to-year variation.

Results: At the Lishu site, productivity was 18.3% lower than at the Zhangye site, and the temporal stability of aboveground biomass for cultivar mixtures was 31.5% higher than that of monocultures. This increase in temporal stability in mixtures corresponded to 6.9% greater productivity overall and 48.1% less variation in productivity than in monocultures at the Lishu site. Complementarity effects were positive and facilitation was much more important at the Lishu site. Temporal stability of aboveground biomass was also positively correlated with complementarity effects ($P < 0.05$) and facilitation ($P < 0.01$). There was no evidence of enhanced stability or facilitation at the Zhangye site.

Conclusions: Our findings emphasize that cultivar mixtures enhance ecosystem functioning under less benign conditions with lower productivity, in part via facilitation, but not under more productive benign conditions.

Implications or significance: Our study highlights that increasing crop cultivar diversity may better respond to more abiotically stressful and fluctuating conditions, and provides insight into why crop cultivar mixtures vary in their effects on stability.

1. Introduction

Cultivar mixtures are promising approaches to increase crop productivity at large scales (Yang et al., 2019), and build on advances in our

understanding species diversity in natural and agricultural systems (Tilman et al., 2001; Li et al., 2021; Yan et al., 2021). Similarly, the ecotypic diversity of wild plants can increase community productivity (Atwater and Callaway, 2015; Yang et al., 2015, 2017; Luo et al., 2016).

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A meta-analysis by Raffard et al. (2019) indicates that intraspecific richness affects ecosystem function at a magnitude similar to that of species richness. The effects of cultivar mixtures on system productivity can be positive, neutral, or negative (e.g., Reiss and Drinkwater, 2018). Cultivar mixtures can also have positive (Creissen et al., 2016; Kong et al., 2022), or negative effects (Lowry et al., 2020) on the year-to-year temporal stability of agricultural productivity. For example, mixed cropping of wheat cultivars with different lodging performances decreases the damage to stalks (lodging) compared to the mean of cultivar monocultures used for the mixture (Kong et al., 2022). This may stabilize yield production through compensation when weaker individuals are protected from damage (Creissen et al., 2013; Doring and Elsalahy, 2022). Winter barley cultivar mixtures also increased yield stability under unpredictable environmental conditions (Creissen et al., 2016). In contrast, Lowry et al. (2020) found that diversity in perennial ryegrass cultivar mixtures was negatively correlated with stability in a three-year experiment. These inconsistencies suggest that the mechanism underlying how cultivar mixture affects the temporal stability of productivity is not well understood.

Yield stability is generally obtained by dividing the average yield by the variation in yield, reflecting the plant community's resistance and resilience to stresses (Tilman and Downing, 1994). Previous studies have shown that biodiversity can increase temporal stability via overyielding, species asynchrony and portfolio effects (Lehman and Tilman, 2000), but direct or indirect facilitation provide other likely mechanisms (Knops et al., 1999; Wright et al., 2017a; b; Wright et al., 2021a; b). Greater temporal stability in yield may result from greater productivity (Li et al., 2021), lower variation in productivity (Tilman et al., 2006), or both. According to the portfolio hypothesis, greater temporal yield stability may also occur when reduction in variation is greater than the reduced mean value if biodiversity decreases community productivity (Lehman and Tilman, 2000; Schindler et al., 2015). However, in cultivar mixtures, it is still unclear which component (average yield or temporal yield variation) affects stability of productivity under different environmental conditions.

Recent models show that species mixtures may increase ecosystem stability via complementarity effects (Wang et al., 2021). In contrast, selection effects, when dominant species in mixtures are the most productive species in monocultures, exhibit low tolerance to perturbations, which are more likely to decrease the stability of productivity (Isbell et al., 2009; Wang et al., 2021). Complementarity effects occur when the average performance of individual species or cultivar is higher in mixtures than in corresponding monocultures (Loreau and Hector, 2001). Cultivar mixtures with different traits can contribute to complementarity, and buffer biotic and abiotic stresses (Fletcher et al., 2019). For example, dwarf cultivars can support taller cultivars and alleviate lodging (Borg et al., 2018). Mixtures of early maturing tall cultivars can improve weed control and increase yield stability (Kaut et al., 2009). Such benefits of cultivar mixtures have been widely reported for lodging resistance (direct facilitation), disease resistance (indirect facilitation), and weed control (Mason et al., 2008; Gigot et al., 2013; Borg et al., 2018).

In our study, in order to compare the effects of mixtures on performance among combinations with varied biomass and grain yield, we standardized the complementarity and selection effects by dividing by the mean value of corresponding monocultures, i.e., relative complementarity and selection effects (Craven et al., 2016). Complementarity effects have generally been thought to function via differences among species in the way they obtain and use resources (niche partitioning). However, recently it has become clear that facilitation, which is usually amalgamated within complementarity effects, is different than niche partitioning (Wright et al., 2017a, 2021a). Facilitation is when one species, or cultivar, increases the performance of other species or cultivars either directly (e.g., via shade, root exudates) or indirectly (e.g., ameliorating negative plant soil feedbacks, reducing herbivory) (Callaway, 2007). Both niche partitioning and facilitation tend to increase species evenness

and maintain the relative abundance of risk-adverse species.

Variation in cultivar diversity effects may be due to variation in the abiotic environment, especially if facilitation is an important mechanism for the biodiversity effect. Facilitation tends to be more common and more intense in relatively low productivity environments (Bertness and Callaway, 1994; Callaway et al., 2002; Brooker et al., 2008; Blaser et al., 2013; He et al., 2013). Considering variation in productivity in the context of biodiversity-ecosystem function (BEF), which is analogous to intercropping, Mulder et al. (2001) established experimental communities of bryophytes in monoculture and diverse mixtures in contrasting living conditions with different humidity and light. They found there was no positive BEF relationships in high-humidity and low-light conditions. However, community biomass increased with species richness when bryophyte communities were exposed to drought and high light. Several lines of evidence indicated that this difference was due to facilitation. Considering this evidence, stronger positive effects of cultivar diversity on system productivity might be more likely in less productive circumstances, such as rainfed crops without irrigation.

Annual rainfall and total water input can affect the traits expressed by crops, which influences yield (Westerband et al., 2021). For example, in arid conditions, plants tend to have high leaf mass per area, a morphological trait that widely used as a good indicator of plant functioning (i.e., photosynthetic and respiratory rates, chemical composition, resistance to herbivory, etc.), with greater nitrogen content per unit area (Cernusak et al., 2011). We conducted experiments with mixtures of different maize cultivars at two sites with different growing conditions and management. The Zhangye site is in Northwest China with irrigated conditions and with higher soil organic matter, total nitrogen, available phosphorus and available potassium. The Lishu site is in Northeast China with rainfed conditions without irrigation, and with lower soil fertility than the Zhangye site. We investigated year-to-year stability of crop yield production and the linkage between stability, complementarity effects, and facilitation. We hypothesized that (1) cultivar mixtures would increase maize productivity and temporal yield stability more at Lishu than at Zhangye and (2) increased temporal stability of productivity would be more correlated with niche partitioning aspects of complementarity at Zhangye, but more correlated with facilitation at Lishu.

2. Materials and methods

2.1. Site description

Our field experiments were based on maize (*Zea mays* L.) cultivar mixtures at Lishu (43°27' N, 124°43' E), Jilin Province, Northeast China, and at Zhangye (38°85' N, 100°38' E), Gansu Province, Northwest China. Lishu has a temperate monsoon climate with annual precipitation of 577 mm, average annual temperature of 6.5 °C, and a frost-free period of 115–188 d. Zhangye has a continental climate with annual precipitation of < 130 mm, average annual temperature of 7.7 °C, and a frost-free period of 170–180 d.

The experiment at Lishu was conducted over four growing seasons from 2017 to 2020; maize was cultivated in May and harvested in October. The mean water supply at Lishu from sowing to maturity during these years was 509 mm/yr. The 0–20 cm soil layer at the Lishu site had an initial pH of 5.8, total organic matter (SOM) of 19.1 g kg⁻¹, total nitrogen (TN) of 1.3 g kg⁻¹, available phosphorus (AP) of 16.5 mg kg⁻¹, available potassium (AK) of 46.8 mg kg⁻¹. All plots received 80 kg ha⁻¹ N fertilizer as urea, 52 kg ha⁻¹ P fertilizer as calcium superphosphate and 83 kg ha⁻¹ K fertilizer as potassium sulfate before sowing. An additional nitrogen fertilizer of 80 kg ha⁻¹ as urea was applied at jointing stage and pre-tasseling stage of maize, respectively, i.e. the system received a total 240 kg N ha⁻¹. The experiment at Zhangye was conducted over five growing seasons from 2016 to 2020; maize was sown in the middle of April and harvested in October. The mean water supply at Zhangye from sowing to maturity (2017–2020) to parallel

Lishu) was 611 mm/yr, 20% more than at Lishu. Soils in the 0–20 cm layer at the Zhangye site had a pH of 7.6, total organic matter (SOM) of 20.6 g kg⁻¹, total nitrogen (TN) of 1.7 g kg⁻¹, available phosphorus (AP) of 24.7 mg kg⁻¹, and available potassium (AK) of 82.0 mg kg⁻¹. All plots received 132 kg ha⁻¹ N fertilizer as urea, 101 kg ha⁻¹ P fertilizer as triple superphosphate before sowing. An additional nitrogen fertilizer of 198 kg ha⁻¹ as urea was applied at jointing stage of maize, i.e. the system received a total 330 kg N ha⁻¹.

2.2. Experimental design

Experiments were arranged in a randomized complete block design with three blocks in the first year (in 2016 at Zhangye and in 2017 at Lishu). The blocks and plots were fixed in the subsequent years during experimental implementation; i.e. a given cultivar combination was grown in the same plot over the course of the experiment, which allows the calculation of temporal stability for each plot. Maize cultivars in mixture were prepared with equal proportions of seed number of each cultivar and each specific place for the cultivars was chosen randomly. Seeds were sown individually by hand. We selected eight maize cultivars with similar growth periods, and sowed and harvested them over two days, and all cultivars were considered to be highly productive and were used commonly in the area around the Lishu site. Cultivars were Zhengdan958 (ZD958), Limin33 (LM33), Xiangyu998 (XY998), Jidan50 (JD50), Liangyu66 (LY66), Jingke968 (JK968), Tiannongjiu (TNJ) and Xianyu335 (XY335). In each block we established experimental treatments of 8 monocultures, 4 two-cultivar mixtures, 1 four-cultivar mixture, 1 six-cultivar mixture and 1 eight-cultivar mixture, totaling 45 experimental plots. Each plot was 5.4 × 6.0 m and contained 9 rows with 30 plants in each row. Detailed cultivar information was shown in Table S1.

The experiment at Zhangye also used eight maize cultivars with similar growth period, were sowed and harvested them over three days, considered to be highly productive and were used commonly in the area around the Zhangye site. Cultivars were Zhengdan958 (ZD958), Jixiang1 (JX1), Shendan16 (SD16), Jinkai2 (JK2), Jinkai6 (JK6), Xianyu335 (XY335), Jinkai7 (JK7), Yuyu22 (YY22) and Jinkai3 (JK3). We established 8 monocultures, 4 two-cultivar mixtures, 4 four-cultivar mixtures and 1 eight-cultivar mixture, with all 51 experimental plots. Each plot size was 2.4 × 6.0 m and contained 4 rows with 25 plants each row. Detailed cultivar information was shown in Table S2.

2.3. Plant sampling and analysis

For both experiments, a central strip of the individual maize cultivars in monoculture (5.0 m long × 1.2 m wide at Lishu and 4.0 m long × 1.2 m wide at Zhangye) was hand harvested in each plot for grain yield and aboveground biomass after full maturity every year. For mixture treatments, all plants in experimental plots were hand harvested separately and then summed to determine the total biomass and grain yield. After harvest, we measured plant height, ear height and shoot diameter characteristics by sampling 10 plants from different individuals in each experimental plot both in monocultures and in mixtures. The above-ground samples were dried at 60 °C for 72 h and weighed.

Soil samples were collected from the top 20 cm of the profile using an auger (10 cm diameter) in 2016 at Zhangye and in 2017 at Lishu. Soil organic matter (SOM), total soil nitrogen (TN), available soil phosphorus (AP) and available soil potassium (AK) were determined using standard protocols (Bao, 2005). Soil pH was measured at a ratio of 1: 2.5 (dry soil: deionized water).

2.4. Calculations

Total water input, and the water and temperature anomalies, were calculated based on long term data (1965–2018 year at Lishu and 1990–2020 at Zhangye) and data during the experimental years, i.e.,

2017–2020 at Lishu, and 2016–2020 at Zhangye. Total water input was calculated as the sum value of growing season precipitation at Lishu, and the sum value of whole growing season precipitation and irrigation at the Zhangye site. The temperature was the average value for the whole growing season. We used the inverse of the coefficient of variation as a measure of temporal stability:

$$S = \mu/\sigma$$

where μ is the temporal mean of grain yield or biomass in a given plot during the experimental years (5 years at Zhangye and 4 years at Lishu), and σ refers the temporal standard deviation of grain yield or biomass in a given plot during the experimental years. Also, we calculated the temporal stability of productivity using the mean value of three blocks using fractal stability, and absolute stability based on Eghball and Power (1995) and Knapp and van der Heijden (2018). Calculations are presented in the Supporting Information.

We calculated the diversity effects using the additive partitioning equation from Loreau and Hector (2001).

$$\begin{aligned}\Delta Y &= Y_O - Y_E = \sum_i RY_{Oj}M_i - \sum_i \Delta RY_{Ej}M_i = \sum_i \Delta RY_i M_i \\ &= N\overline{\Delta RY}M + N\text{cov}(\Delta RY, M)\end{aligned}$$

In this Equation, the complementarity effect is measured by $N\overline{\Delta RY}M$, and the selection effect is measured by $N\text{cov}(\Delta RY, M)$. Specifically, Y_O is the observed yield and biomass of cultivar i in the mixture, Y_E is the expected yield and biomass of cultivar i in the mixture, $RY_{Oj} = Y_{Oj}/M_i$ is the observed relative yield and biomass of cultivar i in the mixture, ΔRY_{Ej} is the expected relative yield and biomass of cultivar i in the mixture, M_i is the yield and biomass of cultivar i in the monoculture, $\Delta RY_i = RY_{Oj} - RY_{Ej}$ is the deviation from expected relative yield and biomass of cultivar i in the mixture, N is the number of cultivars in the mixtures.

To allow comparisons among mixtures with variable productivity, biodiversity effects were standardized to the relative complementarity effect and selection effect by dividing by the average monoculture grain yield and biomass of the component cultivars in a mixture (Craven et al., 2016). The relative complementarity effect and selection effect for each two-, four-, six- and eight-mixture communities were calculated at each site.

We used the relative interaction index (RII) to estimate the intensity of competition and facilitation among cultivars in mixtures (Armas et al., 2004).

$$RII = \frac{Y_{\text{mixture}} - Y_{\text{monoculture}}}{Y_{\text{mixture}} + Y_{\text{monoculture}}}$$

where Y_{mixture} is the aboveground biomass or grain yield of a maize cultivar in mixture, and $Y_{\text{monoculture}}$ is the aboveground biomass or grain yield of the same maize cultivar in monoculture. In this equation, RII has defined limits from -1 to 1 , with negative value indicating competition and positive value indicating facilitation.

Above-ground plant trait plasticity was calculated as follows:

$$\text{Aboveground trait plasticity} = \frac{\text{trait}_{\text{mixture}} - \text{trait}_{\text{mono}}}{\text{trait}_{\text{mono}}}$$

2.5. Statistical analysis

Linear mixed-effect models were used to determine the main effects of cropping system (mixture vs. monoculture) on grain yield, biomass and the year-to-year temporal stability at the two experimental sites. Block, year and experimental site were treated as random effects that tested the effects of cropping patterns and cultivar number (including two-, four-, six- and eight-cultivar combination) on grain yield, biomass and the year-to-year temporal stability at two experimental sites. It is important to note that year was excluded in the analysis of the year-to-year temporal stability. For the factor ‘cropping pattern’, the

monoculture value is the means of the two monocultures with the whole system considered. Post-hoc Tukey HSD tests were used in linear mixed-effect models at the 5% probability level. Package ‘nlme’ was used for linear mixed-effect models (Pinheiro et al., 2017).

To test whether the biodiversity effects (including complementarity and selection), relative interaction index and trait plasticity were significantly different from zero, two-sided one-sample Student's *t*-test was performed for each cultivar mixture treatment and each maize cultivar separately (two, four, six and eight cultivar mixtures) at each site. Moreover, linear regressions with mixed-effects models were applied to examine the relationships between the response variable and

the explanatory variables, with different random effects (in parentheses). These included productivity (including both grain yield and biomass) and cultivar number (experimental year, maize cultivar combination and block), temporal yield stability and cultivar mixture number (maize cultivar combination and block), relationships between temporal deviation and yield mean value (maize cultivar combination, cultivar mixture number and block), relationships between temporal yield stability and the relative biodiversity effects (maize cultivar combination, cultivar mixture number and block), relationships between temporal yield stability and relative interaction index (maize cultivar combination, maize cultivar, cultivar mixture number and

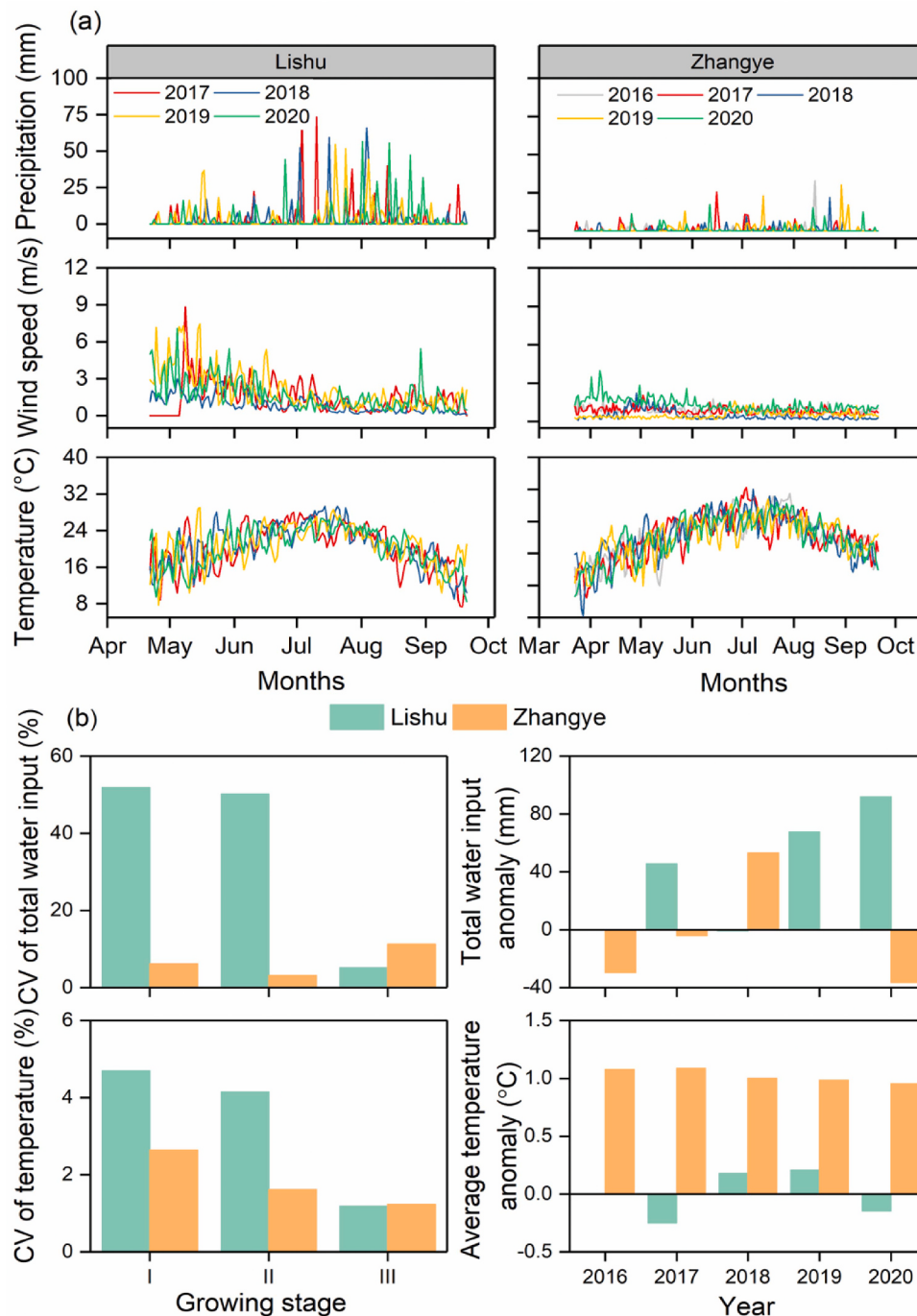


Fig. 1. (a). Precipitation, wind speed and temperature during the experimental years at the two experimental sites (2017–2020 at Lishu, and 2016–2020 at Zhangye). (b) Coefficient of variation (CV) and anomaly of water input and temperature at two experimental sites (2017–2020 year at Lishu, and 2016–2020 year at Zhangye). Growing stage included sowing to jointing (I), jointing to tasseling (II) and tasseling to maturity (III) during growing seasons.

block). We used the function lme () from package ‘nlme’ to fit the mixed models. Parameters were estimated by restricted maximum likelihood (REML). All statistical analyses were conducted with R version 4.1.3 (R Core Team, 2022).

3. Results

3.1. Differences in growing conditions between two sites

Total water supply was 18.5% higher at Zhangye than at Lishu. Windspeed reached higher levels at Lishu, and precipitation and wind

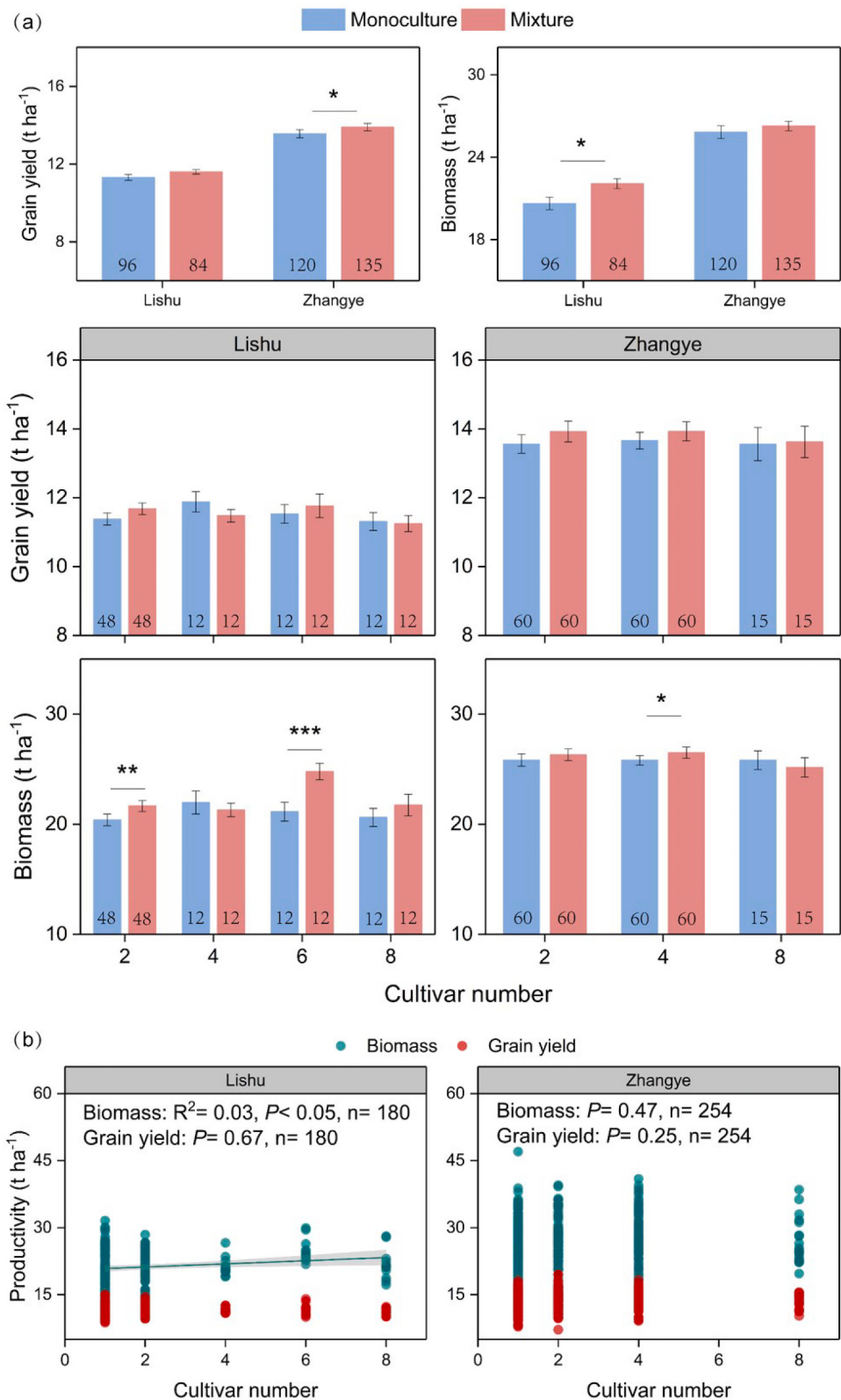


Fig. 2. (a). Means ± standard errors of above-ground biomass and grain yield for mixtures and corresponding monocultures. The experiment at Lishu was conducted from 2017 to 2020, and the experiment at Zhangye was conducted from 2016 to 2020. The values inside the bars refer to the total numbers of dataset in given cultivar combinations × years × replicates. (b) Regression between cultivar number and aboveground biomass, and the regressions between cultivar number and grain yield at the Lishu and Zhangye sites. The grey band refers to the 95% confidence interval. Asterisks indicate significant differences of aboveground biomass and grain yield between monocultures and mixtures (Tukey HSD). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

speed exhibited substantially greater variation at the Lishu site than at the Zhangye site during the experimental years (Fig. 1a). The CVs for total water input were 51.9% vs. 6.9% at the stage from sowing to jointing (stage I), and 50.2% vs. 3.2% at the stage from jointing to tasseling (stage II) at the Lishu and Zhangye sites, respectively (Fig. 1b).

Wind speed was 93.9% higher at Lishu than that at Zhangye during the growing season.

The results also exhibited a greater total water input anomaly, i.e., the cultivated year data minus average value of long-term water input data, at the Lishu site than at the Zhangye site (Fig. 1b). However, the

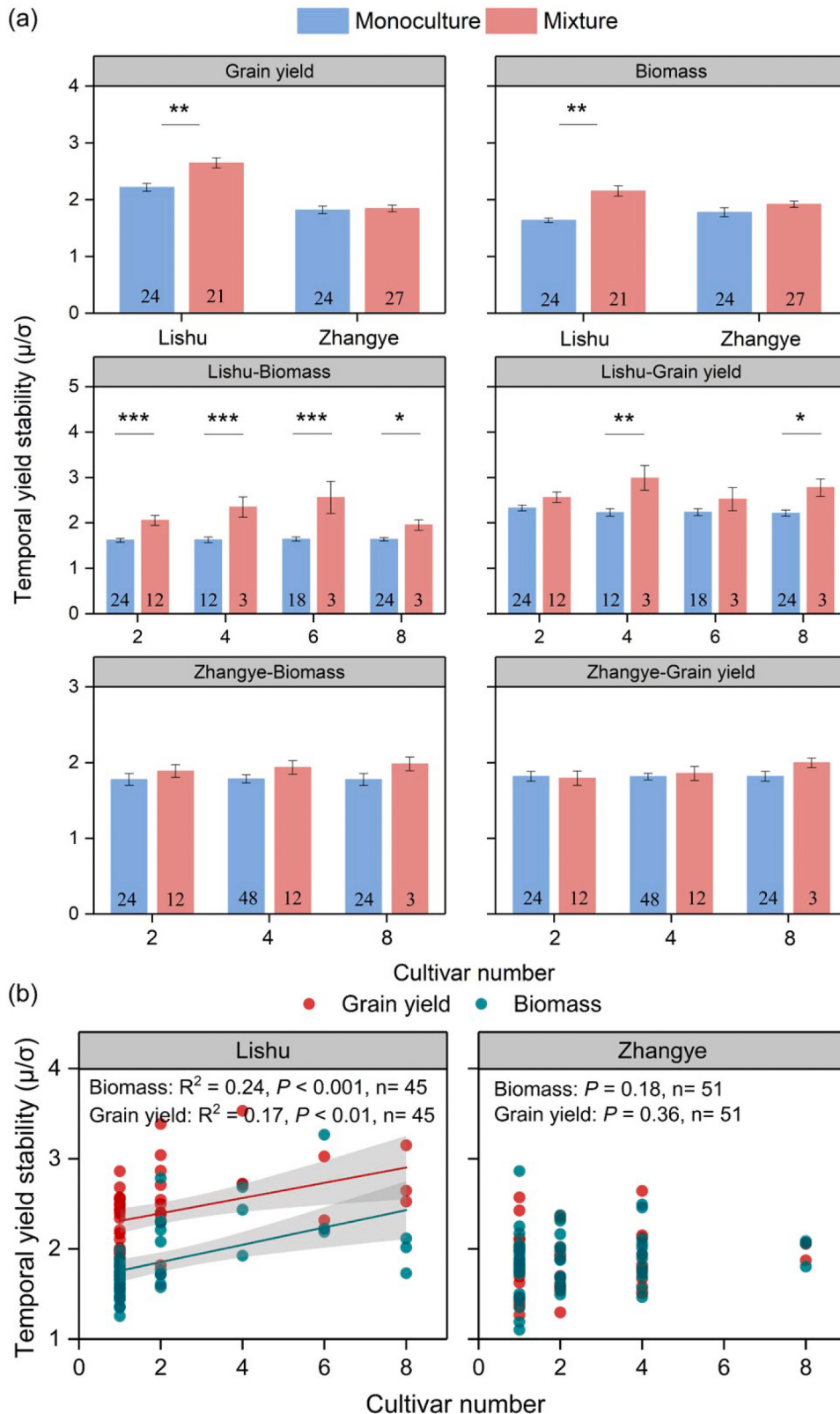


Fig. 3. (a). Means $\pm$ standard errors for temporal stability of biomass and grain yield for mixtures and corresponding monocultures. The values inside the bars refer to the total numbers of dataset in given cultivar combinations $\times$ replicates. (b) Regressions between cultivar number and temporal stability of aboveground biomass, and the regressions between cultivar number and temporal stability of grain yield at the Lishu and Zhangye sites. The grey band shows the 95% confidence interval. Asterisks indicate significant differences of aboveground biomass and grain yield temporal stability between monocultures and mixtures (Tukey HSD). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Zhangye site showed a greater temperature anomaly compared with the temperature anomaly at Lishu.

3.2. Overyielding in maize cultivar mixtures

Overall, productivity was higher at Zhangye than at Lishu; 22.4% for aboveground biomass and 20.0% for grain yield. Maize cultivar mixtures exhibited 7.0% greater ($P < 0.05$) aboveground biomass than monocultures at Lishu and 2.5% greater ($P < 0.05$) grain yield at Zhangye (Fig. 1a). In more detail, the aboveground biomass of two- and six-cultivar mixtures ($P < 0.01$ and $P < 0.001$, respectively) were higher than those of corresponding cultivar monocultures at Lishu. We also found that the grain yield of two- and four-cultivar mixtures ($P < 0.01$ and $P < 0.001$, respectively) were higher than monocultures and that the aboveground biomass of four-cultivar mixture ($P < 0.001$) was higher than those of corresponding monocultures at Zhangye (Fig. 1a). Moreover, aboveground biomass increased ($P < 0.05$) with the increasing number of maize cultivars at Lishu, whereas no such positive relationships were observed at Zhangye, either for grain yield or aboveground biomass (Fig. 2b).

3.3. Temporal yield stability in maize cultivar mixture

The average temporal stability of mixtures with two or more cultivars was greater than those of corresponding monocultures ($P < 0.01$), calculated with aboveground biomass and grain yields, at Lishu but not at Zhangye (Fig. 3a). We also found that the stabilities of two-, four-, six-, and eight-cultivar mixtures were higher than those of corresponding cultivar monocultures for both aboveground biomass and grain yields (except for two- and six-cultivar mixtures), again at Lishu but not at Zhangye (Fig. 3a). The average temporal stability of productivity increased with increasing cultivar number at the Lishu site, both for aboveground biomass ($P < 0.001$) and grain yield ($P < 0.01$), whereas no such positive relationships were observed at the Zhangye site (Fig. 3b).

We also calculated the year-to-year mean value and temporal standard deviation for productivity during the experimental years at two sites. First, we calculated the year-to-year mean value and temporal standard deviation for the productivity of monocultures and mixtures. The temporal standard deviations were lower ($P < 0.001$ for biomass, $P < 0.01$ for grain yield) in mixtures than those in corresponding monocultures at Lishu. We found year-to-year mean aboveground biomass was greater ($P < 0.05$) in mixture than in monoculture at Lishu (Fig. S1a). Temporal standard deviations were positively ($P < 0.05$) correlated with mean grain yields in monocultures rather than in mixtures at Lishu (Fig. S1b). Moreover, we calculated the year-to-year mean value and temporal standard deviation for productivity of each maize cultivar. We found cultivar mixtures increased the year-to-year mean biomass ($P < 0.01$) and average temporal stability ($P < 0.01$) of maize cultivar biomass at Lishu (Fig. S2a). However, there was no difference in temporal standard deviations for both aboveground biomass and grain yields between monocultures and mixture systems at Zhangye (Fig. S1a). The temporal standard deviations of each maize cultivar were positively correlated ($P < 0.001$) with mean aboveground biomass and grain yield in mixtures, but not in monocultures (Fig. S2b).

Cultivar mixture significantly increased the temporal stability and absolute stability that was calculated with the mean value of three blocks of grain yield and biomass than corresponding monocultures along cultivar gradients at Lishu, but not at Zhangye (Figs. S3, S5).

Fractal-calculated stability of biomass and grain yield production did not differ between monocultures and mixtures at the two sites (Fig. S4a). However, fractal-calculated stability of grain yield increased with the increasing maize cultivar number at Lishu, but not at Zhangye (Fig. S4b).

3.4. Relationships between the year-to-year temporal stability and complementarity effects

Relative complementarity effects (rCE) and relative selection effects (rSE) differed between the two experimental sites (Fig. 4a). Most rCEs were positive at both sites, whereas rSEs were significantly less than zero. Positive rCEs occurred for the two-, six- and eight-cultivar mixtures ($P < 0.001$, $P < 0.01$ and $P < 0.05$, respectively) at Lishu, and in two- and four-cultivar mixtures ($P < 0.01$ and $P < 0.01$, respectively) at Zhangye for aboveground biomass. Grain yield-based rCE was significantly positive for the two-cultivar mixtures ($P < 0.05$) at Lishu and two-, four- and eight-cultivar mixtures ($P < 0.01$, $P < 0.001$ and $P < 0.05$, respectively) at Zhangye (Fig. 4a).

Temporal stability was positively correlated with the rCE of biomass ($P < 0.05$; Fig. 4b), rather than rSE, at Lishu. The temporal yield stability was not correlated with rCE or rSE of grain yield and biomass at Zhangye.

3.5. Relationships between the year-to-year temporal stability of productivity and the relative interaction index

The relative interaction index (RII) for aboveground biomass and grain yields differed among maize cultivars at the two experimental sites (Fig. 5a). Most of the RIIs for maize cultivars were greater than zero, indicating facilitation, at Lishu. However, RIIs for only two maize cultivars were higher than zero at Zhangye. Specifically, both biomass and grain yield of ZD958 ($P < 0.01$ for biomass and $P < 0.05$ for grain yield) and LY66 ($P < 0.01$ both for biomass and grain yield) exhibited significantly positive RIIs at Lishu, and SD16 ($P < 0.001$ for biomass and grain yield) and JK3 ($P < 0.001$ for biomass and grain yield) had a positive RII at Zhangye.

Moreover, the temporal stability for aboveground biomass, but not grain yields, was positively ($P < 0.01$) correlated with RIIs at Lishu, indicating positive interactions among cultivars increased the temporal stability of aboveground biomass (Fig. 5b). However, temporal yield stability of grain yields and biomass were not related to RIIs at Zhangye (Fig. 5b).

3.6. Trait plasticity in maize cultivar mixture at two sites

We compared trait plasticity of maize cultivars between mixtures and monocultures based on plant height, shoot diameter, ear height, ear height coefficient and shoot height ratio. The trait plasticity of plant shoot diameter and shoot height ratio between monocultures and mixtures in maize cultivars were significantly higher than zero at Lishu (Fig. 6). However, the trait plasticities of plant height and shoot diameter between monocultures and mixtures in maize cultivars were significantly lower than zero, the trait plasticities of ear height coefficient and shoot height ratio between monocultures and mixtures in maize cultivars were significantly higher than zero at Zhangye (Fig. 6). In addition, the trait plasticity of plant height of ZD958 and XY998 between monocultures and mixtures were significantly lower than zero, the trait plasticity of ear height and ear height coefficient of JK968 between monocultures and mixtures in maize cultivars were significantly higher than zero at Lishu (Table S3).

At Zhangye, the trait plasticity of plant height of all maize cultivars between monocultures and mixtures were significantly lower than zero. The trait plasticity of shoot diameter of ZD958, JX1, JK2 and XY335 between monocultures and mixtures were significantly lower than zero, and the trait plasticity of shoot diameter of JK3 and YY22 between monocultures and mixtures were significantly higher than zero. In addition, both SD16 and JK7 exhibited significantly negative trait plasticity of ear height, and maize cultivar ZD958, JX1, JK2 and JK3 exhibited a positive trait plasticity of ear height coefficient (Table S4).

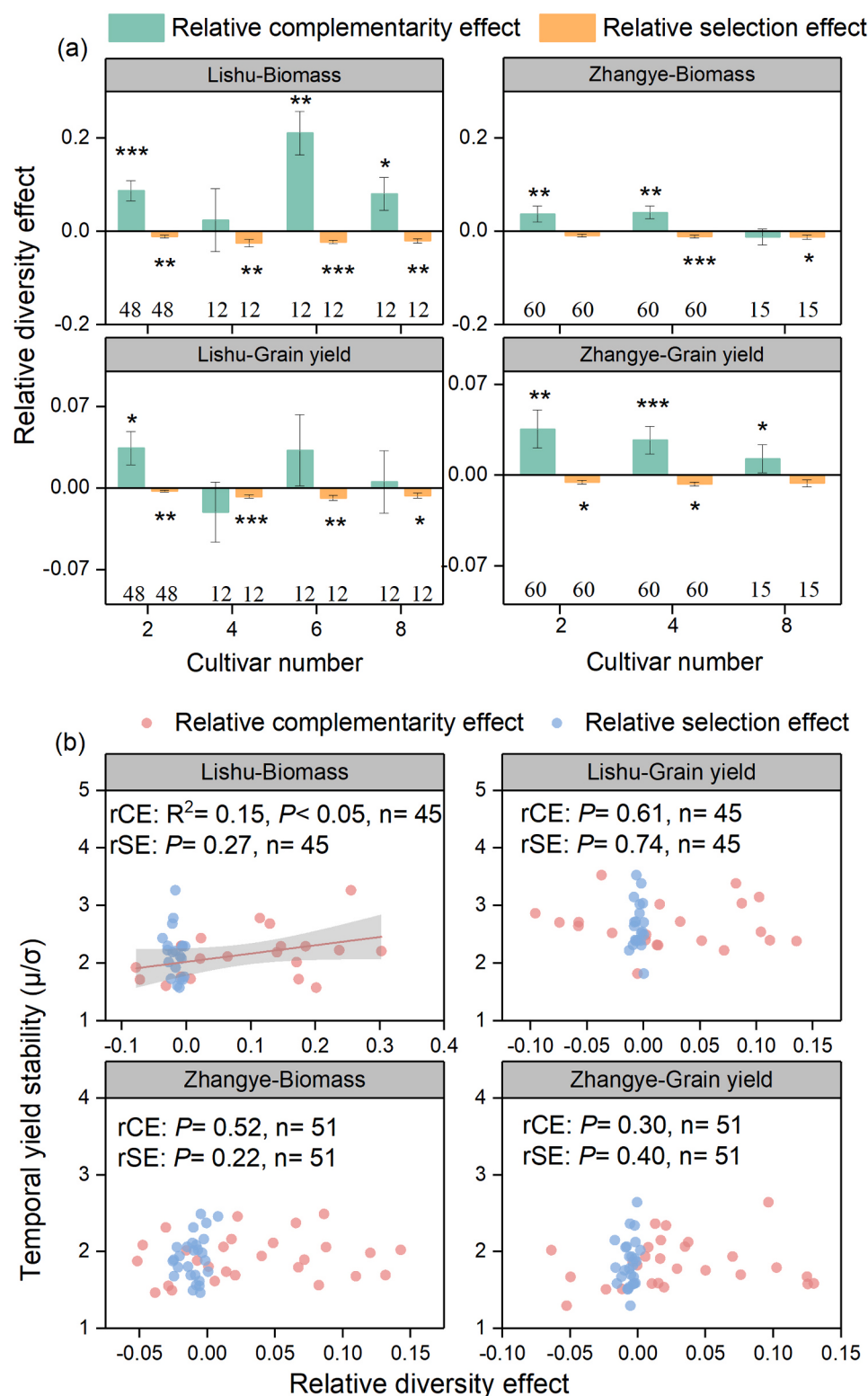


Fig. 4. (a). Means $\pm$ standard errors of relative diversity effects based on aboveground biomass and grain yield of two-, four-, six- and eight-cultivar mixtures at Lishu and Zhangye. Asterisks indicate significant differences between mixtures and zero, using two-sided Student's *t*-test. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The values under the bars refer to the total numbers of dataset in given cultivar combinations $\times$ years $\times$ replicates. (b) Relationships between relative complementarity effects (rCE) and average temporal stability in aboveground biomass and grain yield, and the relationships between relative selection effects (rSE) and average temporal stability in biomass and grain yield. The grey band shows the 95% confidence interval.

4. Discussion

Cultivar mixtures of maize increased the temporal stability of productivity, for both biomass and grain yield, compared to the same cultivars in corresponding monocultures at Lishu. Maize cultivars were more productive than monocultures at both sites. However, cultivar mixtures only increased the temporal stability of productivity at Lishu. This combination of results is consistent with our first hypothesis -

cultivar mixtures will increase maize productivity and temporal yield stability at Lishu under less benign and less productive conditions than at Zhangye under benign and more productive conditions. Our results are also consistent with other studies that have reported that intraspecific crop biodiversity increases temporal stability (Creissen et al., 2016; Reiss and Drinkwater, 2018; Yang et al., 2019). In contrast, however, Brooker et al. (2021) found no statistical interaction between experimentally applied drought and cultivar diversity treatments, concluding

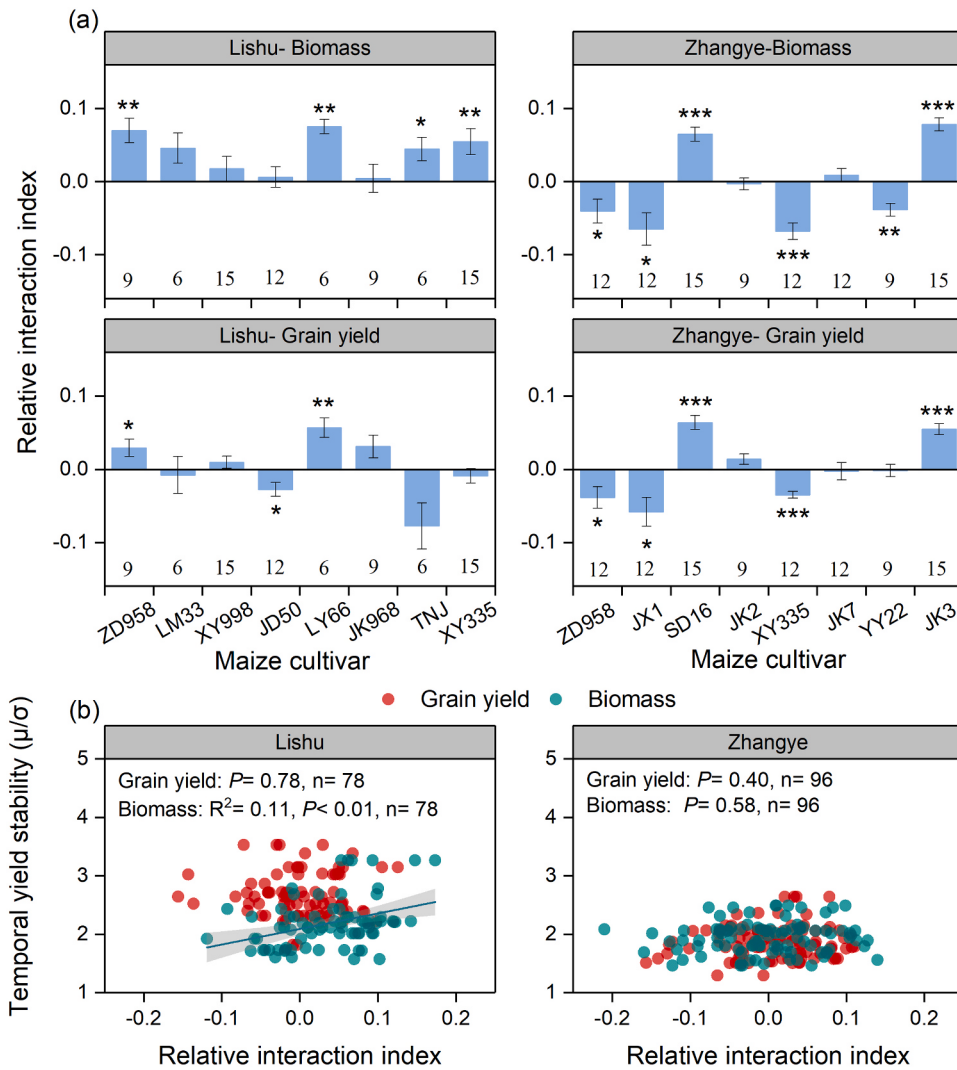


Fig. 5. (a). Means $\pm$ standard errors of the relative interaction index (RII) based on aboveground biomass and grain yield for maize cultivars at two sites. Asterisks indicate RIIs significantly greater or less than zero, using two-sided Student's t -test. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Values under bars refer to the average numbers of cultivar combinations $\times$ replicates. (b) Relationships between the temporal stability of cultivar mixtures for grain yields or aboveground biomass and the relative interaction index of maize cultivars at two sites. The grey band refers to the 95% confidence interval.

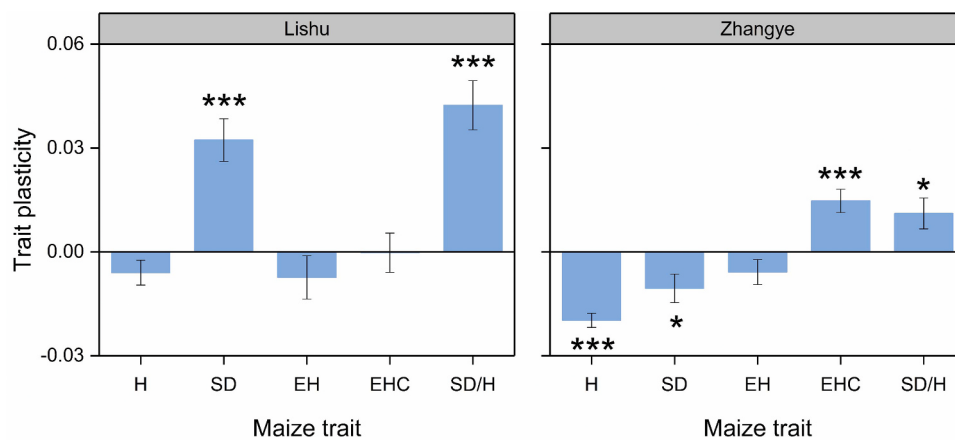


Fig. 6. Means $\pm$ standard errors for trait plasticity based on plant height (H), shoot diameter (SD), ear height (EH), ear height coefficient (EHC) and shoot height ratio (SD/H) for maize cultivars at two sites. $n = 312$ and $n = 480$ for Lishu and at Zhangye, respectively. Asterisks indicate trait plasticity significantly greater or less than zero, using two-sided Student's t -tests. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

that effect cultivar diversity on agroecosystem function did not increase with drought.

The greater temporal yield stability in mixtures at Lishu resulted from both greater productivity and lower yield variation compared to

corresponding monocultures (Fig. S1a). However, the lack of a cultivar diversity effect at Zhangye was mainly due to increases in variation in the yield of maize cultivars in mixtures, with increasing aboveground biomass and grain yield production (Fig. S2b). Biodiversity-driven

increases in community productivity can be accompanied by greater variation in yield (Tilman et al., 2006), however, we found cultivar mixture simultaneously increased yield production and decreased yield variation at Lishu. The difference of mixture effects on temporal stability between the two sites may be related to the difference and variation in total water supply, fertilizer application rate and soil properties. Maize cultivars were more productive and variable at Zhangye (irrigated condition with a relative higher soil fertility than Lishu) compared to Lishu (rainfed condition with a relative lower soil fertility and fertilizer application rate than Zhangye). Cultivar mixtures improved temporal stability for grain yield and aboveground biomass at Lishu where water supply was more variable and fertilizer inputs and soil properties were lower than Zhangye (Fig. 1, M & M). In other words, maize cultivars in mixture had a performance-enhancing effect and a buffering effect in less productive and more variable growing conditions. Temporal stability analysis will improve over more years. However, previous studies have also used 3–4 year field experiments to calculate temporal stability in both ecological and agronomy research. For example, Bocci et al. (2020) and Kong et al. (2022) conducted field trials over four years and three years, respectively, to calculate temporal stability of wheat (agronomy research). Wu et al. (2022) found that the complex shifts in complementarity and competitive intensities are likely to be the key mechanisms that maintain temporal stability in species-diverse agriculture by conducting a 3-year field experiment. Lowry et al. (2020) conducted a 3-year field experiment to study the productivity and stability of ryegrass. Therefore, although we have only 4–5 years of data in this study, the comprehensive analysis of temporal stability based on maize cultivar diversity allows conclusions that are as robust as many in the literature.

Our results are consistent with the two major “insurance effects”: originally proposed by Yachi and Loreau (1999). Biodiversity tends to enhance ecosystem stability by providing insurance or portfolio effects when species differ in their responses to environmental fluctuations (Yachi and Loreau, 1999; Thibaut and Connolly, 2013) or by including individuals with higher resistance to perturbations. This can occur directly through complementarity, which includes niche differentiation and/or facilitation (Wright et al., 2014, 2017a). Complementarity tends to increase community evenness and keep the relative abundance of intolerant individuals, contributing to greater stability (Wang et al., 2021). We found significantly positive complementarity effects in maize cultivar mixtures (Fig. 4a). Here, relative complementarity effects, rather than selection effects, were positively correlated with temporal stability of aboveground biomass of maize cultivar mixture at Lishu (Fig. 4b). Our results were consistent with previous studies (Isbell et al., 2009; Wang et al., 2021), which showed that temporal stability in productivity was also strongly related to complementarity among species.

Importantly, most RIIs for maize cultivars were higher than zero at Lishu, whereas RIIs for only two maize cultivars were higher than zero at Zhangye (Fig. 5a). The higher RIIs for maize cultivars at Lishu could be caused by reduced intraspecific competition in cultivar mixture, but they are likely to be driven to a large degree by facilitation at Lishu, whereas yield advantages at Zhangye were more likely due to niche partitioning. Our results contribute to a growing body of evidence and theory for the importance of facilitation as a driver of biodiversity ecosystem function relationships (Mulder et al., 2001; Brooker et al., 2021; Wright et al., 2017b, 2021b). For example, Wright et al. (2021b) found that six or eight species were suppressed by drought when in monocultures, but not when in diverse mixtures. A likely mechanism for this is facilitation. Often, facilitation is not separated from niche partitioning in the broader context of complementarity. However, niche partitioning is a broader use of resources or an avoidance of competition. In contrast, facilitation is the improved performance of a species or a cultivar because of the presence of another species or cultivar, and unlike niche partitioning indicates some degree of interdependence within the natural or agricultural systems (Callaway, 1998, 2007).

Moreover, we also found a positive correlation between temporal stability for aboveground biomass and relative interaction index of maize cultivar at Lishu (Fig. 4b), which supports our second hypothesis, i.e., the enhanced temporal yield stability is partly related to the facilitation component of complementarity at Lishu.

Plastic responses by crop cultivars can affect interactions among mixture components and might buffer the negative effects of variable environments on productivity and decrease competition (Matias et al., 2018; Wainwright et al., 2019). In our study, maize cultivars showed a significantly positive trait plasticity in plant shoot diameter and shoot height ratio, and negative trait plasticity in ear height and ear height coefficient at Lishu (Fig. 6, Table S3). In contrast, maize cultivar showed significantly negative trait plasticity in plant height and shoot diameter, and positive trait plasticity in the ear height coefficient and shoot height ratio at Zhangye (Fig. 6, Table S4). Positive trait plasticity between mixtures and monocultures indicated that increasing trait values of cultivars in mixtures than in monocultures and vice versa. Previous studies have found that the resistance of maize to stalk lodging is positively correlated with plant ear height and the ear height coefficient, whereas it is negatively correlated to plant shoot diameter (Novacek et al., 2013). In our case, Lishu was variable in precipitation and had higher wind speeds in the growth periods during the experimental years (Fig. 1a). The positive trait plasticities of shoot diameter and shoot height ratio, and the negative trait plasticities of ear height and ear height coefficient for maize cultivars could produce intraspecific facilitation in cultivar mixtures, which may further buffer wind effects on lodging for maize cultivars in mixtures and maintain whole system yield production at Lishu.

We experimentally manipulated cultivar diversity, which is directly related to genotypic diversity and indirectly related to phenotypic diversity. We do not know all of the ways that cultivar diversity may have been expressed as phenotypic diversity (but see Tables S1, S2), but how genotypic, or species, diversity is manifest in phenotypes is important for understanding BEF relationships in general. For example, Madritch and Hunter (2004) found that within-species variation among individual trees in the phenotypic expression of litter chemistry affected carbon and nitrogen fluxes during decomposition. Models suggest that phenotypic variance corresponds with the ability of different species to react to variation in the environment (Norberg et al., 2001), and variation among cultivars or genotypes might do the same. Norberg et al. (2001) also suggested that long-term ecosystem function might increase with high phenotypic variance among species. Krause et al. (2014) argue that mapping microbial phenotypic traits to genotypes might explain the effects of the latter on ecosystem function. Detailed analysis of traits expressed by our cultivars and correlating them to their responses in monocultures and mixtures might provide even more insight into the role of intraspecific diversity in ecosystem function.

5. Conclusions

In conclusion, our results indicated that cultivar mixtures can enhance both crop production and temporal yield stability, especially under fluctuating or relatively high stressful conditions. To a large degree this positive cultivar effect may be driven by facilitation. Our results also suggest that cultivar mixtures might better adapt to fluctuating conditions via greater complementarity and facilitation, which in turn will increase long-term sustainability. Our findings also help to understand why cultivar mixtures enhance temporal stability in some cases but not in other cases. In sum, our results indicate that cultivar mixtures can increase crop productivity at large scales, much like the effect of species diversity.

CRedit authorship contribution statement

Long Li, Jian-Hao Sun and Ye Su designed the experiment. Hua-Sen Xu and Ye Su collected data. Ye Su, Hua-Sen Xu, Jian-Hao Sun, Jian-Hua

Zhao, Wei-Ping Zhang, Hao Yang and Surigaoge Surigaoge managed the field experiment. Ye Su, Rui-Peng Yu, Ray Callaway, and Long Li contribute to analyze the data. Ye Su and Rui-Peng Yu drafted the paper, and Ragan M. Callaway and Long Li contributed substantially to the conceptual framework and revisions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fcr.2023.109046](https://doi.org/10.1016/j.fcr.2023.109046).

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