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Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield

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Abstract. Extensive research has shown that greater plant community diversity leads to higher levels of productivity and other ecosystem services, and such increased diversity has been suggested as a way to improve yield and agricultural sustainability. Increasing intraspecific diversity with cultivar mixtures is one way to increase diversity in agricultural systems. We examined the relationship between intraspecific diversity and yield in cultivar mixtures using a meta-analysis of 91 studies and >3,600 observations. Additionally, we investigated how environmental and management factors might influence this relationship, and if the yield stability of cultivar mixtures differed from that of monocultures. We found that the yield increased by 2.2% overall in cultivar mixtures relative to their monoculture components. Mixtures with more cultivars and those with more functional trait diversity showed higher relative yields. Under biotic stressors, such as disease pressure, and abiotic stressors, such as low levels of soil organic matter and nutrient availability, this diversity effect was stronger, resulting in higher relative yields. Finally, cultivar mixtures generally showed higher yield stability compared to monocultures, especially in response to annual weather variability at a site over time. This practice of mixing cultivars can be integrated into intensified cropping systems where species monocultures dominate, as well as in smallholder cropping systems where low-cost improvements are in demand. Overall, these results suggest that cultivar mixtures are a viable strategy to increase diversity in agroecosystems, promoting increased yield and yield stability, with minimal environmental impact.

Key words: agroecosystems; biodiversity–ecosystem function; ecological intensification; environmental stress; food crops; small grains; stability; yield.

Introduction

There is increasing pressure on global agriculture to increase yields and feed a growing population (Godfray et al. 2010, Tilman et al. 2011). Simultaneously, there is demand to reduce the environmental impact of agricultural production (Tilman et al. 2011). Ecological intensification may be one way to achieve both of these goals (Bommarco et al. 2013, Garibaldi et al. 2016). Ecological intensification uses biological understanding to replace inputs and restore ecosystem functions to agroecosystems and maintain or increase yields (Petersen and Snapp 2015). Increasing diversity within and across agricultural systems is a key principle of ecological intensification proposed to improve agroecosystem performance and minimize the need for external inputs (Bommarco et al. 2013). Agricultural intensification has decreased both spatial and temporal diversity, and as a rule, agricultural systems have reduced plant species diversity within fields and across landscapes (Meyer et al. 2013). Furthermore, because of crop-breeding goals, which aim to optimize varieties for specific environments and agricultural markets, the genetic diversity within fields tends to be very low.

Experiments in unmanaged ecosystems have shown that increased diversity, typically measured as species richness, is positively related to the overall ecosystem functioning of the community, often measured as total productivity (Hooper et al. 2005, Cadotte et al. 2008, 2009, Cardinale et al. 2011, Grace et al. 2016). A high-functioning community is often a more productive one, where all available resources are utilized by the diverse set of individuals present (Hooper et al. 2005). We are still isolating the specific mechanisms responsible for this increase in functioning, but they likely vary by site and community (Grace et al. 2016). However, the diversity of functional traits present in the community is a very good predictor of ecosystem function (Cadotte et al. 2011). Functional traits ultimately relate to how an organism extracts and utilizes resources from the environment (McGill et al. 2006). Diversity of these traits in a community increases partitioning of the ecosystem resources by organisms, resulting in more complete resource utilization (Cadotte et al. 2011).

Though the types and levels of diversity in agricultural systems may differ from unmanaged systems, we would expect the underlying ecological principles to remain the same, allowing us to enhance agroecosystem functions through increased diversity, which we can do through a number of strategies (Jackson et al. 2007, Costanzo and Bàrberi 2014, Martin and Isaac 2015, Wood et al. 2015).

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Many annual crops are currently grown in continuous monocultures or in rotations that include only two plant species. Temporal plant diversity can be increased by expanding crop rotations to include additional cash crop species, as well as species that serve other functions such as cover crops (Davis et al. 2012). Spatial diversity can also be increased within fields, farms, or across landscapes. Hedgerows or other between-field vegetation, as well as the cultivation of multiple crops in a region, can increase landscape-scale diversity (Staley et al. 2013). Intercropping (increasing interspecific diversity by growing two or more crops together in a field) has been shown to increase productivity (Vandermeer 1989, Lithourgidis et al. 2011). Intercropping is not a common practice in mechanized systems due to the greater complexity of managing two or more species, but there are many examples of intercropping in smallholder systems (Lithourgidis et al. 2011). Cultivar mixtures, the simultaneous cultivation of multiple cultivars of the same species, can increase the intraspecific diversity of monocultures by increasing the genetic diversity present in a species and field. This use of intraspecific diversity is well suited to mechanized systems, which are designed to manage one species at a time, and can provide benefits ranging from reduced disease, weed, and insect pressure as well as improvements in yield and quality (Newton et al. 2009, Grettenberger and Tooker 2015).

Currently, the use of cultivar mixtures in industrial, mechanized agriculture is on the rise and has already become a standard of practice in several regional production systems, mainly for grain production. Cultivar mixtures have been successfully used on a large scale, over 3,000 ha, to reduce disease and increase yield in rice in China and in wheat in East Germany (Wolfe 1985, Zhu et al. 2000, Newton et al. 2009). In Poland, Denmark, and Switzerland, up to 90,000 ha are planted in cereal cultivar mixtures each year (Newton and Swanston 1999, Newton et al. 2009).

Exploitation of the intraspecific diversity present within crop species has a long history in agricultural research, and crop breeding has led to the development of increasingly specialized crop cultivars (Duvick 2005, Fu 2015). Crop breeding selects for desired characteristics and traits to improve yields, and against traits that limit productivity or are not compatible with agricultural management regimes (e.g., mechanical harvest) or consumer expectations. Thus, while a limited number of crop species dominate food production worldwide, there are many cultivars of these species, which are functionally distinct. For example, the domesticated apple has over 7,500 cultivars. While most are selected for their taste and other palatability traits, disease resistance and climate sensitivity also vary widely (Elzebroek 2008). Even in a primarily vegetatively propagated crop like potato, there remains a diversity of several thousand cultivars and landraces (Brush 1995). Despite this diversity, it was the use of a single-cultivar clone that was responsible for the potato late blight epidemic and ensuing famine in 19th-century Ireland, an extreme example of the consequences of low diversity (Machida-Hirano 2015).

Experiments comparing cultivar mixtures (particularly of small grains) to single cultivars dates back to the first half of the 20th century (Frankel 1939). This work has been concentrated in North America, with substantive contributions from around the world. The basic experimental design has changed very little since early work was done, allowing for comprehensive data collection and comparison. Two reviews and one meta-analysis in the last two decades have shown some of the benefits of cultivar mixtures. The earliest review (Smithson and Lenne 1996) provided qualitative conclusions along with a simple quantitative analysis, and showed a slight yield benefit overall across multiple crops, as well as some disease reduction benefits. More recent studies have focused exclusively on small grains. One review (Mundt 2002) highlighted how cultivar mixtures can successfully reduce disease in small grains. A recent meta-analysis (Kiær et al. 2009) was done on a small data set of wheat and barley cultivar mixtures (26 studies, all located in temperate regions). As part of the selection criteria, this study only included studies that reported a measure of experimental variation. Overall, it showed a slight yield benefit for cultivar mixtures in these two crops.

In this study, we conducted a global meta-analysis using an extensive database of 94 studies to assess the impact of intraspecific diversity in a wider range of food crops and growing conditions. First, we compared cultivar mixtures to their component monocultures to determine the effect of mixing on yield, a critical ecosystem service of agricultural systems. We also investigated the impact of environmental factors and growing conditions, as well as how experimental and mixture design might influence yield. We expected that cultivar mixtures would have a greater impact on yields under stressful growing conditions (e.g., nutrient or water limitation). Finally, we tested our prediction that cultivar mixtures would have greater yield stability compared to single-cultivar monocultures over multiple seasons and across sites. Our meta-analysis is the first to examine the yield response and stability of increased intraspecific diversity through cultivar mixtures in a wide range of food crops and environments.

METHODS

Using the *Web of Science* database, we searched the literature for a variety of search terms to target cultivar mixtures of important annual food crops (excluding rice, due to its specialized and varied cultivation) and limited our search to journal articles published in English that fell within the *Web of Science* categories related to ecology or agriculture. While all the results included the matching search terms, there were also papers that that did not test cultivar mixtures as the terms were not used in the context we intended (e.g., individual “cultivar” trials treated with a "mixture" of herbicides). As further search term revisions eliminated some of the cultivar mixtures studies that met our criteria, we reviewed individual titles and abstracts to eliminate nearly 90% of the papers that were clearly not studies of cultivar mixtures. We also reviewed relevant studies referenced in the selected studies, including all digitally accessible papers from two previous reviews (Smithson and Lenne 1996, Kiær et al. 2009). We then individually assessed the remaining >200 papers related to the mixing of cultivars. We included papers in the meta-analysis if they met all of the following specific selection criteria: (1) the study was field based (not conducted in a greenhouse or microcosm) and conducted for at least one full growing season; (2) the study reported either actual yields for all treatments, or relative yield of cultivar mixtures compared to component monocultures; (3) the study included only simultaneous plantings of cultivar mixtures and monocultures, with only one harvest (i.e., not relay planting or multiple cuttings for forage); and (4) a replacement series experimental design was used. Ultimately, 91 papers published between 1939 and 2014 met our four criteria and were included in the meta-analysis (see Appendix S1 for references and full search details). Our database has an additional 77 papers compared to the previous 2009 meta-analysis (Kiær et al. 2009), expanding the range of crops beyond wheat and barley, as well as the geographic extent beyond the temperate region.

Building the database

We built a database of the yield performance of cultivar mixtures along with information on management and environmental conditions that could influence productivity (Tables 1 and 2). For each observation we recorded year, crop species, crop type (legume, non-legume), cultivar count in mixture (two to nine), evenness of cultivar proportions in seeded mixture (even, uneven), and location of the experimental site. Other variables were not reported consistently in all studies, but where available, we included the following: soil organic matter (converted to percentage if not reported as such), N, P, K fertilizer applied, row spacing, seeding rate (kg/ha or number of seeds/m^2), elevation (kilometers above sea level), soil N, P, K levels and soil pH, water management, and disease management. We used DataThief v.1.6 (Tummers 2006) to extract data reported in figures.

We modified and categorized some of the raw data to facilitate analysis of the role played by environmental and management conditions in determining cultivar mixture performance. Latitude was converted to the absolute value, effectively measuring distance from the equator. We categorized climate zone as tropical where the latitude fell between the Tropics of Cancer and Capricorn at 23° and −23° latitude. We approximated the potential of abiotic and biotic stressors using the reported information on soil pH, fertilizer application, water management, and disease management. As optimal soil pH levels are crop specific we categorized site pH as high, optimal, or low using available extension information on recommended growing conditions. For the four crops where pH was reported (seven studies), the optimal ranges were defined as follows: wheat, 6.0–7.0 (Vitosh 1998); barley, 6.0–6.5 (Mallory and Kersbergen 2013); sugarbeet, 6.5–7.0 (Steinke 2014); and field pea, 5.5–7.0 (Pavek 2012). Fertilizer application: While an appropriate indicator of nutrient availability is actual soil nutrient levels, less than 10% of observations reported this information. However, nearly one-half of the studies provided information about fertilizer use so we designated two levels of nutrient availability for these studies as fertilizer applied, yes or no. For water management, we grouped studies as sufficient rain or irrigated, where rainfall was specifically noted by the authors as sufficient or irrigation was used, and rainfed,

TABLE 1. Number of observations (n), between-group heterogeneity (Q_{b}), and P values for relative yield (RY) of categorical variables analyzed as part of meta-analysis of cultivar mixtures.

		RY		
Variable	Levels	n	Q_{b}	P
Crop	barley, corn, legumes, oats, sorghum, soybean, wheat	3,582	0.6065	$\ll$0.001
Crop type	legume, non-legume	3,612	0.0117	0.254
Number of cultivars in mixture	two, three, four or more	3,612	0.1169	0.002
Mixture intention	specified basis, unspecified basis	3,612	0.0486	0.020
Mixture composition basis	disease, physical, both	2,554	0.3615	$\ll$0.001
Soil pH	high, optimal, low	303	0.2317	$\ll$0.001
Fertilizer applied	no, yes	1,432	0.0476	0.020
Water management	rainfed, sufficient rain or irrigated	1,553	0.000	0.950
Disease pressure	high, low	1,315	0.0494	0.015
Mixture evenness	even, uneven	3,612	0.0064	0.406
Purpose of experiment	disease, height, lodging, management, maturity, mixing ability, seeding proportions, spacing, stability, yield	3,612	0.024	0.971
Climate zone	temperate, tropical	3,612	0.6522	$\ll$0.001

Notes: The legumes group includes common bean, common vetch, cowpea, field pea, moth bean, all represented by one study each. Significant Q_{b} values indicate significant differences between classes (Scheiner and Gurevitch 1993).

Table 2. Number of observations (n) and regression results (intercept, slope, slope P values, and adjusted R^2) for relative yield (RY) and continuous variables analyzed as part of meta-analysis of cultivar mixtures.

Variable	n	Intercept†	Slope	P	Adj. R^2
Soil organic matter (%)	240	1.075	−0.028	≪0.001	0.075
Fertilizer applied, N (kg/ha)	1,148	1.004	0.000	0.018	0.004
Fertilizer applied, P (kg/ha)	1,013	1.018	0.000	0.048	0.003
Fertilizer applied, K (kg/ha)	957	1.017	0.000	0.085	0.002
Row spacing (cm)	2,827	1.008	0.000	≪0.001	0.007
Seeding rate (kg/ha)	236	0.991	0.000	0.014	0.022
Seeding rate (no. seeds/m^2)	2,624	1.030	0.000	0.016	0.002
Year	3,180	1.685	0.000	0.016	0.002
Latitude	3,332	1.070	−0.001	≪0.001	0.012
Kilometers above sea level	459	0.991	0.038	0.005	0.015
Soil N (ppm)	259	1.021	0.000	0.079	0.008
Soil P (ppm)	275	1.017	0.000	0.972	−0.004
Soil K (ppm)	86	1.030	0.000	0.561	−0.008

†$P \ll 0.001$ for all.

where it was stated that the experiment was rainfed, but without an indication of rainfall amount or actual water deficit. For disease management, disease pressure was classified as high when reported as moderate to high (typically due to no control methods or inoculation with a pathogen), and low when reported as absent or minimal, or when a control (i.e., fungicide) was used.

To assess the impact of experimental design features on mixture performance, we compiled information from the *Introduction* and *Methods* sections of the papers. Here authors outlined the experimental purpose and selection basis for the cultivars they used in mixtures, and we based our categories for both on author terminology. First, we noted the goals of the experiment in terms of what the authors hoped cultivar mixtures would do compared to the monocultures (for example, improve yield or reduce disease). We then characterized their rationale for the particular cultivar mixtures they tested. When the authors described specific traits or general basis for cultivar selection and mixing, we categorized that as specified and noted the particular characteristics used to construct the mixtures. We classified studies where there was no discussion of mixture rationale as unspecified. For those mixtures where the authors explained a rationale, classified as specified, we also categorized the type of characteristics used to construct mixtures from the component cultivars as either disease or physical, or both. Mixtures created based on physical characteristics included breeding history, heading date, height, lodging susceptibility, growth habit, maturity group, phenology, phenotype, yield potential, and competitive ability against weeds. Anywhere the authors noted the disease response of a cultivar, such as susceptibility or resistance, we categorized the mixtures as having a disease basis. A sizable percentage (~25%) of mixtures considered both disease and physical traits for selection of cultivars.

Few studies reported the complete set of information on experimental design, management practices, and growing conditions necessary for testing all of our hypotheses. When data on yield or critical variables were missing, we contacted the authors and incorporated the data received from these inquiries into the data set. Despite these measures, it was still not possible to collect the full range of variables for all studies, so we conducted some analyses on subsets of the data. Tables 1 and 2 show all the variables collected and analyzed, categorical and continuous, respectively. Also shown are the results for the measures between-group (Q_b) heterogeneity. These are similar to partitioning of variation in an ANOVA; specifically, model sums of squares and error sums of squares, respectively (McDaniel et al. 2014).

Meta-analysis calculations

In meta-analyses, an effect size is calculated to compare evaluate the treatment relative to the control, allowing quantification of trends across a range of experiments and environments. The response ratio, r, which is commonly used as the effect size in meta-analyses is calculated as the mean of the experimental treatment over the mean of the control treatment (Koricheva and Gurevitch 2014). For cultivar mixtures, the experimental treatment is the actual mixture yield, and the control is the expected mixture yield calculated based on the component monoculture yields. Consequently, r is the same as the relative yield (RY) of the cultivar mixtures.

Relative yield (RY) is the metric most commonly used in competition or mixture experiments to compare the productivity of plants grown as monocultures and those grown in combination with others (Weigelt and Jolliffe 2003). This is a useful index for cultivar mixture trials as it indicates when a mixture is more or less productive than expected based on the mixture components in monoculture. This measure automatically accounts for area and seeding proportions when the monocultures and mixtures are grown at the same seeding density (replacement series design). This design is by far the most commonly used in this field. Relative yield for each mixture was calculated as

$$\mathrm{RY} = Y_{\mathrm{mx}}/(Y_{\mathrm{mo1}} \cdot P_1 + Y_{\mathrm{mo2}} \cdot P_2, \mathrm{etc.})$$

where Y_{mx} is the total yield of the mixture, Y_{mo1} is the yield of cultivar 1 in monoculture, and P_1 is the proportion of cultivar 1 in the mixture. An RY > 1 indicates a yield benefit from mixing, an RY < 1 indicates a yield penalty from mixing, and an RY = 1 indicates no change in yield from mixing compared to the component monoculture yields. Converting RY to percentage change in yield for the mixture compared to the component monocultures is calculated as (RY − 1) 100.

We calculated RY using the above formula for the majority of the studies. A small percentage, less than 15% of studies, reported only RY without reporting the corresponding component monoculture yields. For these, we took RY directly as reported in the study. Our final database includes 3,612 mixture treatments, "observations," from 94 experiments reported in 91 published papers.

With RY as the effect size, the measure of the magnitude of the effect of mixing, we used MetaWin version 2.1 software (Rosenberg et al. 2000) to explore the mean response of RY to a variety of environmental and experimental variables (Tables 1 and 2). As RY = r, and RY is already normally distributed (Fig. 1), no transformation was needed to change it to a normally distributed effect size (Tonitto et al. 2006). Very few papers reported study variance. Consequently, we performed an unweighted meta-analysis, assigning a variance of 1 to all observations. To improve the statistical significance of our results without experimental variance, we calculated the mean RY and a bias-corrected 95% confidence interval using a bootstrapping method with 9999 iterations (Tonitto et al. 2006, McDaniel et al. 2014). Means are considered significant if the 95% confidence interval does not cross 1 (Adams et al. 1997). Significant Q_{b} values indicate significant differences between classes, where nonoverlapping confidence intervals can be used as an informal evaluation to distinguish significant contrasts (Scheiner and Gurevitch 1993). However, classes are considered significantly different where Q_{b} is significant even when confidence intervals overlap (see Fig. 5b, for example, and Table 1). Following convention, we acknowledge the lack of independence between mixture observations from the same experiment, from studies in the same journal, and studies by the same author. We have not modified the data set, but rather used a more conservative significance level ($P < 0.03$; Gurevitch et al. 1992). We ran regression analyses of RY and the continuous variables (Table 2) with study as a random effect. As this effect was not significant, we removed it from the final regression results. All regression analyses were performed using R Version 3.1.2 (R Core Team 2014).

Before conducting further analyses of environmental and management effects using subsets of the data, we checked for bias, outliers, and confounding variables. The vast majority (80%) of studies had fewer than 50 observations, with only six studies containing more than 100 observations. We used funnel plots to test for bias, with number of observations in the study as the explanatory variable. Overall, the shape of the scatter remained consistent over the range of observation values, and did not suggest any bias in the data set (Philibert et al. 2012, McDaniel et al. 2014). We identified two observations as outliers in the data for RY. They both came from the same study and were the results of near-complete crop failure of the monoculture plots for three of the four cultivars in one year at one site. Due to extremely low monoculture yields, the RYs of the mixtures were skewed high and did not accurately reflect the effect of mixtures as represented by all other experimental results. We removed these two points (greater than eight standard deviations away from the mean) from the data set. Finally, when we assessed each variable for its effect on RY, we examined possible confounding variables, especially when there was a small sample size. Where there may have been confounding factors, we made a note in the figure legend or the text.

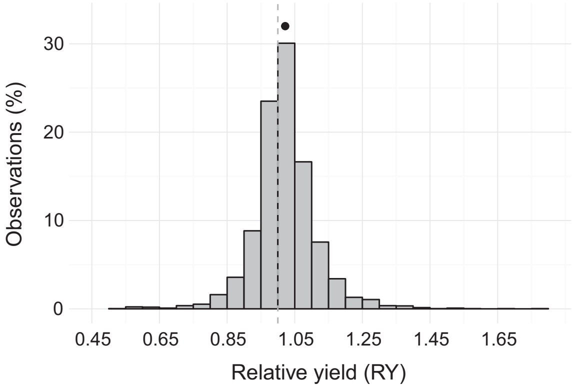

FIG. 1. Distribution of cultivar mixture observations by relative yield (RY). Overall mean shown at RY = 1.0217 (black dot) with 95% bias-corrected confidence interval (1.0187–1.0247), though not visible due to point size. Dashed line at RY = 1, indicating no change in yield from mixing.

Yield stability analysis

A subset of the meta-analysis data set was used to assess the yield stability in monocultures and mixtures in response to varying environmental conditions (e.g., soils, precipitation, rainfall) across spatial and temporal scales. In crop production, stability is the maintenance of yield or productivity at a consistent amount in the face of differing environmental conditions (Newton et al. 2009). For this analysis, we included studies comparing monocultures and mixtures over multiple years at a single site, as well as those across multiple sites for one year.

For the yield stability analysis, we used actual yields rather than relative yields to compare the monocultures and mixtures. We calculated the coefficient of variation (CV) for each cultivar monoculture or mixture either across multiple years for each site (stability over time), or across multiple sites for each year (stability across different environments). Where studies included both multiple sites and multiple years, data were included in both analyses. Additionally, where there were multiple treatments at one site (for example, crops inoculated with disease and disease controlled with fungicide), we separated these treatments for the stability calculation so that this additional treatment did not add to the variability. We averaged the CV for all the monocultures and all the mixtures across sites or years for that study and treatment. We then compared the average monoculture CV to that of the mixtures in a study and classified it as either higher or lower. We counted these classifications to assess the proportion (χ^2 test) of experiments where the variability of the monocultures was higher or lower than that of the mixtures. We also did a Wilcoxon signed rank test on the average CV for monocultures and mixtures for stability across space and across time.

Results

We found studies that tested cultivar mixtures across a wide variety of crops and agricultural regions, but small grains in temperate regions dominated the data set. Small grains accounted for 80% of the mixture observations (wheat, 43%; barley, 20%; oats, 17%), with soybean and corn accounting for 10.5% and 3.5% of the observations, respectively. For the common vegetable crops that we searched, we found no cultivar mixture studies that met our criteria. Most experiments were conducted in temperate regions, with North America accounting for 80% of the observations, with Europe (7.8%) and Asia (6.8%) making up the next largest groups. Oceania, Africa, and South America accounted for very small percentages of the observations (2.7%, 2.2%, 0.7%, respectively).

Many studies of cultivar mixtures share similar characteristics and research goals. Replacement series designs and relative yield have been used from the earliest study in 1939 through to the present. Interestingly, the work on cultivar mixtures has not evolved over this time to include substantive investigations into the mechanisms underlying differences in ecosystem services between cultivar monocultures and mixtures. The experimental purpose varied across studies and often included multiple goals. Yield improvement, particularly in terms of quantity and/or stability, was the most common purpose (91%) for testing cultivar mixtures, with disease control and grain quality improvement accounting for the remainder. Though not included in the data set because they did not report yield, an increasing number of studies in the last 20 yr have investigated the ability of cultivar mixtures to provide supporting ecosystem services such as disease reduction, insect pest and weed suppression, and improved water use efficiency. Only a handful of studies specifically evaluated yield stability, though more than one-half of the studies reported results from either multiple years or multiple sites or both. There was very little overlap in the cultivars used for these experiments so we could not reach any conclusions about whether specific cultivars are better suited for use in mixtures. For example, the 42 studies of wheat mixtures used a total of 77 cultivars with only 13 cultivars used in more than one study.

Relative yield response and impact of growing conditions

Overall, mixtures yielded 2.2% (RY = 1.0217) more than expected based on their monoculture yields (Fig. 1). We observed a significant yield increase for all crops tested in three or more studies, with the exception of sorghum (Fig. 2). Though they have different nutrient acquisition and utilization traits, legume and non-legume crops did not differ in their RY (Table 1). Overall, the RYs of mixtures in the data set closely follow a normal distribution. Fewer than 7% of the mixtures had RY reductions of greater than 10%, which made it difficult to detect patterns leading to such yield losses. In contrast, 14% had RY increases greater than 10%. While most studies only examined two- or three-cultivar mixtures, resulting in mean RYs of 1.02, mixtures with four or more cultivars had a much higher mean RY (RY = 1.05; Fig. 3a). Relative yields did not change with year over the range of the data set, showing the consistency of the

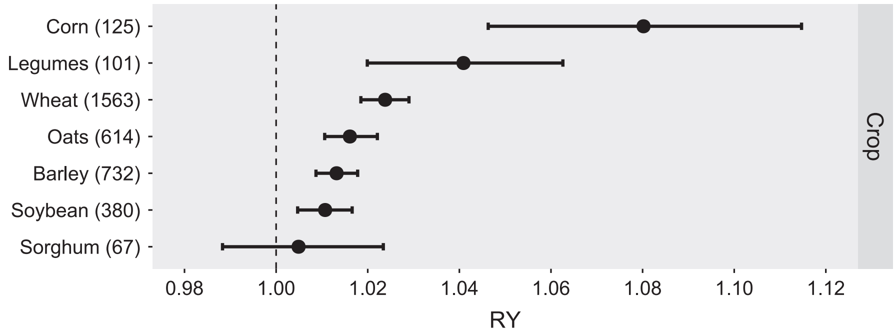

Fig. 2. Effect of crop on RY of mixtures. Mean values and 95% bias-corrected confidence intervals for the RY are shown, with the number of mixture observations in parentheses. Dashed line at RY = 1, indicating no change in yield from mixing. The legumes group includes common bean, common vetch, cowpea, field pea, moth bean, all represented by one study each. Not shown here are one study of rye and sugarbeet each. All other crops or groups are represented by three or more studies.

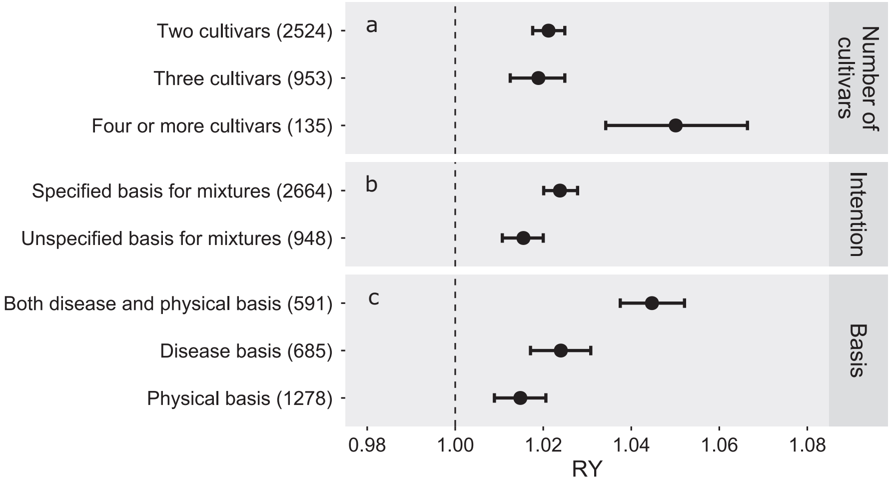

FIG. 3. Effect of mixture composition on RY of mixtures. (a) Number of cultivars in mixture (the four or more cultivar group contains observations from 20 studies, across eight crops). (b) Mixture intention, specified or unspecified by study author. (c) Mixture composition basis, characteristics of cultivars in mixtures with a specified basis. Mean values and 95% bias-corrected confidence intervals for the RY are shown, with the number of mixture observations in parentheses.

effect of cultivar mixtures across time, even with substantial changes in management, such as breeding and input use, over the seven decades (Table 2).

Experimental design

Some decisions around experimental design and management can have a substantial impact on RY of mixtures, while others are insignificant. The experimental purpose and/or intent of the study did not have a significant impact on the RY of the mixtures in the trials (Table 1). However, mixtures constructed with a specified basis for selecting particular cultivars had higher RYs compared to mixtures where no rationale was stated (Fig. 3b). Planned mixtures based on both disease and physical characteristics were significantly better than those mixtures based on either a physical or a disease basis alone (Fig. 3c). Management decisions related to seeding of cultivars in mixtures (row spacing and seeding rates) had no effect on the RY outcome. The evenness of the mixture did not have a significant impact on the RY, though even mixtures had a greater mean and were almost four times more frequent in the data set (Table 2).

Effect of abiotic and biotic stressors

We found that a variety of environmental characteristics and related biotic and abiotic stressors influenced the performance of cultivar mixtures and RY. Reporting of certain variables was inconsistent across studies, making it necessary to use subsets of the data to test hypotheses about the role of environmental and biotic stress (see *Data limitations and further research*). We found a negative correlation between soil organic mater (SOM) and RY (Fig. 4), suggesting that, in environments where nutrient supply from organic matter mineralization may be more limited, mixtures resulted in greater yield benefits. Soil pH levels that were below crop-optimum levels positively affected RY, while soils with pH levels above crop optima substantially reduced the RY of mixtures (Fig. 5a), possibly due to reduced availability of nutrients such as phosphorus. Following the trend suggested by the impacts of SOM content and pH on RY, we found that RY was greater in studies where no fertilizers were applied (Fig. 5b). When we used actual fertilizer rates as a continuous variable, the slope of the relationship between amount of fertilizer applied and RY was near zero for N, P, and K (Table 2). Soil nutrient content (N, P, and K) had no detectable relationship with RY, similar to fertilizer applications (Table 2). We also did not detect any differences in the RY of irrigated mixtures compared to those grown under rainfed conditions (Fig. 5c).

Disease pressure was the only biotic stress we were able to quantify in the database. Mixtures in environments with high disease pressure had greater RY compared to those grown under conditions with little or no disease pressure (Fig. 5d). However, when mixtures were intentionally constructed based on disease characteristics, there was no difference in RY under high or low disease pressure (Fig. 6a). This may be due to poor selection of cultivars, or limited resistance. It is possible that mixtures reduced disease compared to the monocultures, without a corresponding yield increase. However, where mixtures were constructed based on both disease and physical traits, there was a significant RY increase under high disease pressure conditions. In environments with low disease pressure, RY did not differ between mixtures constructed with only a disease basis and those with a combined disease and physical basis (Fig. 6b).

The effects of larger scale abiotic conditions on RY, such as those dependent on latitude, had a greater effect

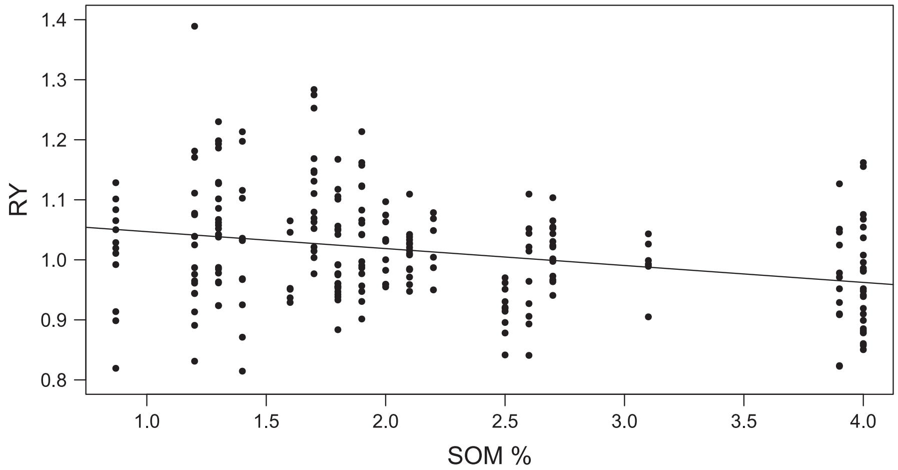

FIG. 4. The relationship between soil organic matter percent (SOM %) and RY shows an increase in RY with lower SOM % (black line, $R^2 = 0.0748$, $F_{1,\ 238} = 20.32$, $P \ll 0.001$, $y = 1.075–0.0282x$). Data from six papers (240 observations), encompassing sites with 17 unique SOM levels.

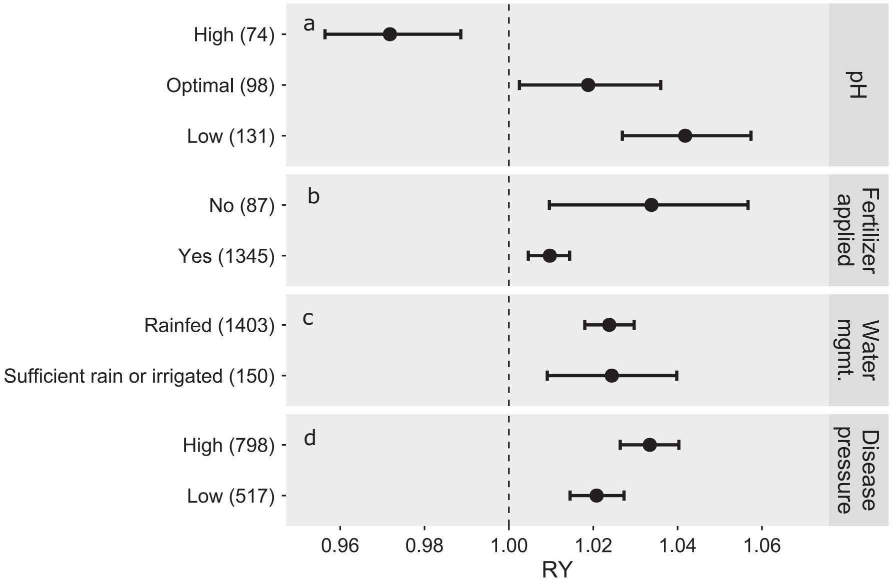

FIG. 5. Effect of environmental stress on RY of mixtures. (a) The pH of soil categorized by suitability for individual crops. Both the high and low pH categories consist of observations from three unique studies, while one study containing multiple sites provided observations in all three categories. (b) Nutrient stress evaluated as fertilizer applied or not. The group with no fertilizer applied included six studies of three crops and three continents). (c) Water stress evaluated as water management (mgmt.): only rainfed or sufficient rain or irrigated. (d) Disease stress evaluated as disease pressure: high (when disease was present and/or no control was used) or low (when control was applied and/or no disease was present). Mean values and 95% bias-corrected confidence intervals for the RY are shown, with the number of mixture observations in parentheses.

than those driven by elevation. Those studies conducted closer to the equator in the tropical region had significantly higher RYs than those studies conducted in the temperate region, which constituted the vast majority of observations (Fig. 7). Latitude as a continuous variable follows the trend suggested by the climate zones with a weak, but significant, negative relationship with RY (Table 2). The weak and insignificant relationship between the elevation of the experimental site and RY, suggests that latitudinal position has a stronger influence on RY than the effects of elevation (Table 2).

Yield stability analysis

Overall, we found that, compared to mixtures, monocultures tended to have greater yield variability, as measured by average CV of yield (Fig. 8). However, the yield stabilizing effect of cultivar mixtures in response to

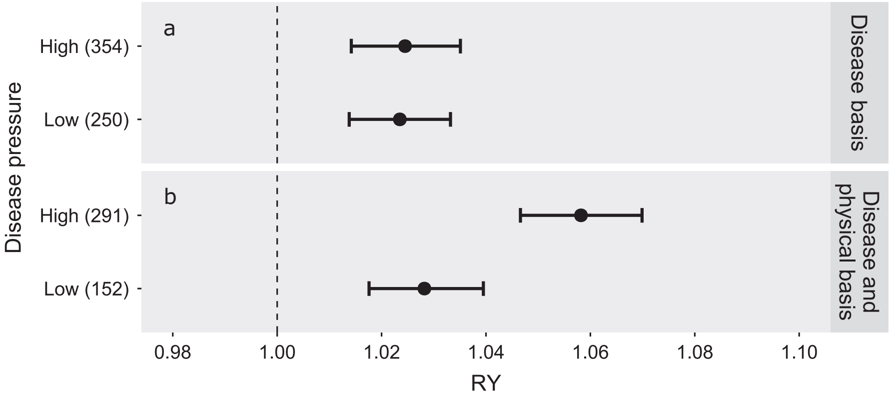

FIG. 6. Effect of mixture basis on RY of mixtures under high and low disease pressure. (a) Mixtures based on disease characteristics of component monocultures. (b) Mixtures based on both disease and physical characteristics. Mean values and 95% bias-corrected confidence intervals for the RY are shown, with the number of mixture observations in parentheses.

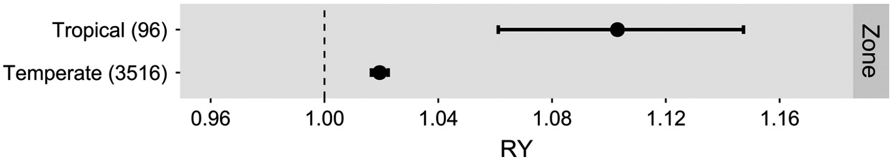

FIG. 7. Effect of climate zone on RY of mixtures. Mean values and 95% bias-corrected confidence intervals for the RY are shown, with the number of mixture observations in parentheses.

seasonal fluctuations in weather in one location over time was stronger compared to the response to variation in one season from environmental conditions across a study area (Fig. 8). In fact, there was no difference between average CV of monocultures and mixtures over multiple sites in the same year (Fig. 8). The percentage of trials where the monoculture is more variable than the mixture was significant only when examined over time (61%, $\chi^2 = 5.24$, df = 1, $P = 0.022$), and not over space (59%, $\chi^2 = 1.59$, df = 1, $P = 0.208$). Using both average CV and the percentage of trials showing increased variability in monocultures, mixtures have a stronger stabilizing effect on yield over multiple growing seasons, compared to their weaker effect on yield stabilization over a geographic area in one growing season (Fig. 8).

DISCUSSION

Reincorporating diversity into agroecosystems to promote ecosystem services is one viable approach for reducing environmental impacts while maintaining and even increasing yields (Kremen and Miles 2012). The practice of planting cultivar mixtures, which increases intraspecific diversity in monoculture fields where diversity is very low, contributes to increased overall diversity from the field to landscape scale. This additional diversity promotes ecosystem services, including increasing and stabilizing yield. The 2.2% overall yield increase we found for cultivar mixtures compared to the expected yield from their component monocultures is small, but comparable to the average annual rate of yield gain due to plant breeding improvements of between 1% and 3% (Fernandez Cornejo 2004). The prospect of this small yield gain from breeding regularly drives farmers to purchase the newest cultivars. The fact that the RY benefit from mixtures has not changed over the seven decades in this review shows that the practice of mixing cultivars is robust and compatible with the consistent improvement of plant genetics and other changes in management (Table 2). In addition to the overall yield benefit that we found, stressful environments appear to strengthen the positive diversity response, fitting with the stress-gradient hypothesis (Li et al. 2007, He et al. 2013, Tang et al. 2016). Finally, we found that the yield stability of mixtures from one growing season to the next is generally higher than that of monocultures, a potentially important factor for farmers as climate-influenced environment conditions become more variable.

Increased yield

While we are limited in our ability to isolate the specific mechanisms responsible for the RY increase observed in cultivar mixtures, the ability of the community as a whole to maximize available resource use through distinct functional traits is likely a major driver. Functional traits characterize an organism's response to the environment and/or effect on the ecosystem functioning, which relates to resource use by individuals and ultimately the community as a whole (Díaz and Cabido

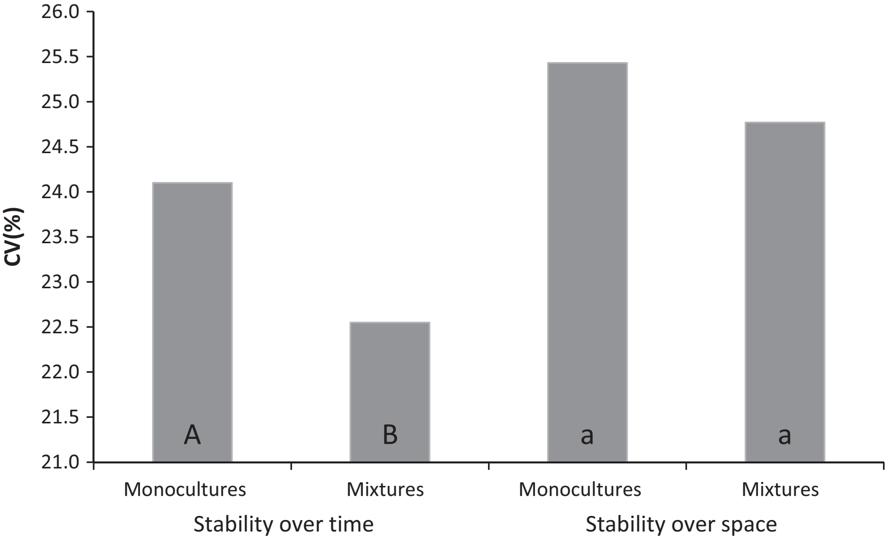

FIG. 8. Yield stability over time (multiple years at the same site, n = 2,191 observations) and over space (multiple sites in the same year, n = 1,412 observations). Bars show the average coefficient of variation (CV), with monocultures more variable than mixtures when examined over time only (Different letters within each measure of stability indicated significant differences based on a paired Wilcoxon signed rank test, over time, V = 3198, P = 0.035; and over space: V = 757, P = 0.380).

2001). Functional diversity encompasses the values and range of these traits in the community (Díaz and Cabido 2001). A more functionally diverse community has greater resource partitioning, potentially utilizing the available resources more efficiently and ultimately increasing overall productivity and function (Cadotte et al. 2011). Recent reviews of studies in unmanaged ecosystems, both aquatic and terrestrial, have confirmed an overall relationship between various measures of diversity, including species richness and functional diversity, as well as productivity response (Weiss et al. 1990, Cadotte et al. 2011, Cardinale et al. 2011). As cultivars are specifically bred for desirable and distinct functional traits, we would expect mixtures of cultivars to be functionally diverse, and display a similar relationship between functional diversity and productivity. Specifically, we would expect cultivar richness, as well as targeted trait selection in mixtures, to increase functional diversity and ultimately productivity.

Three lines of evidence from this study demonstrate the positive relationship between functional diversity in cultivar mixtures and increases in RY. First, we saw that higher cultivar richness, specifically mixtures with four or more cultivars, results in higher RY compared to mixtures with a richness of two or three, and all had increased RY compared to the monocultures (Fig. 3a). Second, beyond the simple richness effect, the impact of cultivar mixtures is increased when they are specifically designed to include greater functional diversity. The specification of a basis or rationale for selection of specific cultivars in the mixtures by the authors suggests an awareness and intentionality related to traits that may result in more functionally diverse mixtures. We do in fact see greater RYs in mixtures constructed with a specified basis for the selection of component cultivars compared to mixtures without such a specified basis (Fig. 3b). Third, where mixture composition was intentionally based on both disease and physical traits, we see a substantial increase in RY (Fig. 3c). We would expect these mixtures to have greater functional trait diversity, compared to mixtures based on either disease or physical traits in isolation, as the traits for disease resistance or physical characteristics rarely overlap, providing a larger range of functional traits. This independence of disease and physical traits is supported by the fact that there was no difference in the RYs of mixtures where cultivar selection was based on these traits alone.

Stress and environmental conditions

The response of cultivar mixtures to certain environmental conditions and stress may be responsible for the wide range of RY responses we found in the data set (Fig. 1). The insurance hypothesis predicts that ecosystem function will be maintained in more diverse communities due to the divergent responses of species (or other organismal groupings) to environmental conditions (Naeem and Li 1997, Yachi and Loreau 1999, Jackson et al. 2007). Though the mechanisms responsible for this maintenance of function may differ slightly at the cultivar level, there is likely overlap with those suggested for higher levels of diversity (e.g., species). Additionally, landraces (heterogeneous populations of locally adapted crop species) have long been known to be more successful than modern cultivars in stressful conditions (Newton et al. 2010, Dwivedi et al. 2016). The genetic and phenotypic diversity in these landraces is very high, resulting in great functional diversity (Dwivedi et al.

2016). Therefore, we expected that under stressful environments cultivar mixtures might provide greater benefits in terms of yield outcomes. Fundamentally, stressful conditions may make the improved function and associated productivity of a diverse community more apparent, as efficient use and sharing of resources is more important. As an example, one experiment found no relationship between species richness and productivity of bryophytes under constant conditions, but under drought conditions, higher species richness increased survivorship of all species, due to facilitation (Mulder et al. 2001). The results of a recent meta-analysis of global plant communities support the stress-gradient hypothesis and showed that most plant interactions respond to stress, and typically shift toward facilitation and reduced competition (He et al. 2013).

Across the range of abiotic stresses we were able to quantify in the database, we found a clear trend toward higher RY outcomes under more stressful conditions, but the strength varied between the different stresses. The lack of consistent reporting of environmental conditions in the studies reduced our ability to make strong conclusions (see *Data limitations and further research*). However, we were able to analyze the impact of two key soil characteristics: soil organic matter (SOM) and pH. SOM correlates with higher water-holding capacity, improved aeration, and greater aggregate stability of soils. SOM is not only a key source of plant nutrients during decomposition, but it also helps to retain nutrients in the soil, and subsequently enhance their availability to plants by increasing cation exchange capacity (Hudson 1994, Reeves 1997). We observed a clear trend of increasing RY with decreasing SOM levels, which would indicate conditions that are more stressful for plant growth (Fig. 4). We tried to isolate the effect of nutrient stress specifically in two ways: fertilizer application and soil nutrient status. The small set of unfertilized mixtures had a substantially higher mean RY compared to those where fertilizer was applied (Fig. 5b), and even with the large range, was significantly different from the fertilized set (Table 1). The lower RYs for mixtures under more ideal, fertilized conditions suggest that there is less benefit of mixtures when resources are not limiting. This may be because the differential and more complete root exploitation by cultivar mixtures is not as necessary in these better conditions. Alternately, mixtures could yield as well as monocultures with less inputs, reducing associated environmental impacts and costs (Elser et al. 2014). Soil nutrient status showed no significant trends for N, P, or K, likely due in large part to the underreporting of these conditions, which were available for less than 10% of observations in data set (Table 2).

Our results showing a significant impact of soil pH on RY also support this relationship between plant nutrient stress and diversity. Mixtures performed substantially better in more acidic conditions than basic ones (Fig. 5a). Macronutrient (N, P, K, S, Ca) concentrations tend to be less in acidic soils (Brady and Weil 2008). In contrast, micronutrient cations are often more available at lower pH, but can sometimes become too available and toxic, especially manganese and aluminum (Barak et al. 1997, Fageria et al. 2002, Brady and Weil 2008). Where pH is low, the coexistence of multiple cultivars may be able to ameliorate the potentially toxic conditions. First, multiple cultivars are able to more completely exploit the soil profile with different root architectures, increasing the overall production and distribution of root exudates. These exudates promote microbial decomposition, the products of which form complexes with aluminum, reducing its toxicity (De la Fuente-Martínez and Herrera-Estrella 1999, Brady and Weil 2008).

We observed an enhanced yield response under the biotic stress of high disease pressure, especially in the most functionally diverse mixtures. Overall, mixtures experiencing disease stress had higher RYs, perhaps because of mortality and compensation by other cultivars, or some form of facilitation reducing the spread of disease (Fig. 5d; Brophy and Mundt 1991). Mixtures constructed with a disease-trait basis had the same RY response regardless of the disease pressure (Fig. 6a). However, the more functionally diverse mixtures had significantly higher RY responses under high disease compared to low disease pressure (Fig. 6b). These functionally diverse mixtures were those constructed with both disease and physical traits in mind. The benefit of increased functional diversity in these mixtures was most important in this high-stress (high disease) environment. From these two comparisons, we might conclude that not only is the diversity effect strengthened under stressful conditions, but also that the inverse is true: we may not see a stress response if the community is not sufficiently diverse (as in the mixtures with a disease basis). With disease pressure expected to increase with climate change, this benefit of mixtures may be particularly relevant (Tripathi et al. 2016).

Yield stability

Stability (low variation of yield over time or space) under stressful or less than ideal conditions is gaining in importance for breeding, but is rarely a goal on its own, as achieving acceptable yields when conditions are favorable remains paramount. Landraces have persisted for hundreds to thousands of years, not because of their high yields, but rather their ability to adapt to environmental conditions and maintain adequate yields (Newton et al. 2010, Dwivedi et al. 2016). In environments where uniform conditions are achieved with inputs and where there is a favorable climate, modern cultivars excel and outperform the genotypically and functionally diverse landraces (Mohammadi et al. 2014, Yahiaoui et al. 2014). As we found in this study, cultivar mixtures with their increased intraspecific diversity generally showed improved yield stability compared to monoculture (Fig. 8). Cultivar mixtures may be a way to integrate the yield benefits of modern breeding with the stability from genetic diversity similar to landraces.

Ecologically, our understanding of the relationship between stability and diversity is still developing. A recent review found that both productivity and stability over time increased with increasing diversity across a range of unmanaged ecosystems; however, the effects were independent of one another (Cardinale et al. 2013). Mechanistically, there is not yet a clear understanding of what drives this diversity–stability relationship. However, the insurance hypothesis again provides a useful framework. For example, cultivar-specific mortality in an early drought allows better adapted cultivars to exploit this additional space, compensating for the loss of individuals and maintaining productivity (Cadotte et al. 2012). This may be particularly true for small grains with the ability to tiller and fill space left by less successful cultivars. Facilitation may also play a role, with some cultivars providing a more hospitable growing environment for others that might otherwise fail under the given conditions (Mulder et al. 2001).

In our study, we observed a much stronger yield-stabilizing effect of diversity in response to weather variability as opposed to the broader environmental variability of sites in a region. We assessed yield stability by splitting the data set in two ways, each capturing a different type of variability. Yield stability of the cultivars and mixtures over multiple seasons at one site primarily reflects the response to weather variability, specifically, tolerance or resistance to annual variations in rainfall and temperature, keeping constant other environmental conditions (i.e., other ecosystem state factors such as soil properties). In contrast, yield stability across multiple sites in one season reflects the response to the variability of environmental conditions across an experimental region in addition to localized weather variability. While we might expect mixtures to increase the yield stability across sites, as different cultivars might each thrive in different sites and conditions, we are not able to separate this variation from that of the weather. Additionally, the interactions between weather variability and site conditions may have inhibited our ability to detect a stronger diversity effect across sites (Fig. 8). Where only annual weather variation is concerned, there is a clear stability-over-time advantage of mixtures compared to monocultures. We see this in terms of both average CV and the percentage of trials where monocultures were more variable (Fig. 8). Recent climate modeling of crop performance has shown that, as annual weather variation increases, so does yield variability (Porter and Semenov 2005). More specifically, when temperature variation is increased and mean temperature held constant, yield variability responds much more dramatically than absolute yield losses (Porter and Semenov 2005). Weather variability is a powerful driver of yield-stability outcomes, and mixtures appear to be able to buffer some of that variability.

Data limitations and further research

As our technical ability to analyze large data sets through meta-analyses and other methods increases, it is critical that all researchers report complete experimental methods and site conditions in as much detail as possible. This additional information will allow us to advance our understanding of the mechanisms underlying the effect of intraspecific diversity on yield and other ecosystem functions. Specifically, authors should prioritize the reporting of basic soil and climate conditions for the site, along with standard management practices including fertilizer and pesticide applications and water management. With these data and an improved understanding of mechanisms, we can better isolate the conditions where cultivar mixtures will be either beneficial or detrimental to RY. For example, with more extensive reporting of soil pH and SOM, our findings would be applicable to a larger range of conditions. Additionally, we could have investigated interactions between these basic soil characteristics with management practices such as fertilizer application, a critical assessment for practical applications.

A specific challenge to advancing our understanding of mechanisms in cultivar mixtures is the difficulty of separating the component cultivars in the mixture after harvest for measurement and analysis. The few studies in this meta-analysis that were able to separate cultivars used characteristics such as seed color, or developed clever methods of planting and hand-harvesting to track cultivars in the mixture and maintain separation at harvest (Brophy and Mundt 1991, Finckh et al. 1999, Worster and Mundt 2007, Fang et al. 2014). More work along these lines will help us to understand the mechanisms behind improved, or depressed, RY in cultivar mixtures.

In addition to a more detailed understanding of the drivers behind yield increases in cultivar mixtures, we should broaden our scope to include other important ecosystem services. Though still limited, more papers are looking at the relationship between intraspecific diversity and water use efficiency (Song et al. 2010, Haghshenas et al. 2013, Fang et al. 2014, Adu-Gyamfi et al. 2015) and insect pest regulation (Weiss et al. 1990, Vera et al. 2013, Pan and Qin 2014). Specifically, compared to mono-cultivar planting, cultivar mixtures can reduce the abundance of herbivore pests such as aphids and whiteflies, which have similar characteristics to pathogens and thus may be controlled well with intraspecific diversity (Tooker and Frank 2012). However, there is less data on the potential for cultivar mixtures to affect natural enemy populations and this area particularly warrants additional attention (Jones et al. 2011, Tooker and Frank 2012). Other services relevant to agroecosystems that may respond to increased diversity include nutrient retention and use efficiency, soil organic matter accumulation, weed suppression, and crop pollination.

Management implications

Diversifying our monoculture-dominated landscape with cultivar mixtures is a tractable first step toward ecological intensification for farmers globally. In the long term, increasing species diversity and other larger scale spatial and temporal diversification strategies aimed at increasing agricultural diversity will likely be more important and effective in enhancing ecosystem services (Davis et al. 2012). Cultivar mixtures can be integrated into mechanized and input-intensive systems where single-crop cultivation is the norm, and increased yield potential a constant goal. Specifically, mixtures may be one tool to reduce external inputs, such as fertilizers and pesticides, which are often fossil-fuel intensive and known to have negative effects on surrounding environments (Tilman et al. 2011, Schipanski et al. 2016). This may result in increased profitability, as there are fewer costs, with a similar or increased yield. Additionally, cultivar mixtures may help to manage pest resistance as demonstrated by the use of Bt and non-Bt corn to create integrated refuges. As of 2014, almost one-half of all growers surveyed in 2014 exclusively planted seed mixtures for this purpose (Grettenberger and Tooker 2015). Of course, proper selection of cultivars is important to ensure a similar maturation time and compatibility with existing mechanical management such as combine height settings for harvesting beans.

Wider acceptance of cultivar mixtures in the marketplace would likely increase adoption of mixtures by growers. Modern malting operations prefer single cultivars as there is the assumption of greater homogeneity, however this view is increasingly challenged with mixtures delivering equivalent quality for a range of metrics (Newton and Swanston 1999, Newton et al. 2009). Additionally, for other uses such as alcohol production for distilling or biofuels, single cultivars are still the norm, but there may be no benefit for pure batches, and mixtures may in fact allow for greater total production (Newton et al. 2009). Cultivar mixtures can be indistinguishable from single cultivars in terms of baking and end-loaf quality for bread wheat (Manthey and Fehrmann 1993, Mille et al. 2006). While more research demonstrating the viability of cultivar mixtures for a range of end uses would be helpful, collaborations that ensure growers will have a buyer for their cultivar mixtures will likely do more to advance cultivar mixture acreage.

For small-scale farmers or those in low-input systems where stress may be more intense, the diversity benefits for yield would have an even greater impact. It is not uncommon for farmers in these systems to grow both modern varieties as well as local varieties or landraces (Kolech et al. 2015). Additionally, as farmers are already familiar with cultivating landraces tailored to specific regional and farm-level conditions, creating cultivar mixtures with available modern varieties already grown in the area might be an accessible next step. This intraspecific diversity increase is also compatible with existing technologies and practices to reduce the yield gap, as the fundamental structure of the plant community is not different from existing monoculture production. As these smallholder and low-input systems occupy more heterogeneous environments compared to more typical, mechanized systems, increased reliance on participatory breeding, rather than traditional, centralized breeding, will be more important (Dawson et al. 2008).

Our results showing increased yield stability with cultivar mixtures have important implications for management strategy, especially as climate change is projected to result in more variable weather and environmental extremes. Mixtures alone may not substantially reduce the variability associated with multiple fields on a farm, but they can reduce the variability that might be experienced over years within one field. For farmers concerned about yield stability, planting a portion of their farm in cultivar mixtures may help to provide consistency in production in the face of weather variability. The importance and impact of yield stability may differ for farmers around the world. For farmers in the developed world, consistent and predictable yields influence planting decisions, cash flow, and long-term farm viability (Koesling et al. 2004). In the developing world, widely variable yields can have a direct impact on food security, as well as market prices and cash flow (Sinebo 2005, Asrat et al. 2010). Cultivar mixtures are a practical way for all farmers potentially to reduce their yield variability over time.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1629/full

DATA AVAILABILITY

Data available from Cornell University's eCommons: https://doi.org/10.7298/x4tx3chf