Field Crops Research 221 (2018) 298–313

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Unfolding the potential of wheat cultivar mixtures: A meta-analysis perspective and identification of knowledge gaps

J. Borg[a,*], L.P. Kiær[b], C. Lecarpentier[a], I. Goldringer[a], A. Gauffreteau[c], S. Saint-Jean[d], S. Barot[e], J. Enjalbert[a]

[a] UMR Génétique Quantitative et Evolution le Moulon INRA, CNRS, UPS, 91190 Gif-sur-Yvette, France
[b] Department of Plant and Environmental Sciences, University of Copenhagen, DK-1871 Frederiksberg, Denmark
[c] UMR Agronomie INRA, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon, France
[d] UMR ECOSYS INRA, AgroParisTech, Université Paris-Saclay, 78850 Thiverval-Grignon, France
[e] IEES-Paris (IRD, CNRS, UPEC), 7 quai Saint Bernard, 75005 Paris, France

A R T I C L E I N F O

Keywords:
Wheat
Cultivar mixtures
Meta-regression
Overyielding
Disease reduction
Stress gradient hypothesis

A B S T R A C T

Increasing the biodiversity of cropped plants is a key leverage for agroecology, aiming to replace chemical inputs by ecological processes and regulations. Cultivar mixtures are a straightforward way to increase within-crop diversity, but they have so far been poorly used by farmers and they are not encouraged by advisory services. Based on the methodology developed by Kiær et al. (2009), we achieved a meta-analysis of cultivar mixtures in wheat. Among the 120 publications dedicated to wheat, we selected 32 studies to analyze various factors that may condition the success or failure of wheat mixtures by calculating overyielding, i.e. the difference in productivity of a variety mixture compared with the weighted mean of its component varieties in pure stand. The analysis highlighted a significant global overyielding of 3.5%, which reached 6.2% in condition of high disease pressures. Overyielding was not affected by seeding density or plot size. Under high disease pressure, overyielding increased by 3.2% point per added component variety. Overyielding was respectively 5.3% and 3.3% higher for mixtures heterogeneous in disease resistance or phenology than for homogeneous ones, and did not vary when considering height. Overyielding reached its highest values in the 1980s and 1990s, which reflects the predominance of disease-focused studies during this period. Our results confirm that cultivar mixtures are a potential way to increase yield relatively to pure varieties, especially under low pesticide cropping systems. Literature suggests that mixture practice is impeded by the lack of general rules that could help to mixing varieties. To design such rules it is needed to (1) achieve new experiments manipulating the heterogeneity in variety traits, (2) determine experimentally the ecological mechanisms underlying mixture performance and (3) develop new models allowing testing and analyzing these mechanisms.

1. Introduction

High yield gains have been achieved during the 20th century through the breeding of elite crop lines or hybrids adapted to the homogeneous cropping conditions of modern agriculture (Tilman et al., 2001) that strongly relies on chemical inputs and simplified rotations. However, this agricultural model seems to reach its limits, and many authors point out the side effects of intensification: water and air pollution, greenhouse gas emissions, deleterious impacts on natural ecosystems and human health issues (Carpenter et al., 1998; Robertson et al., 2000; Vitousek et al., 1997). Besides, agriculture is facing global climate changes, which is in part responsible for an increase in annual variability and, for some crops, a stagnation of yields (Brisson et al., 2010; Grassini et al., 2013). Stabilizing the production and switching to a more sustainable agriculture requires a paradigm shift, as advocated by many authors (Altieri, 1989; Malézieux, 2011). Adopting agroecological practices is one of the options for such a shift. Covering a wide range of practices, agroecology aims to replace chemical inputs by ecological processes and regulations. Biodiversity, whether species diversity (Loreau et al., 2001) or genetic diversity within species (Hughes et al., 2008) has been shown to play a critical role for the functioning of natural ecosystems, and increasing diversity of cropped plants has been proposed as a key leverage for agroecology (Malézieux, 2011). Many ecological mechanisms identified in natural ecosystems, such as complementarity and facilitation, are also at play within crop fields, both in co-culture of multiple species (Gaba et al., 2015; Litrico and Violle,

* Corresponding author.
E-mail address: julie.borg@inra.fr (J. Borg).

http://dx.doi.org/10.1016/j.fcr.2017.09.006
Received 13 June 2017; Received in revised form 22 August 2017; Accepted 7 September 2017
Available online 28 September 2017

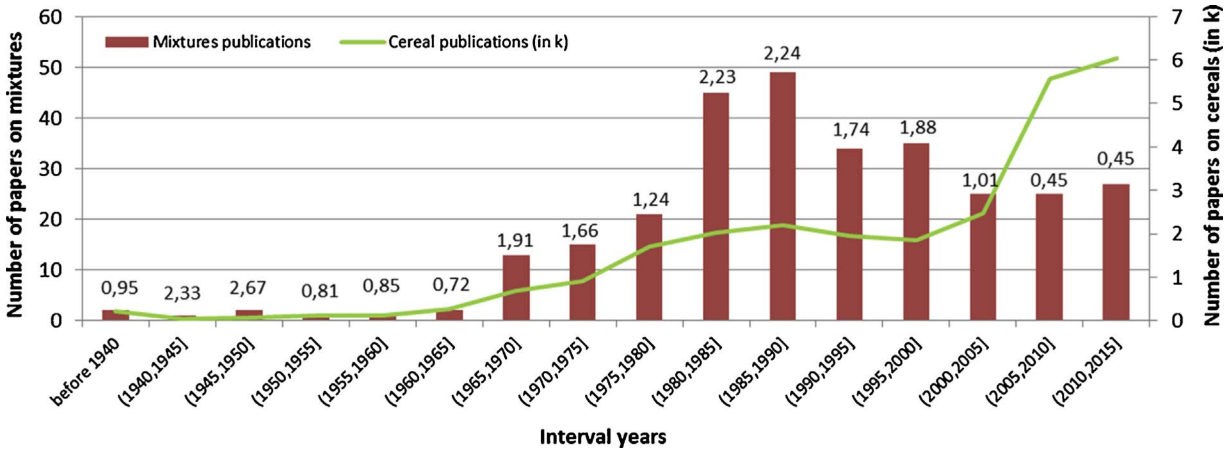


Fig. 1. Global evolution of publications concerning cereal cultivars (26,250 papers) and cereal cultivar mixtures (298 papers) between 1939 and 2015. The proportion of publications on mixtures compared to publications on cereals is represented at the top of the bars.

2015) and in cultivar mixtures (Barot et al., 2017). Cultivar mixtures (variety blends) are certainly the most straightforward way to increase within-crop diversity and their documented use in agriculture dates back to the eighteenth century (Wolfe, 1985). The interest of scientists for genetic diversity and cultivar mixtures in cereals rose in the late 1960s and remained constant during twenty years, as illustrated by the number of publications on the subject (Fig. 1).

However, after the 1990s the number of publications on cultivar mixtures dropped to approximately 4 publications/year since year 2000. Indeed, such stagnation denotes a declining interest of scientists for the subject, when compared to the strong increase in publications dealing with cereals genetics and agronomy in general (Fig. 1). Interestingly, the main themes addressed by publications on cereal mixtures also varied across years (see Fig. 2 and also supplementary material). First, one predominant question has been whether mixtures can outperform in yield their pure component varieties, i.e. present “overyielding”. Second, the burst in cultivar mixtures studies between 1970 and 1990 was mainly carried by phytopathologists encouraged by success stories such as spring barley mixtures in Germany that reduced powdery mildew incidence and fungicide use by 80% during 1984–1990 (Wolfe et al., 1992). Third, more recently, new interests for cultivar mixtures have emerged due to raising concerns about the sustainability of agriculture, leading to a diversification of research themes (Fig. 2), more oriented towards a better understanding of the ecological mechanisms involved in the ecosystem services potentially provided by mixtures (Gaba et al., 2015). Examples include exploitation of water (Adu-Gyamfi et al., 2015; Fang et al., 2014; Wang et al., 2016), control of insect pests (Shoffner and Tooker, 2013; Smith et al., 2014) and weed suppression (Kiær et al., 2009).

Despite some success stories in the past (Finckh et al., 2000), there has been a very limited use of cultivar mixtures by farmers in developed countries, and an even more limited incitation by most farm advisory services. Besides practical and legal barriers in the wheat chain that can impede cultivar mixture adoption, two main explanations can be proposed for the poor use of cultivar mixtures. First, the strong positive effects of cultivar mixtures might have been demonstrated under specific environmental and cropping conditions that do not correspond to dominant cropping systems. For example, mixtures could present positive effects under high disease pressures and low input levels that are not common under intensive agriculture. Indeed, according to the stress gradient hypothesis (Lortie and Callaway, 2006), overyielding should increase with disease pressure and abiotic stress because stresses can foster positive interactions and complementarity and compensation between the varieties of the mixture (Creissen et al., 2013). Second, academic researchers might have missed to address key questions on mixtures, partly because the development of alternative studies (as in agroecology) has stayed on the margins of dominant policy and research objectives, leading to a lock-in situation (Vanloqueren and Baret, 2009). For example, multi-resistant varieties that can contribute to the reduction of pesticides use have a little commercial success, partly due

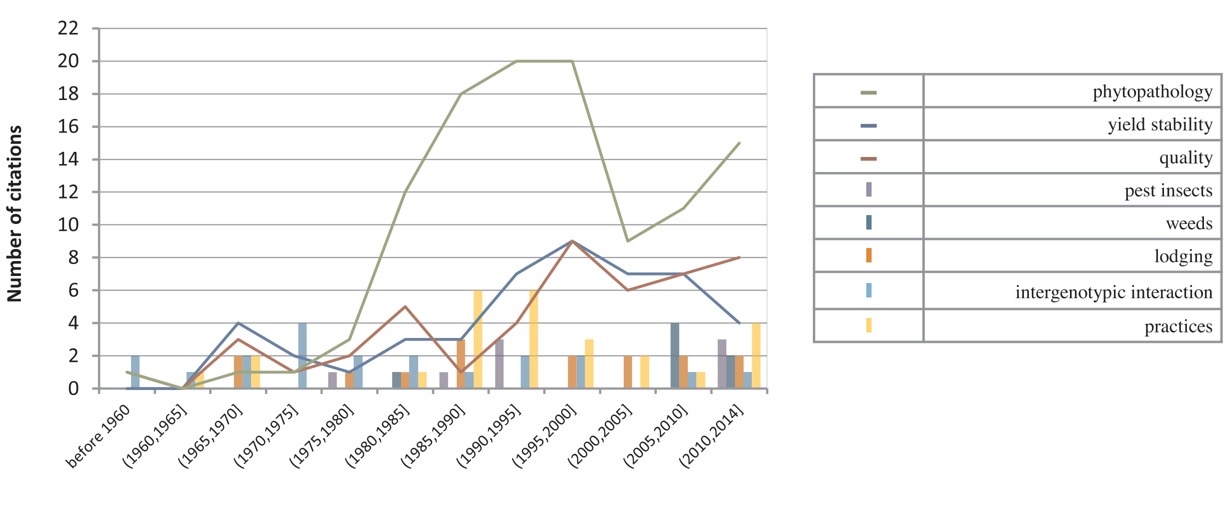


Fig. 2. Evolution in the main themes addressed by publications dedicated to cultivar mixtures. (298 papers analyzed).

to the fact that the same companies often sell pesticides and seeds (Vanloqueren and Baret, 2008). Considering the seed market, its business is mainly relying on rapid innovation and registration of new cultivars. Public and private researches are therefore mainly oriented toward genetic engineering of varieties and not on their durability, as potentially provided by mixtures or multi-resistant varieties. The required changes in scientific objectives are indeed impeded by high overcosts for scientists (knowledge, reputation, networks, access to research grants) (Vanloqueren and Baret, 2009). Finally, the use of mixtures by farmers might have also been impeded by the lack of practical rules derived from available scientific knowledge, a prerequisite for helping farmers to design cultivar mixtures.

In order to assess the validity of these different hypotheses, we developed an up-to-date review of publications on cultivar mixtures in wheat, a crop for which an informal practice of mixtures is currently spreading in France and other countries (Faraji, 2011). Building on an earlier meta-analysis (Kiær et al., 2009), we scrutinized additional experimental factors that may condition mixture performance to better understand the mechanisms involved in the success or failure of wheat mixtures. Specifically, we analyzed how overyielding responds to disease pressure and heterogeneity in traits of the mixed varieties. The response to disease pressure was used to test the stress gradient hypothesis, which assumes that interactions between varieties in mixtures become more significant as stress increases (Barot et al., 2017). We also tested whether the knowledge about mixtures has been accumulated over time, allowing mixtures to better perform in recent experiments than in former ones. We finally reviewed the published rules for blending cultivars, and highlighted the missing knowledge on mechanisms at the origin of mixtures performances.

2. Materials and methods

2.1. Literature review

We compiled publications on cereal cultivar mixtures included in The Science Citation Index Expanded database (Web of Science, Clarivate), published between 1900 and 10 October 2015, using Boolean search targeting cereal cultivar mixtures (Table S1). Over the 278 papers reported, 16 were discarded after abstract checking and 36 were added after additional research in the cited references of principal review papers, resulting in a total of 298 papers.

Among these 298 publications, 120 were dedicated to wheat, of which we selected 32 studies between 1939 and 2010 clearly reporting the yields of pure stands and their mixtures in field experiments: Akanda and Mundt, 1996; Bacon et al., 1987; Baker, 1977; Brophy and Mundt, 1991; Chapman et al., 1969; Cowger, 2008; Cox, 2004; Dai, 2012; Dubin and Wolfe, 1994; Finckh, 1992; Frankel, 1939; Gallandt, 2001; Gieffers and Hesselbach, 1988; Jackson, 1997; Karjalainen and Salovaara, 1987; Kaut, 2009; Khalifa, 1974; Knott and Mundt, 1990; Kovacs and Abranyi, 1985; Mahmood et al., 1991; Manthey, 1993; Mengistu et al., 2010; Mille, 1997; Mundt, 2002b; Mundt, 1995b; Pridham and Martin, 2007; Sage, 1971; Salovaara and Karjalainen, 1987; Sammons, 1985; Sarandon, 1995; Sharma and Dubin, 1996; and Swanston et al., 2005. These data allow the calculation of overyielding (see 2.2.1.). Overyielding is defined as the ratio between the yield of a variety mixture and the mean yield of its component varieties in pure stand (if necessary weighted by the proportion of the varieties sown). Note that the majority of studies were conducted in North America (18 studies) and in Europe (9 studies), two important areas but not fully representative of all world wheat producing areas.

The final data set included 386 mixtures (356 mixtures of winter wheat) for a total of 1320 entries, i.e. area-based grain yields of a pure stand or a mixture, in a given combination of year, location and agronomic management (in some cases, data were pooled in a mean yield including several sites), and yield variance. Variance estimates of each reported yield were derived from provided measures of yield variability, following Kiær et al. (2009).

In addition to yield data, a number of background variables were extracted to describe the study context: main study objective (yield, yield stability, disease control, quality, survival, lodging reduction, weed suppression), spring/winter type, plot size, seed density, number of replicates, agricultural management system (conventional/organic/low-input), disease pressure in relation to fungicide applications (low disease pressure *i.e.* intensive fungicides applications, moderate disease pressure *i.e.* fungicides applications and high disease pressure *i.e.* no fungicides applications and fungal inoculations), type of disease (rusts, septoria, mildew…) and harvesting year. Mixture characteristics were also extracted, *i.e.* number of component varieties, cultivar traits considered for mixing (disease resistance, crop height, phenological traits, yield potential, quality…) and whether heterogeneous or homogeneous associations of each trait were used as mixing criteria. A mixture was considered homogeneous for disease resistance if all its components were either resistant or susceptible to a specific disease. For other traits such as height or earliness, a mixture was qualified as heterogeneous when studies explicitly mentioned these traits as mixing criteria. Some characteristics were retrievable from all studies, whereas others were retrievable from subsets of the studies (see Appendices for further data description).

2.2. Statistical analyses

We followed the general methodology developed by Kiær et al. (2009), performing the meta-analysis on the basis of computed effect sizes or inputed ones when missing, and paying attention to effect size independence. A total of 606 mixture entries were thereby collated.

2.2.1. Effect size

Overyielding was quantified as the log-response-ratio, having $\text{lnRR} = \ln(\overline{X}_M/\overline{X}_C)$, where $\overline{X}_M$ and $\overline{X}_C$ denote mean yields of mixtures and component varieties, respectively, the latter being averaged over k varieties as $\overline{X}_C = \sum_{i=1}^{k} \overline{X}_i/k$

Assuming that genotypic yields were independently distributed within trials, the variance of lnRR was calculated as

$$\text{Var}(\text{lnRR}) = \text{Var}(\ln(\overline{X}_M) - \ln(\overline{X}_C))$$

$$= \frac{s_M^2}{n_M \overline{X}_M^2} + \frac{s_C^2}{k \cdot n_C \overline{X}_C^2}$$

where s_M^2 denotes the variance of the mixture yield, s_M^2 denotes the mean variance of component yields, and n_M and n_C denote the corresponding sample sizes. Notice that average component performance is estimated more precisely than mixture performance, being averaged over k times the number of observations for the mixture, where k is the number of component varieties of the mixture.

2.2.2. Imputation of missing values

In order to keep a maximum number of studies, we chose to impute SD when missing. Effectively, Ellington et al. (2015) demonstrated that omission of studies (‘complete case removal’) can lead to biased and imprecise coefficient estimates, concluding that multiple imputation in ecology and evolution performed particular well when the imputed values were weighting variables, such as SD. Multiple imputation was used to derive Var(lnRR) for the studies not reporting this information (59%). First, coefficients of variation were calculated for each mixture with a standard deviation, dividing this by the overyielding, lnRR. Missing coefficients of variation were then imputed by random sampling with replacement among this set of coefficients, either among all (when continuous moderators were tested) or a sub-set of observations within the same category level (when categorical explanatory variables were tested). Finally, each imputed value was converted back to standard deviation by multiplying with the reported mean of the imputed overyielding, allowing all mixtures to be included in quantitative meta-analysis. This procedure was repeated 100 times, and final parameter estimates were obtained as the average across runs (Ellington et al., 2015; Wiebe et al., 2006).

2.2.3. Modelling of non-independence

Conflicting with the assumption of effect size independence, many studies reported yields of specific genotypes and mixtures from multiple field trials (*e.g.* in different sites or years), and some studies used the same mixtures as others (*i.e.* from the group of C.C. Mundt). To account for this multi-level (*hierarchical)* structure in the data, effect sizes based on the same cultivar mixture, and evaluated under the same crop management and disease pressure regime, were assigned an additional shared (*group-specific*) random effect. Thus, following the three-level notation of Konstantopoulos (2011), the *i*'th effect size estimate T_{ig} in 1, …, *k* effect sizes, belonging to the *g*'th of 1,…, *m* groups, is given as

$$T_{ig} = \gamma_{\cdot\cdot} + \upsilon_{\cdot g} + \eta_{ig} + \varepsilon_{ig},$$

where $\gamma_{\cdot\cdot}$ is the overall mean, $\upsilon_{\cdot g}$ is a normally distributed level-3 unit (*group*) specific random effect, η_{ig} is a normally distributed level-2 unit (study-specific) random effect, and ε_{ig} is a normally distributed overall error term.

2.2.4. Meta-analysis

Meta-estimates of overyielding were obtained from random effects meta-analysis models in which calculated effect sizes were weighted by the inverse of their respective variances (Hedges and Olkin, 1985). A range of 'mixed effect' meta-regression models were used to evaluate (as regression coefficients) the change in overyielding over the different a priori selected background variables (moderators; see Viechtbauer, 2010 for details). Where appropriate, multiple meta-regressions were used to compare the correlation with continuous moderators in various categorical groups. Among the subset of studies using multiple mixing criteria (as defined above), pairwise contingency tables of combined mixing criteria were set up. By disregarding small sample sizes and searching for the most meaningful contrast among the remaining levels of the combined factors (i.e. compared groups sharing one mixing criteria and each having reasonable sample size, using 15 mixtures as the threshold), we were able to test the correlation of combined mixing criteria with overyielding. It should be noted that individual analyses can only be regarded as exploratory and do not prove cause-effect relationships, acknowledging also the possibility of collinearity among moderators.

Uncertainty of regression coefficients was quantified by 95% confidence intervals. Overyielding is presented in the text as percentage of yield change (in mixtures compared to weighted mean of pure stands), following exponential back-transformation ($e^{\ln RR}$). All analyses were run in the R environment, version 3.2.1 (R Development Core Team, 2011), using matrix notation as implemented in the *metafor* package (Viechtbauer, 2010). R code is available upon request.

3. Results of the meta-analysis

3.1. General overyielding

The distribution of raw overyielding values gathered for the meta-analysis range from −40% up to +60%, with a positive mean of 2.9% (Fig. 3). There was no overall publication bias in the dataset, as tested with linear regression (Egger et al., 1997) and the trim-and-fill method (Duval and Tweedie, 2000; results not shown). Mixtures of winter wheat provided a global overyielding (4.3%) that was significantly higher (p-value < 0.05) than mixtures of spring wheat, for which global overyielding was not significant (Table 1). A significant level of residual heterogeneity indicated substantial variability across the data set. Overall, overyielding was not systematically affected by number of component varieties in mixture (2–5), plot size (1.3–2500 m^2) or seeding density (40–395/m^2) (Table 1). Overyielding was significantly affected by trial year (1935–2010) according to a quadratic regression with a maximum fitted value of 4.4% in 1987 (Appendix A.4.1.)

3.2. Effect of diseases on overyielding

Overyielding from mixtures generally increased with disease pressure (Fig. 4). Global overyielding was significant under high disease pressure only (6.2%), based mostly on studies where mixtures were

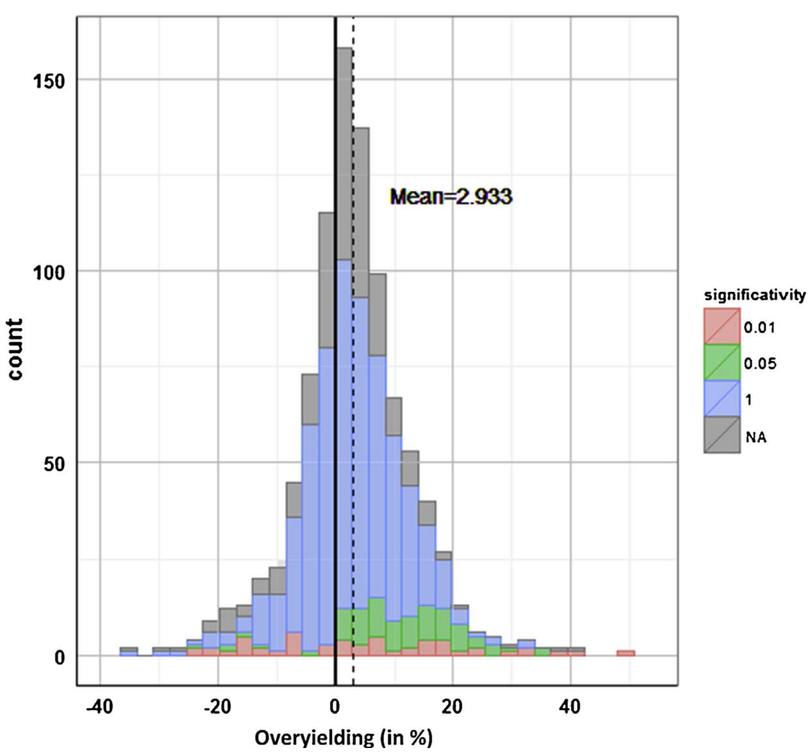


Fig. 3. Distribution of overyielding values used for the meta-analysis. Green and pink bars represent the values reported as significant (p.value. 0.05 and 0.01 respectively), blue bars are the non-significant values, and grey bars are values with missing significance test. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Meta-Metaestimates of overyielding and effects of season, number of mixed component cultivars, plot size, seeding density and trial year, including number of mixtures in the group (k), confidence limits (CL) and test probabilities (*p*-values).

	k	Meta-estimate	CL (lower)	CL (higher)	p-value
Overall	606	0.0351	0.024416	0.04576	< 0.001
Springwheat	150	0.0142	−0.00843	0.036858	0.232
Winter wheat	456	0.0418	0.029721	0.05395	< 0.001
Component number	606	0.0113 #	−0.00365	0.026196	0.160
Plot size	578	0.0000 #	−0.00002	0.00002	0.833
Seedingdensity	425	0.0000 #	−0.00020	0.00016	0.743

Slope from meta-regression.

inoculated (56% of the studies) rather than naturally infected by fungal spores. This was significantly higher (*p*-value < 0.05) than the global overyielding under low disease pressure (2.6%; *p*-value = 0.093) where mixtures were treated with fungicides. Within trials involving winter wheat, overyielding under low disease pressure turned to be significant (2.6%; *p*-value < 0.05: see Appendix A.1.). The number of spring wheat mixture studies providing information on disease pressure was too small for analysis. Under high disease pressure, overyielding was found to generally increase by 3.2% point (respectively 3.3% for winter wheat only, Fig. 5) per added component variety (*p*-value < 0.05), mostly when moving from two to three component varieties). Seeding density differed significantly between disease pressure groups (t-test; not shown), with averages of 286, 231 and 320 seeds per m^2 for low, moderate and high disease pressure, respectively. Overyielding was not influenced by seeding density within any of these groups (meta-regressions; see Appendix A.2.). Plot size had no significant influence on overyielding under any disease pressure (see Appendix A.3.). We found no systematic change in studied disease pressures over studied years (see Appendix A.4.2.).

3.3. Effects of trait heterogeneity within mixtures

Mixtures composed of varieties with contrasting levels of resistance towards one or more fungal diseases (15 studies) were distributed evenly among trials with low, moderate and high disease pressure. These mixtures tended to provide larger overyielding, but with a marginally significant test (+2.5%;p-value < 0.1), than mixtures composed of cultivars with similar disease resistance or without any reported consideration of resistance. As expected, this overyielding was enhanced when handled resistances were specific to a disease seriously affecting the plots (2.9%; p < 0.05; see Appendices B.1. and B.2.) (Fig. 4). Mixtures with declared objective to enhance disease control, based on resistance diversity rather than resistance similarity provided higher overyielding (+5.2%) but with a marginally significant test (*p*-value < 0.1; Appendix B.4.). The 9 studies presenting diversity for resistance levels for rust or mildew diseases do not exhibited a significantly higher overyielding than the 6 other studies addressing other diseases (even if with a higher mean, see Appendix B.3.).

Mixtures without reported consideration of height, and certainly displaying homogeneity for this trait, had significantly lower overyielding when compared to mixtures diverse in height (3.8%; *p*-value < 0.05). This result was also true for the winter wheat subset (see Appendix B.5.).

Considering multiple mixing criteria within the 433 mixtures designed for resistance diversity, the mixtures presenting height diversity (176) presented a higher overyielding (+3.6%) than mixtures for which no information on height diversity was provided (183 mixtures, p < 0.05) (see Appendix B.7.).

Finally, different contrasts show that diversity for plant height or earliness in mixtures never provide a significant negative impact on overyielding when compared to mixtures composed of varieties with similar height or earliness, or with no information (and even a positive trend, see Appendices B.5., B.6. and B.8.).

4. Discussion

We have surveyed the wheat bibliography to update a published meta-analysis on overyielding in cereals cultivar mixtures (Kiær et al., 2009), gathering more publications (a total of 32 studies), and collecting complementary information on methods implemented in these experiments. We first interpret and discuss the results of the meta-analysis. This is followed by a broader discussion on the conditions required for a generalization of the use of mixtures, based both on the meta-analysis and a qualitative assessment of the literature on mixtures.

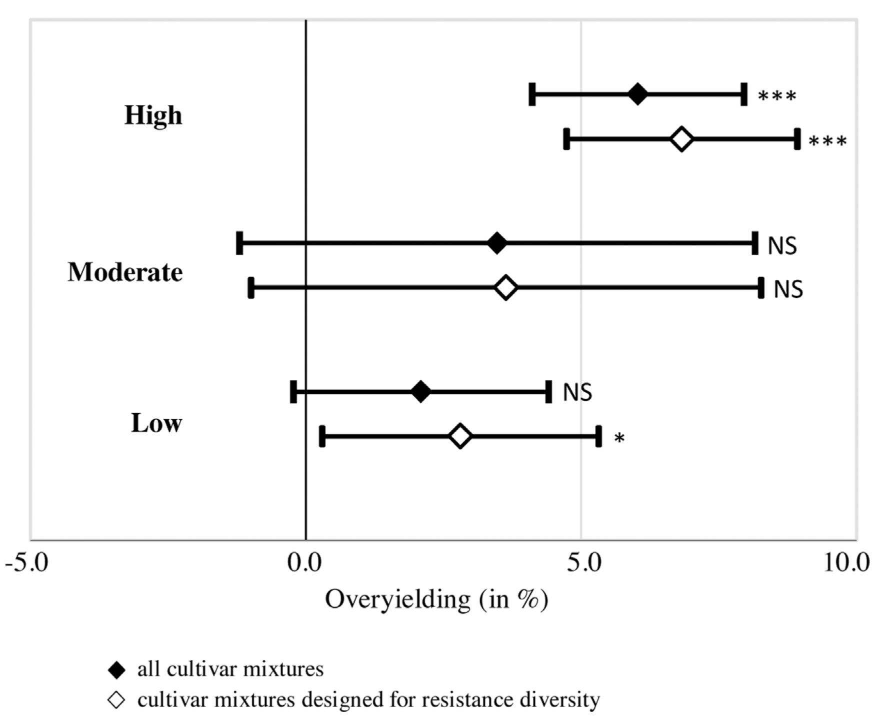


Fig. 4. Meta-estimates (and confidence intervals) of mixture overyielding under high, moderate and low disease pressure, shown for all cultivar mixtures (full diamonds) and the subset of mixtures designed for component diversity in resistance towards diseases specific to the testing field (open diamonds).

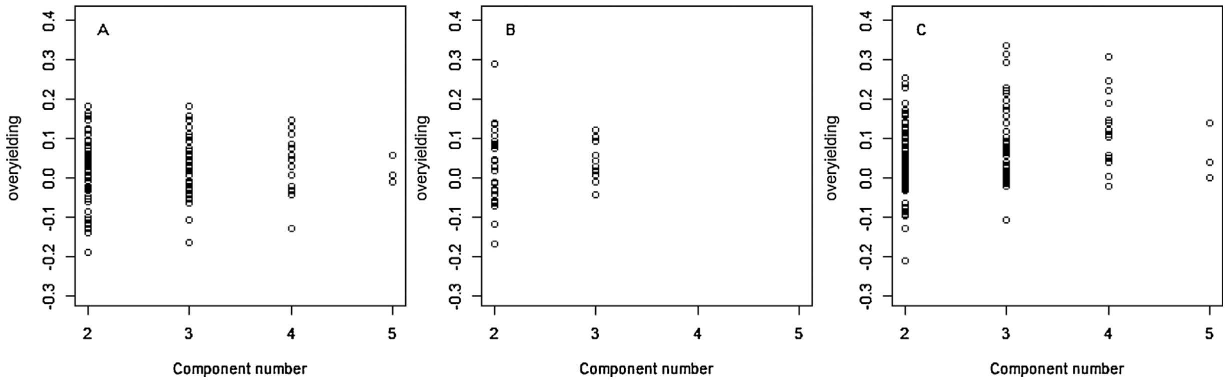


Fig. 5. Overyielding as a function of the number of component variety associated in mixtures, in groups based on season and disease pressure: winter-low (A), winter-moderate (B), winter-high (C).

4.1. The global view from the meta-analysis

4.1.1. Global overyielding patterns

Our meta-analysis first highlighted a significant global overyielding of 3.5% in wheat cultivar mixtures. This aligns with previous results (5.4% in the unweighted analysis of Smithson and Lenne, 1996); 3.9% in the meta-analysis of Kiær et al. (2009), confirming the potential of cultivar mixtures for increasing crop yield relatively to pure varieties. When considering general experimental features, we did not find any significant influence of seeding density or plot size, and no linear effect of the number of cultivars in the mixture. Seeding density is known to affect interactions between individual plants in pure stands. Therefore, increasing seeding density potentially would increase between-cultivar interactions, which could in turn increase the intensity of synergy/compensation/competition mechanisms and support positive mixing effects. Likewise, higher mixture efficiency might be expected in large plots (Cowger and Weisz, 2008; Mille et al., 2006; Wolfe, 1985; Zhu et al., 2000) as inoculum dispersal is maintained into plots (Mundt and Leonard, 1986). An explanation of the absence of significant effect of seeding densities and plot size in our meta-analysis could be that these parameters were not variable enough in the studies taken into account. The number of cultivars in mixtures (generally 2–5) has been found to be positively correlated to overyielding (Kiær et al., 2009; Mundt et al., 1995a; Smithson and Lenne, 1996), and in our analysis this correlation was significant under high disease pressure only, as suggested by Mundt and Leonard (1986).

Finally, we tested a historical question: has the accumulation of knowledge over the years allowed designing more effective mixtures, and resulted in a gradual increase in overyielding? Instead of such progress, the highest performance of mixtures was found in the 1980s and 1990s, reflecting the changes in research focus over time, and the importance of disease-focused studies during this period. This highlights the need to disentangle the ecological mechanisms behind mixture performance that can both impact the effect of mixtures on the disease reduction and on the abiotic stress tolerance.

4.1.2. Testing the stress gradient hypothesis

4.1.2.1. Biotic stresses. There was a clear increase in overyielding with the disease pressure (Fig. 4). This suggests that mixtures of varieties could be more beneficial in low pesticide cropping systems. When mixtures were designed to control specific diseases occurring on the study area, the overyielding was 2.9% higher than mixtures designed without disease consideration, both under low and high disease pressure (Fig. 4). In the publications addressing disease control, the mixed varieties were generally heterogeneous in their resistance capacity and complementary on specific resistance genes, offering little power to disentangle these two resistance components. On the basis of experiments on rusts, mildews and septoria, numerous authors (Finckh and Mundt, 1992; Mundt et al., 1995a; Østergård, 1983; Ram et al., 1989; Wolfe, 1985) have highlighted how cultivar mixtures improve the control of airborne diseases through 5 mechanisms: dilution and barrier effects, induced resistance, disruptive selection and compensation effects (Fig. 6).

As for single variety stands, the mixture ability to control diseases is strongly dependant on the nature of resistances mobilized. Major genes can provide immunity to the plant (often pathogen race specific) and quantitative resistance genes lower pathogen fitness (less pathogen race specific). In a cultivar, the combination of quantitative and major resistances have complex and synergistic interactions, the latter potentially increasing the durability of the former (Palloix et al., 2009). Heterogeneity in resistance mechanisms within a mixture of varieties impacts strongly the genetic structure of pathogen populations. Managing non-specific resistance can promote disruptive selection, fostering pathogen diversity and subsequently competition between pathogen genotypes and reducing the general fitness and aggressiveness (i.e. “virulence” in ecology) of the pathogen (Mundt, 2002b; Sapoukhina et al., 2013). Published studies have illustrated that the type of pathogen and the type of resistance influence the ability of a mixture to limit the disease impact. However, there are so far too few studies, and too sparse information in these studies on resistance and pathogen characteristics, to test the generality of these findings through a meta-analysis. For example, we were unable to detect a significant difference in overyielding between mixtures affected by rusts and mildews, or by other pathogens, possibly due to a lack of statistical power, as well as confounding effects. Nevertheless, we found that overyielding is 2.5% higher for mixtures heterogeneous in the resistance capacity than for mixtures homogeneous in this capacity. We were not able to test the effect of the proportion of resistant/susceptible varieties because most studies did not manipulate this proportion. The higher overyielding in “diversified” mixtures can be explained by the protection provided to their more susceptible varieties by their more resistant varieties, while homogeneous mixtures do not foster any protection effect.

Theoretical work has highlighted how within-field genetic diversity mobilizes the five mechanisms listed above and increases disease control. This is especially true for airborne pathogens (such as rusts), as they usually perform many cycles of multiplication per year due to a short life-cycle duration and most of all are easily transmitted between neighboring plants (low self-contamination rates: Garrett and Mundt, 1999; Gigot et al., 2013; Mundt and Leonard, 1986). The few studies on Septoria confirmed a moderate to low impact of resistance complementarity on disease progression (Gigot et al., 2013; Jackson and Wennig, 1997; Manthey and Fehrmann, 1993). Indeed, the Septoria is spread through a short distance by rain-splash, therefore dilution mechanism (Fig. 6 ***(a)***) in mixture is less effective. Also, very few cultivars are resistant and cultivar resistant levels to Septoria are not wide, compared to rust diseases. Similarly, mixtures may be less efficient on soil-borne diseases, as they have a single cycle each year and develop within the plant since an early host infection (see for e.g. eyespot due to

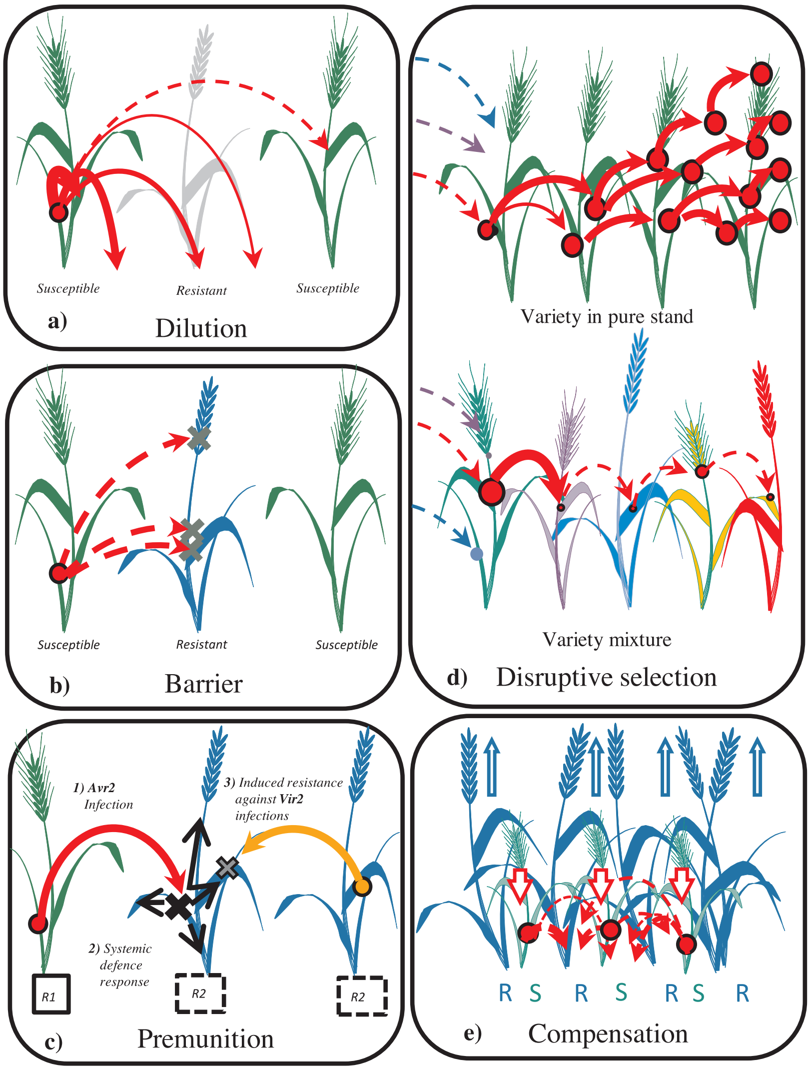


Fig. 6. illustration of the different mechanisms involved in diseases regulation. Control of airborne diseases can be summarized through 5 principal mechanisms (Finckh and Mundt, 1992; Mundt et al., 1995a,b): (a) the lower density in susceptible plants results in a lower probability for spores to find a susceptible host (dilution effect); (b) the presence of resistant plants among susceptible plants constitutes a physical barrier, restraining the dispersion of a virulent pathogen; (barrier effect) (c), the genetic diversity of varieties leads to more diverse pathogen populations where virulent and avirulent spores coexist. Therefore, the stimulation of plant defenses, especially through systemic responses, by avirulent spores allows preventing or limiting further infections by virulent spores (induced resistance); (d) In a mono-genotypic field, the best fitted pathogenic strain are quickly selected, while in mixtures selection pressures on pathogens are more diverse and reduce the overall speed of adaptation of pathogens to the crop species (disruptive selection); (e) In a cultivar mixture the individuals of the most susceptible varieties have a poor growth or yield, but this can be compensated by individuals of less susceptible varieties that better use available resources (compensation effect).

Pseudocercosporella herpotrichoides in Saur and Mille (1997). However, some studies have detected a reduction in the impact of some soil-borne diseases in mixed-crop mixtures. For example, wheat-barley mixtures reduced by 5–30% the severity of an attack by *Rhizoctonia cerealis* because of larger inter-root distances in mixed-crop systems (Hiddink et al., 2010). Potentially the same mechanisms could also allow mixtures of varieties to be less impacted by soil-borne pathogens.

The phytopathologists' extensive studies of air-borne disease control by cultivar mixtures highlight the overall interest of within field diversity in the context of biotic stresses, a finding in agreement with the stress gradient hypothesis.

4.1.2.2. Abiotic stresses. Many other major regulations potentially provided by mixtures have been neglected and certainly deserve better attention. The stress gradient hypothesis also predicts that mixtures could be more beneficial when growing or abiotic conditions are not optimal, i.e. (1) when low quantities of fertilizers are used, (2) when irrigation is insufficient, (3) in the presence of heat/drought/frost climatic stresses, (4) on infertile/degraded soils. Evidence of these complementary relationships among varieties can be found in some publications. Such complementarity necessarily requires some phenotypic diversity among the mixed cultivars. The phenological diversity within a mixture leading to differing precocity at key phenological stages (heading, maturity) can be responsible for an increased grain yield (Gallandt et al., 2001) through (i) an improved resources use (complementarity), because it allows nutrient uptake to occur at different times (Essah and Stoskopf, 2002; Francis, 1989; Sarandon and Sarandon, 1995), (ii) compensation mechanisms, as the deficiencies in yield or grain quality of the cultivars hit by a stress during a critical development phase can be balanced by the cultivars escaping to this same stress (Sammons and Baenziger, 1985; Stutzel and Aufhammer, 1990). For example, compensation has been exemplified when a component of a cultivar mixture is damaged from frost (Bowden et al., 2001). In relation to the stress gradient hypothesis, because compensation mechanisms require the temporal variability in growing condition (occasional occurrence of stressful conditions during short period of time) and because complementarity mechanisms might become ineffective in optimal conditions when all resources are abundant (e.g. with an intensive use of fertilizers), the benefits of mixture-associated phenotypic diversity should decrease in optimal growing conditions. Our attempt to test the influence of abiotic stress was however unsuccessful, in part because statistical power is too low to test potential mixture effects. It is possibly due to: (i) a lack of relevant studies, (ii) missing information on agricultural practices in the published studies, and most of all (iii) missing information on the principal abiotic stresses impacting the experiments. However, our meta-analysis revealed two other interesting effects of trait diversity. First, mixtures with different heights provided on the average an additional overyielding of 2.8% compared to mixtures designed without consideration of height although they did not differ significantly from mixtures designed with similar heights. Second, overyielding was 3.3% higher in mixtures with heterogeneous phenology than in mixtures with homogeneous phenology. Similar trends were found in studies using multiple mixing criteria: combined heterogeneity in height and in phenology between mixed varieties chosen for resistance diversity leads to a 3.6% and 2.1% overyielding, respectively, in comparison to mixtures for which no information on height or phenology diversity is provided. These effects are likely due to complementarity and selection/compensation effects between varieties and should thus depend on abiotic conditions. Hence many questions remain to be addressed for the key height and earliness traits, while many other architectural or physiological root/shoot traits might foster complementarity/compensation effects, and these aspects remain fully absent from the bibliography (see 4.2.2.).

These results on cultivar mixture performance under biotic or abiotic stresses are overall in accordance with the stress gradient hypothesis, but point to the need of in-depth studies addressing specific hypothesis testing, in order to build the knowledge necessary for handling multiple trait diversity, and potentially reach higher overyielding.

4.2. Finding rules to design mixtures

In this meta-analysis, 17 studies over 32 had a declared objective to enhance disease control through mixing cultivars with complementarity in resistances, but most of them did not explicit any assembly rules. Much fewer publications paid attention to diversity for other cultivar traits, considering first the diversity in plant height (7 studies) and earliness (6 studies), but in most of the cases as secondary traits in disease oriented studies (only 3 studies were dedicated to height/earliness complementarity). Scientists seem to have used dominant or well-studied cultivars, certainly missing part of the available genetic variability. Relatively few scientists paid a thorough attention at the individual characteristics of each cultivar used in the mixture. Hence, publications rarely address the following issues: What are the important traits when designing mixtures? What trait combinations allow providing particular services under given circumstances? When mechanisms allowing for a beneficial effect of a mixture have been identified, can these mechanisms be mapped into rules to design mixtures for breeders and farmers?

4.2.1. Mixing varieties for disease control

As seen in 4.1.2.1., a pivotal issue when mixing varieties for disease control is the impact of heterogeneity for resistance, *i.e.* how susceptible and resistant varieties interact and impact the disease progression. However the extended scientific knowledge available on disease control has been only very recently (and only partly) translated in practical rules to design mixtures. Phytopathologists have tested how the proportion of susceptible plants (S:R ratio) affect the control of diseases, with extended studies on barley mildew (Cox et al., 2004), wheat stripe rust (Huang et al., 2012; Sapoukhina et al., 2013), and septoria (Gigot et al., 2013, 2014). Manthey and Fehrmann (1993) and de Vallavieille-Pope (2004) reported that a proportion of 1:3 susceptible:resistant allows to protect the mixtures from mildew and rust. Here scientists provided very practical advices, converting scientific knowledge in simple criteria to mix varieties. In direct link with the combination of resistances, the question of the optimal number of cultivars has been addressed by epidemiologists, stating that it is highly depending on the number of resistances carried by each cultivar, as well as the epidemic cycle of the pathogen (Leonard and Czochor, 1980; Mikaberidze et al., 2014; Wolfe, 1985), varying from 2 to 3 cultivars to a hundred. However, experiments (Mille et al., 2006) and recent models (Sapoukhina et al., 2013) have reduced this number to 4–5, stressing that the cultivar number (genetic diversity) is less influential than the type of cultivar resistances assembled (functional diversity). Note that in our meta-analysis, the overyielding was increased by 3.3% per added component variety (over a range of 2–5 components per mixtures), for winter wheat under high disease pressure (Fig. 5).

When refining the interplay between quantitative and specific resistances, assembly strategies have not been subject to the same simplification effort, certainly because of the poor knowledge available on quantitative resistances in registered varieties. Even if recommendations are to mix seed instead of sowning the different cultivar on separate rows, the spatial arrangement of component cultivars within plot (Garrett and Mundt, 1999; Gigot et al., 2014; Newton and Guy, 2011; Xu, 2011) has not been fully investigated. Likewise, impacts of heterogeneity in plant height and canopy structure have been studied (microclimate effect on Blast: Zhu et al., 2005), but this knowledge has never been used to design rules to provide optimized cultivar mixtures.

4.2.2. Mixing varieties for other synergies

While some mixing rules have been developed for disease resistance, very few recommendations have been proposed for other traits. Plant height and earliness have been the subject of some attention, due to their known role in plant competition. To maintain a balanced proportion of cultivars in the mixtures under study, as well as for general technical concerns (i.e. harvest), agronomists and phytopathologists generally advice for homogeneous height and earliness between cultivars (Bowden et al., 2001; Dai et al., 2012). Strong differences in earliness and height can indeed induce competition for light and nutrients, as the earlier cultivar can get an advantage over the later one (Faraji, 2011) or the taller cultivar can disturb grain filling of smaller ones (Khalifa and Qualset, 1974; Mille and Jouan, 1997; Rao and Prasad, 1984; Wolfe, 1985). However, we were unable to find any publication demonstrating a real negative impact of diversity for these two traits on mixture performance, and our meta-analysis even suggests higher overyielding in mixtures presenting diversity in earliness and height. Indeed differences in plant height have been cited as a way to (i) limit lodging − generally the shorter varieties may support the growth of taller ones, (ii) improve light interception, (iii) create a wavy canopy affording water losses reduction by evaporation (Adu-Gyamfi et al., 2015; Faraji, 2011) and (iv) improve competitive ability toward weeds (Mason et al., 2008). Combining height and earliness diversity can further improve weed control: a mixture of early maturing varieties with tall varieties could provide a higher competitive ability and yield stability (Kaut et al., 2009).

More than general effect of height or earliness, defining assembly rules need to quantify the effect of differences in height/earliness between varieties on overyielding and competitiveness and very few references addressed these issues (but see Khalifa and Qualset, 1974; Thomas and Schaalje, 1997).

Providing assembly rules based on height, earliness or other traits of potential interest such as the stem, leaf and root architecture therefore require additional and dedicated researches. As the impact of the assembly rules may depend on the cropping environment, it should be advised that those experiments focused on the mechanisms of competitions and facilitations in mixtures submitted to various levels of stress and resources. This implies a precise and dynamic description of the experimental conditions (technical and environmental), the use of models to disentangle the mechanisms underneath the observed mixture effects and a phenotyping effort to measure the proportion of each component variety in mixture at least in the harvest and even better in the vegetation cover.

Finally, it should not be forgotten that those assembly rules must be compatible with the technical constraints of the farmer. For instance, the difference in maturity earliness may complicate the harvest calendar and the difference of height may complicate the disease surveillance in the crop.

5. Perspectives

Agriculture is increasingly required to be multifunctional and thus to provide other services (e.g. climate regulation, maintenance of soil fertility, water quality or conservation of biodiversity), in addition to the quantity of food produced. In the present meta-analysis, we emphasize that the conclusions of our meta-analysis have been limited by the fact that published studies (1) focus on yield and do not document other ecological functions or ecosystem services or the stability of yield, (2) only intentionally manipulate a limited number of traits (3) do not describe well enough the experimental conditions (e.g. major agronomic limiting factors, as nitrogen, water…).

Therefore a huge work is still required to understand and disentangle the physiological and ecological mechanisms (facilitation, complementarity, compensation, and competition) that may coexist and determine the type of interactions between mixed varieties, or between mixtures of varieties and other organisms. This will in particular require knowledge, so far nearly missing, on the links between the traits of varieties and other services than grain production. Grain quality, essential for the wheat supply chain (protein content, specific weight, baking quality…) is little affected in mixtures (Gallandt et al., 2001; Mille et al., 2006). However some positive interactions were also reported (Belhaj Fraj, 2003) and deserve better attention. Similarly, few studies have directly tested the hypothesis that cultivar mixtures could be more efficient in exploiting water or mineral nutrients, through specific characteristics of root systems (Adu-Gyamfi et al., 2015; Fang et al., 2014; Newton et al., 2012; Wang et al., 2016). Interactions between mixtures and other organisms are also important for providing potentially important services such as weed control, pest control or increase in nutrient uptake. Mixtures have already been shown to increase the population of natural enemies of some plant pests (Smith et al., 2014). Mixtures could increase populations of spiders by providing diverse food resources or more complex crop architecture (Chateil et al., 2013). Mixtures can directly control pests through dissemination of volatile organic compounds that might influence the growth rate and size of aphid populations (Shoffner and Tooker, 2013), and through the use of pest resistance genes as illustrated for wheat midges (Vera et al., 2013).

Many traits of the varieties that are mixed are probably often interacting to determine the provision of each service. When analyzing competitive ability, 2 key traits are earliness (spike emergence), or plant height (Essah and Stoskopf, 2002; Zhou et al., 2014) that can be broken down in many developmental/architectural parameters such as phyllochron, photoperiod or vernalization sensitivity, branching, leaf surfaces, leaf insertion angles, specific leaf area, and specific root length. However, the causal links between combinations of these traits and beneficial ecological mechanisms are still poorly known, in part because cultivar choices have been confined in the past to components with comparable heights and maturation times, following agronomic recommendations (Bowden et al., 2001). Dedicated research integrating a broader germplasm and manipulating many traits is really needed to decipher the effects of diversity in various traits, before assembly rules can be provided to farmers and breeders.

Finally, there is a lack of experiment dedicated to the study of cultivar mixtures, and their better knowledge requires a similar effort (field trials) than the one dedicated to cultivars. Then, the experimental evaluation of all possible mixtures is a vain goal, due to the almost infinite number of variety combinations. A first solution, already mentioned above, is to study the ecological mechanisms through case studies and to use traits to predict how these mechanisms can be used in mixtures that have never been tested but for which the traits of the mixed varieties are known. A second solution would be to use models to better understand specific mechanisms involved in mixture performances. Statistical models could be used to estimate experimentally “mixing abilities” (Lopez and Mundt, 2000), without specific attention to traits (Barot et al., 2017). The trait-based alternative is to build ecophysiological models to study and even predict the mixture performance, as for example the simulation of epidemic progress in a cultivar mixture (Sapoukhina et al., 2013; Xu, 2011) or the light partitioning within heterogeneous crops (Barillot et al., 2014; Zhu et al., 2015). New models should be also developed to address other issues: e.g. the capacity of a mixture to exploit mineral nutrients and water, or to interact with soil communities.

More and more farmers are turning towards cultivar mixtures to face economic and climatic constraints, calling for intensified research efforts as well as new practical recommendations. Due to the complexity of cultivar assembly, such a challenge requires coordinated research efforts and the implication of all wheat supply chain actors who can be mobilized through participatory approaches.

Acknowledgments

This work was supported by the ANR WHEATAMIX project, grant ANR-13-AGRO-0008 of the French National Research Agency, and by the grant 34009-14-0800 from The Danish Agricultural Agency. The authors are grateful to Bruno Andrieu, Vincent Allard, Claude Pope, Pierre Labarthe and Emmanuelle Porcher for early discussions and helpful comments on earlier versions of the manuscript.

Appendices

Details of the meta-analysis results

Appendix A. Effect of diseases on overyielding

A.1 Disease pressure vs. season

Here and below, the first lines − the first time each moderator level is mentioned − provides the number of mixtures in the group (k), the *meta*-estimate of that group, its standard deviation and confidence limits, as well as test probabilities for the metaest < > 0 for each moderator level separately. The p(Q_mods) and AIC are probability value for the test if the moderator significantly explains variability in the data, and the Akaikes Information Criterion for the same. All additional lines provide pairwise comparisons of moderator levels − given in two lines. As an extra model check, the first line provides output on one moderator level. The second line provides the estimated between-level difference in *meta*-estimates and a test probability of this difference.

Winter wheat mixtures gave the largest overall significant effect of mixing under high disease pressure (6.25%) but also under low disease pressure (2.6%). The number of spring wheat mixtures providing information on disease pressure was much smaller and hence not comparable.

	m	Meta-estimate	
spring-high (1)	13	0.040 (−0.037;0.117)	
spring-low (2)	17	−0.017 (−0.089;0.055)	
winter-high (3)	183	0.061 (0.0410;0.080)	***

winter-low (4)	129	0.026 (0.001;0.050)	*
winter-moderate (5)	44	0.035 (−0.012;0.081)	
2:1		−0.057 (−0.163;0.049)	
3:1		0.021 (−0.059;0.101)	
4:1		−0.014 (−0.095;0.066)	
5:1		−0.005 (−0.096;0.085)	
3:2		0.078 (0.002;0.153)	*
4:2		0.042 (−0.034;0.119)	
5:2		0.051 (−0.035;0.138)	
4:3		−0.035 (−0.067;-0.004)	*
5:3		−0.026 (−0.077;0.025)	
5:4		0.009 (−0.044;0.062)	

A.2 Disease pressure vs. seeding density

Overyielding was not affected by the seeding density under any disease pressure, indicating also that overyielding under disease did not change with seeding density.

	m	Meta-estimate
intcpt low (1a)	146	0.074 (−0.0164;0.1652)
intcpt moderate (2a)	44	0.008 (−0.2678;0.2838)
intcpt high (3a)	196	0.07 (−0.018;0.1579)
slope low (1b)		0 (−0.0005;0.0001)
slope moderate (2b)		0 (−0.001;0.0012)
slope high (3b)		0 (−0.0003;0.0003)
2b:1b		0 (−0.0015;0.0009)
1b:3b		0 (−0.0003;0.0006)
2b:3b		0 (−0.0013;0.001)

A.3 Disease pressure vs. plot size

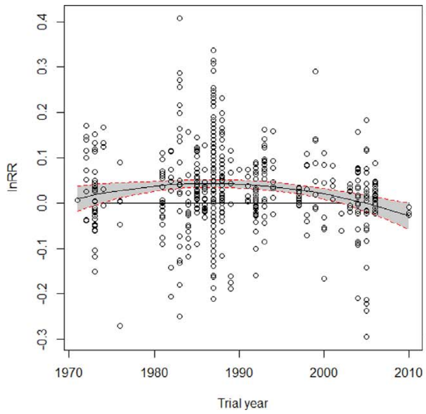
Overyielding under different disease pressure was not affected by the plot size.

	m	Meta-estimate	
intcpt low (1a)	382	0.013 (−0.0463;0.072)	
intcpt moderate (2a)	382	0.04 (−0.026;0.1069)	
intcpt high (3a)	382	0.066 (0.0443;0.0873)	***
slope low (1b)		0.001 (−0.0064;0.0086)	
slope moderate (2b)		0 (−0.0012;0.001)	
slope high (3b)		0 (0;0)	
2b:1b		0.001 (−0.0063;0.0088)	
1b:3b		−0.001 (-0.0086;0.0064)	
2b:3b		0 (−0.001;0.0012)	

A.4 Harvest year

A.4.1 Quadratic regression

Overyielding in lnRR showed a quadratic relationship with the latest harvest year of trials, peaking in 1987.



Coefficients:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-5.256e+02	1.442e+02	-3.646	0.00029 ***
year	5.291e-01	1.448e-01	3.653	0.00028 ***
year_sq	-1.332e-04	3.638e-05	-3.660	0.00027 ***

P-value of quadratic fit:
p = 8.053e-05 ***

Maximum (and 95% CI):
Trial year: 1987
lnRR: 0.043 (0.035;0.052)
Overyielding (%): 4.44 (3.56;5.34)

A.4.2 Disease pressure vs. harvest year

Overyielding under different disease pressure was not affected by the harvest year.

	m	Meta-estimate
intcpt low (1a)	386	2.770 (−6.1504;11.6913)
intcpt moderate (2a)	386	1.809 (−15.0002;18.6175)
intcpt high (3a)	386	−0.754 (−12.6310;11.1227)
slope low (1b)		−0.001 (−0.0059;0.0031)
slope moderate (2b)		0.001 (−0.0093;0.0075)
slope high (3b)		0 (−0.0056;0.0064)
2b:1b		0 (−0.0100;0.0091)
1b:3b		0.002 (−0.0057;0.0092)
2b:3b		0.001 (−0.0091;0.0116)

Appendix B. Effects of trait diversity

B.1 Resistance diversity

Mixtures designed for diversity in resistance toward fungal diseases generally provided larger overyielding than mixtures with similar disease resistance or without consideration of resistance:

	m	Meta-estimate	
Similarity (1)	19	0.017 (−0.0044;0.0383)	
Diversity (2)	433	0.041 (0.0289;0.0535)	***
2:1		0.024 (−0.0004;0.0489)	(*)

B.2 Specific resistance diversity

Overyielding was larger in mixtures designed for diversity in specific disease resistance to the testing area, compared to mixtures designed for similar disease resistance or without consideration of resistance:

	m	Meta-estimate	
Similarity (1)	17	0.018 (−0.0009;0.0359)	(*)
Diversity (2)	393	0.046 (0.0326;0.0589)	***
2:1		0.028 (0.0056;0.0508)	*

B.3 Types of diseases

The majority of mixtures with specific resistance diversity targeted rust and mildew disease, as compared to other types of disease. The effect of mixing was not significantly higher:

	m	Meta-estimate	
Other (1)	42	0.019 (−0.0267;0.0655)	
Rust or mildew (2)	350	0.047 (0.0338;0.0609)	***
2:1		0.028 (−0.0201;0.076)	

B.4 Study objective

Studies with the declared objective to improve disease control by the use cultivar mixtures provided larger overyielding, overall, but not significantly:

	m	Meta-estimate	
Not disease-related (1)	172	0.023 (0.0036;0.0429)	*
Disease-related (2)	433	0.041 (0.0288;0.0541)	***
2:1		0.018 (−0.0052;0.0416)	

Among the studies explicitly using mixtures for disease control, overyielding tended to be 5.3% higher in mixtures based on resistance diversity compared to mixtures based on resistance similarity:

	m	Meta-estimate	
ResSim:DisCtrlObj (1)	18	−0.007 (−0.0591;0.0459)	
ResDiv:NotDisCtrl (2)	53	0.022 (−0.0107;0.0538)	
ResDiv:DisCtrlObj (3)	380	0.045 (0.0318;0.0586)	***
N/A:NotDisCtrl1 (4)	20	0.027 (0.0016;0.0518)	*
N/A:DisCtrlObj (5)	33	−0.009 (−0.0763;0.0589)	
2:1		0.028 (−0.0335;0.0898)	
3:1		0.052 (−0.0024;0.1061)	(*)
4:1		0.033 (−0.0249;0.0917)	
5:1		−0.002 (−0.0878;0.0836)	
3:2		0.024 (−0.0112;0.0585)	
4:2		0.005 (−0.0357;0.046)	
5:2		−0.03 (−0.1052;0.0447)	
4:3		−0.019 (−0.0471;0.0099)	
5:3		−0.054 (−0.1229;0.015)	
5:4		−0.036 (−0.1079;0.0368)	

B.5 Height diversity

Overyielding did not differ systematically between mixtures designed for diversity or similarity in height, but mixtures designed for height diversity gave significantly larger effect than mixtures without reported consideration to height:

	m	Meta-estimate	
Similarity (1)	119	0.029 (0.0031;0.0552)	*
Diversity (2)	221	0.05 (0.0331;0.0674)	***
N/A (3)	265	0.023 (0.0066;0.0387)	**
2:1		0.021 (−0.01;0.0523)	
3:1		−0.006 (−0.0371;0.0242)	
3:2		−0.028 (−0.0511;-0.0041)	*

Also when focusing solely on winter crops, overyielding did not differ systematically between mixtures designed for diversity or similarity in height:

	m	Meta-estimate	
Similarity:Spring (1)	45	−0.012 (−0.0657;0.0412)	
Similarity:Winter (2)	74	0.046 (0.0142;0.0772)	**
Diversity:Spring (3)	40	0.02 (−0.0233;0.064)	
Diversity:Winter (4)	181	0.055 (0.0359;0.0744)	***
2:1		0.058 (−0.0041;0.12)	(*)
3:1		0.033 (−0.0364;0.1017)	
4:1		0.067 (0.0101;0.1244)	*
3:2		−0.025 (−0.0792;0.0285)	
4:2		0.009 (−0.0277;0.0465)	
4:3		0.035 (−0.0135;0.0825)	

B.6 Phenological diversity

Overyielding was overall significant in mixtures designed for phenological diversity, whereas overyielding was overall lower and insignificant in mixtures designed for phenological similarity but not significant:

	m	Meta-estimate	
Similarity (1)	78	0.013 (−0.0213;0.047)	
Diversity (2)	296	0.045 (0.0303;0.0594)	***
N/A (3)	229	0.027 (0.0093;0.045)	**
2:1		0.032 (−0.0051;0.0694)	
3:1		0.014 (−0.0243;0.0528)	
3:2		−0.018 (−0.0408;0.0053)	

Within the group of winter crops, mixtures designed for phenological diversity yielded more than double compared to mixtures designed for phenological similarity, but this difference was not significant:

	m	Meta-estimate	
Similarity:Spring (1)	376	−0.005 (−0.0537;0.043)	
Similarity:Winter (2)	376	0.02 (−0.0213;0.0622)	
Diversity:Spring (3)	376	0.022 (−0.005;0.05)	
Diversity:Winter (4)	376	0.052 (0.0363;0.0684)	***
2:1		0.026 (−0.0381;0.0897)	
3:1		0.028 (−0.0278;0.0835)	
4:1		0.058 (0.0062;0.1094)	*
3:2		0.002 (−0.0479;0.052)	
4:2		0.031 (−0.0149;0.0773)	
4:3		0.029 (−0.0032;0.0621)	(*)

B.7 Height diversity vs. resistance diversity

Based on the contingency table of resistance diversity and height diversity, all groups of mixtures with resistance similarity were disregarded due to small sample sizes.

	h-div		
r-div	**-1**	**1**	**NA**
-1	1	7	11
1	74	176	183
NA	44	38	71

The additional effect of height diversity among the mixtures with resistance diversity was 3.6% yield increase, compared to the group of mixtures without any provided information on height diversity. However, among mixtures with resistance diversity, there was no significant difference between mixtures based on height diversity and mixtures based on height similarity:

	m	Meta-estimate	
Sim:Div (1)	604	−0.019 (−0.1147;0.0771)	
Sim:Unknown (2)	604	−0.003 (−0.0654;0.0596)	
Div:Sim (3)	604	0.044 (0.0133;0.0744)	**
Div:Div (4)	604	0.058 (0.0394;0.0775)	***
Div:Unknown (5)	604	0.023 (0.0038;0.0418)	*
Unknown:Sim (6)	604	−0.01 (−0.0609;0.0404)	
Unknown:Div (7)	604	0.03 (−0.0139;0.0731)	
Unknown:Unknown (8)	604	0.032 (−0.0022;0.0652)	(*)
…			
6:3		−0.054 (−0.1133;0.0051)	(*)
5:4		−0.036 (−0.0625;-0.0087)	*
6:4		−0.069 (−0.1228;-0.0146)	*
4:3		0.015 (−0.0215;0.0506)	

B.8 Phenological diversity vs. resistance diversity

Based on the contingency table of resistance diversity and phenological diversity, all groups of mixtures with resistance similarity were disregarded due to small sample sizes.

	p-div		
r-div	**-1**	**1**	**NA**
-1	0	6	13
1	28	254	151
NA	50	38	65

The additional effect of phenological diversity among the mixtures with resistance diversity was 2.1% yield increase, compared to the group of mixtures without any provided information on phenological diversity, but this difference was not significant:

	m	Meta-estimate	
Sim:Div (1)	604	−0.019 (−0.1147;0.0771)	
Sim:Unknown (2)	604	−0.003 (−0.0654;0.0596)	
Div:Sim (3)	604	0.044 (0.0133;0.0744)	**
Div:Div (4)	604	0.058 (0.0394;0.0775)	***
Div:Unknown (5)	604	0.023 (0.0038;0.0418)	*
Unknown:Sim (6)	604	−0.01 (−0.0609;0.0404)	
Unknown:Div (7)	604	0.03 (−0.0139;0.0731)	
Unknown:Unknown (8)	604	0.032 (−0.0022;0.0652)	(*)
…			
6:3		−0.054 (−0.1133;0.0051)	(*)
5:4		−0.036 (−0.0625;-0.0087)	*
6:4		−0.069 (−0.1228;-0.0146)	*
4:3		0.015 (−0.0215;0.0506)	

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fcr.2017.09.006.

References

Østergård, H., 1983. Predicting development of epidemics on cultivar mixtures. Phytopathology 73, 166–172.
Adu-Gyamfi, P., Mahmood, T., Trethowan, R., 2015. Can wheat varietal mixtures buffer the impacts of water deficit? Crop Pasture Sci. 66, 757.
Akanda, S.I., Mundt, C.C., 1996. Effects of two-component wheat cultivar mixtures on stripe rust severity. Phytopathology 86, 347–353.
Altieri, M., 1989. Agroecology — a new research and development paradigm for world agriculture. Agric. Ecosyst. Environ. 27, 37–46.
Bacon, R., Collins, F., Marx, D., 1987. Comparison of wheat blends with pure-line cultivars. Cereal Res. Commun. 15, 183–186.
Baker, R.J., 1977. Yield of pure and mixed stands of two spring wheat cultivars sown at five rates of seeding. Can. J. Plant Sci. 57, 1005–1007.
Barillot, R., Escobar-Gutierrez, A.J., Fournier, C., Huynh, P., Combes, D., 2014. Assessing the effects of architectural variations on light partitioning within virtual wheat-pea mixtures.

Ann. Bot. 114, 725–737.
Barot, S., Allard, V., Cantarel, A., Enjalbert, J., Gauffreteau, A., Goldringer, I., Lata, J.-C., Le Roux, X., Niboyet, A., Porcher, E., 2017. Designing mixtures of varieties for multifunctional agriculture with the help of ecology. A review. Agron. Sustain. Dev. 37.
Belhaj Fraj, M., 2003. Évaluation de la stabilité et la faisabilité des associations variétales de blé tendre d'hiver à destination meunière en conditions agricoles. ENSAR.
Bowden, R.L., Shroyer, J.P., Roozeboom, K., Claassen, M., Evans, P., Gordon, Heer, Janssen, Long, Martin, et al., 2001. Performance of wheat variety blends in Kansas. Kans. State Univ. Agric. Ext. Bull. 128.
Brisson, N., Gate, P., Gouache, D., Charmet, G., Oury, F.X., Huard, F., 2010. Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. Field Crops Res. 119, 201–212.
Brophy, L., Mundt, C., 1991. Influence of plant spatial patterns on disease dynamics, plant competition and grain-yield in genetically diverse wheat populations. Agric. Ecosyst. Environ. 35, 1–12.
Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., Smith, V.H., 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. 8, 559–568.
Chapman, S., Allard, R., Adams, J., 1969. Effect of planting rate and genotypic frequency on yield and seed size. Crop Sci. 9, 575.
Chateil, C., Goldringer, I., Le Viol, I., Tarallo, L., Kerbiriou, C., 2013. Crop genetic diversity benefits farmland biodiversity in cultivated fields. Agric. Ecosyst. Environ. 171, 25–32.
Cowger, C., Weisz, R., 2008. Winter wheat blends (mixtures) produce a yield advantage in north carolina. Agron. J. 100, 169–177.
Cox, C.M., Garrett, K.A., Bowden, R.L., Fritz, A.K., Dendy, S.P., Heer, W.F., 2004. Cultivar mixtures for the simultaneous management of multiple diseases: tan spot and leaf rust of wheat. Phytopathology 94, 961–969.
Creissen, H.E., Jorgensen, T.H., Brown, J.K.M., 2013. Stabilization of yield in plant genotype mixtures through compensation rather than complementation. Ann. Bot. 112, 1439–1447.
Dai, J., Wiersma, J.J., Nolen, D.L., 2012. Performance of hard red spring wheat cultivar mixtures. Agron. J. 104, 17–21.
de Vallavieille-Pope, C., 2004. Management of disease resistance diversity of cultivars of a species in single fields: controlling epidemics. C. R. Biol. 327, 611–620.
Dubin, H., Wolfe, M., 1994. Comparative behavior of 3 wheat cultivars and their mixture in India. Nepal Pak. Field Crops Res. 39, 71–83.
Duval, S., Tweedie, R., 2000. Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. Biometrics 56, 455–463.
Egger, M., Smith, G.D., Schneider, M., Minder, C., 1997. Bias in meta analysis detected by a simple graphical test. Br. Med. J. 315, 629–634.
Ellington, E.H., Bastille-Rousseau, G., Austin, C., Landolt, K.N., Pond, B.A., Rees, E.E., Robar, N., Murray, D.L., 2015. Using multiple imputation to estimate missing data in meta-regression. Methods Ecol. Evol. 6, 153–163.
Essah, S.Y.C., Stoskopf, N.C., 2002. Mixture performance of phenotypically contrasting barley cultivars. Can. J. Plant Sci. 82, 1–6.
Fang, Y., Xu, B., Liu, L., Gu, Y., Liu, Q., Turner, N.C., Li, F.M., 2014. Does a mixture of old and modern winter wheat cultivars increase yield and water use efficiency in water-limited environments? Field Crops Res. 156, 12–21.
Faraji, J., 2011. Wheat cultivar blends: a step forward to sustainable agriculture. Afr. J. Agric. Res. 6, 6780–6789.
Finckh, M.R., Mundt, C.C., 1992. Stripe rust, yield, and plant competition in wheat cultivar mixtures. Phytopathology 82, 905–913.
Finckh, M.R., Gacek, E.S., Goyeau, H., Lannou, C., Merz, U., Mundt, C.C., Munk, L., Nadziak, J., Newton, A.C., de Vallavieille-Pope, C., et al., 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. Agronomie 20, 813–837.
Francis, C.A., 1989. Biological efficiencies in multiple-cropping systems. Adv. Agron. 42, 1–42.
Frankel, O.H., 1939. Analytical yield investigations on New Zealand wheat IV. Blending varieties of wheat. J. Agric. Sci. 29, 249–261.
Gaba, S., Lescourret, F., Boudsocq, S., Enjalbert, J., Hinsinger, P., Journet, E.-P., Navas, M.-L., Wery, J., Louarn, G., Malézieux, E., et al., 2015. Multiple cropping systems as drivers for providing multiple ecosystem services: from concepts to design. Agron. Sustain. Dev. 35, 607–623.
Gallandt, E.R., Dofing, S.M., Reisenauer, P.E., Donaldson, E., 2001. Diallel analysis of cultivar mixtures in winter wheat. Crop Sci. 41, 792–796.
Garrett, K.A., Mundt, C.C., 1999. Epidemiology in mixed host populations. Phytopathology 89, 984–990.
Gieffers, W., Hesselbach, J., 1988. Effects of fungicides on the yield of pure stands and cultivar mixtures of spring barley and winter wheat. Z. Pflanzenkrankh. Pflanzenschutz-J. Plant Dis. Prot. 95, 486–494.
Gigot, C., Saint-Jean, S., Huber, L., Maumené, C., Leconte, M., Kerhornou, B., de Vallavieille-Pope, C., 2013. Protective effects of a wheat cultivar mixture against splash-dispersed septoria tritici blotch epidemics. Plant Pathol. 62, 1011–1019.
Gigot, C., de Vallavieille-Pope, C., Huber, L., Saint-Jean, S., 2014. Using virtual 3-D plant architecture to assess fungal pathogen splash dispersal in heterogeneous canopies: a case study with cultivar mixtures and a non-specialized disease causal agent. Ann. Bot. 114, 863–875.
Grassini, P., Eskridge, K.M., Cassman, K.G., 2013. Distinguishing between yield advances and yield plateaus in historical crop production trends. Nat. Commun. 4, 1–11.
Hedges, L.V., Olkin, I., 1985. Statistical methods for meta-analysis, First edition. Academic Press, pp. 369.
Hiddink, G.A., Termorshuizen, A.J., van Bruggen, A.H.C., 2010. Mixed cropping and suppression of soilborne diseases. In: Lichtfouse, E. (Ed.), Genetic Engineering, Biofertilisation, Soil Quality and Organic Farming, pp. 119–146.
Huang, C., Sun, Z., Wang, H., Luo, Y., Ma, Z., 2012. Effects of wheat cultivar mixtures on stripe rust: a meta-analysis on field trials. Crop Prot. 33, 52–58.
Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N., Vellend, M., 2008. Ecological consequences of genetic diversity. Ecol. Lett. 11, 609–623.
Jackson, L.F., Wennig, R.W., 1997. Use of wheat cultivar blends to improve grain yield and quality and reduce disease and lodging. Field Crops Res. 52, 261–269.
Karjalainen, R., Salovaara, H., 1987. Spring wheat mixtures in Northern crop production: quality characteristics. J. Agric. Sci. Finl. 59, 51–55.
Kaut, A.H.E.E., Mason, H.E., Navabi, A., O'Donovan, J.T., Spaner, D., 2009. Performance and stability of performance of spring wheat variety mixtures in organic and conventional management systems in western Canada. J. Agric. Sci. 147, 141–153.
Khalifa, M., Qualset, C., 1974. Intergenotypic competition between tall and dwarf wheats. I. In mechanical mixtures. Crop Sci. 14, 795–799.
Kiær, L.P., Skovgaard, I.M., Østergård, H., 2009. Grain yield increase in cereal variety mixtures: a meta-analysis of field trials. Field Crops Res. 114, 361–373.
Knott, E., Mundt, C., 1990. Mixing ability analysis of wheat cultivar mixtures under diseased and nondiseased conditions. Theor. Appl. Genet. 80, 313–320.
Konstantopoulos, S., 2011. Fixed effects and variance components estimation in three-level meta-analysis. Res. Synth. Methods 2, 61–76.
Kovacs, G., Abranyi, A., 1985. Study of the yielding ability of variety mixtures of winter-wheat. Novenytermeles 34, 81–86.
Leonard, K.J., Czochor, R.J., 1980. Theory of genetic interactions among populations of plants and their pathogens. Annu. Rev. Phytopathol. 18, 237–258.
Litrico, I., Violle, C., 2015. Diversity in plant breeding: a new conceptual framework. Trends Plant Sci. 20 (10), 604–613.
Lopez, C.G., Mundt, C.C., 2000. Using mixing ability analysis from two-way cultivar mixtures to predict the performance of cultivars in complex mixtures. Field Crops Res. 68, 121–132.
Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., et al., 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294, 804–808.
Lortie, C.J., Callaway, R.M., 2006. Re-analysis of meta-analysis: support for the stress-gradient hypothesis. J. Ecol. 94, 7–16.
Mahmood, T., Marshall, D., Mcdaniel, M., 1991. Effect of winter-wheat cultivar mixtures on leaf rust severity and grain-yield. Phytopathology 81, 470–474.
Malézieux, E., 2011. Designing cropping systems from nature. Agron. Sustain. Dev. 32, 15–29.
Manthey, R., Fehrmann, H., 1993. Effect of cultivar mixtures in wheat on fungal diseases, yield and profitability. Crop Prot. 12, 63–68.
Mason, H.E., Goonewardene, L., Spaner, D., 2008. Competitive traits and the stability of wheat cultivars in differing natural weed environments on the northern Canadian Prairies. J. Agric. Sci. 146, 21–33.
Mengistu, N., Baenziger, P.S., Nelson, L.A., Eskridge, K.M., Klein, R.N., Baltensperger, D.D., Elmore, R.W., 2010. Grain yield performance and stability of cultivar blends vs. component cultivars of hard winter wheat in Nebraska. Crop Sci. 50, 617–623.
Mikaberidze, A., Mcdonald, B., Bonhoeffer, S., 2014. How to Develop Smarter Host Mixtures to Control Plant Disease?.
Mille, B., Jouan, B., 1997. Influence of varietal associations on the development of leaf and glume blotch and brown leaf rust in winter bread wheat. Agronomie 247–251.
Mille, B., Fraj, M.B., Monod, H., Vallavieille-Pope, C., 2006. Assessing four-Way mixtures of winter wheat cultivars from the performances of their two-Way and individual components. Eur. J. Plant Pathol. 114, 163–173.
Mundt, C., Leonard, K., 1986. Analysis of factors affecting disease increase and spread in mixtures of immune and susceptible plants in computer-simulated epidemics. Phytopathology 76, 832–840.
Mundt, C., Brophy, L., Schmitt, M., 1995a. Disease severity and yield of pure-line wheat cultivars and mixtures in the presence of eyespot yellow rust, and their combination. Plant Pathol. 44, 173–182.
Mundt, C.C., Brophy, L.S., Schmitt, M.S., 1995b. Choosing crop cultivars and cultivar mixtures under low versus high disease pressure: a case study with wheat. Crop Prot. 14, 509–515.
Mundt, C.C., 2002b. Performance of wheat cultivars and cultivar mixtures in the presence of Cephalosporium stripe. Crop Prot. 21, 93–99.
Newton, A.C., Guy, D.C., 2011. Scale and spatial structure effects on the outcome of barley cultivar mixture trials for disease control. Field Crops Res. 123, 74–79.
Newton, A.C., Guy, D.C., Bengough, A.G., Gordon, D.C., McKenzie, B.M., Sun, B., Valentine, T.A., Hallett, P.D., 2012. Soil tillage effects on the efficacy of cultivars and their mixtures in winter barley. Field Crops Res. 128, 91–100.
Palloix, A., Ayme, V., Moury, B., 2009. Durability of plant major resistance genes to pathogens depends on the genetic background, experimental evidence and consequences for breeding strategies. New Phytol. 183, 190–199.

Pridham, J., Martin, E., 2007. Mixtures of Modern and Historical Wheat Cultivars Under Organic Management in Western Canada. (Germany).
R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput., Vienna Austria.
Ram, B., Redhu, A., Singh, S., 1989. Development of rusts and powdery mildew in mixtures of wheat-Varieties. Cereal Res. Commun. 17, 195–201.
Rao, B.R., Prasad, R., 1984. Intergenotypic competition in mixed stands of spring wheat genotypes. Euphytica 33, 241–247.
Robertson, G.P., Paul, E.A., Harwood, R.R., 2000. Greenhouse gases in intensive agriculture: contributions of individual gases to the radiative forcing of the atmosphere. Science 289, 1922–1925.
Sage, G., 1971. Inter-varietal competion and its possible consequences for the production of F1 hybrid wheat. J. Agric. Sci. 77, 491–498.
Salovaara, H., Karjalainen, R., 1987. Spring wheat mixtures in Northern crop production: quality characteristics. J. Agric. Sci. Finl. 59, 51–55.
Sammons, D., Baenziger, P., 1985. Performance of 4 winter-Wheat cultivars in blended populations. Field Crops Res. 10, 135–142.
Sapoukhina, N., Paillard, S., Dedryver, F., de Vallavieille-Pope, C., 2013. Quantitative plant resistance in cultivar mixtures: wheat yellow rust as a modeling case study. New Phytol. 200, 888–897.
Sarandon, S., Sarandon, R., 1995. Mixture of cultivars − pilot field trial of an ecological alternative to improve production or quality of wheat (triticum-aestivum). J. Appl. Ecol. 32, 288–294.
Saur, L., Mille, B., 1997. Développement du piétin-verse dÛ à Pseudocercosporella herpotrichoides sur des associations variétales de blé tendre d'hiver. Agron. EDP Sci. 17, 113–118.
Sharma, R.C., Dubin, H.J., 1996. Effect of wheat cultivar mixtures on spot blotch (Bipolaris sorokiniana) and grain yield. Field Crops Res. 48, 95–101.
Shoffner, A.V., Tooker, J.F., 2013. The potential of genotypically diverse cultivar mixtures to moderate aphid populations in wheat (Triticum aestivum L.). Arthropod-Plant Interact. 7, 33–43.
Smith, M. a. H., Wise, I.L., Fox, S.L., Vera, C.L., DePauw, R.M., Lukow, O.M.1, 2014. Seed damage and sources of yield loss by Sitodiplosis mosellana (Diptera: Cecidomyiidae) in resistant wheat varietal blends relative to susceptible wheat cultivars in western Canada. Can. Entomol. 146, 335–346.
Smithson, J.B., Lenne, J.M., 1996. Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. Ann. Appl. Biol. 128, 127–158.
Stutzel, H., Aufhammer, W., 1990. The physiological causes of mixing effects in cultivar mixtures − a general hypothesis. Agric. Syst. 32, 41–53.
Swanston, J.S., Newton, A.C., Brosnan, J.M., Fotheringham, A., Glasgow, E., 2005. Determining the spirit yield of wheat varieties and variety mixtures. J. Cereal Sci. 42, 127–134.
Thomas, J.B., Schaalje, G.B., 1997. Winter survival and competition in a mixture of winter wheat cultivars. Crop Sci. 37, 732–738.
Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. Science 292 (281), 284.
Vanloqueren, G., Baret, P.V., 2008. Why are ecological, low-input, multi-resistant wheat cultivars slow to develop commercially? A Belgian agricultural 'lock-in' case study. Ecol. Econ. 66, 436–446.
Vanloqueren, G., Baret, P.V., 2009. How agricultural research systems shape a technological regime that develops genetic engineering but locks out agroecological innovations. Res. Policy 38, 971–983.
Vera, C.L., Fox, S.L., DePauw, R.M., Smith, M. a. H., Wise, I.L., Clarke, F.R., Procunier, J.D., Lukow, O.M., 2013. Relative performance of resistant wheat varietal blends and susceptible wheat cultivars exposed to wheat midge, Sitodiplosis mosellana (Gehin). Can. J. Plant Sci. 93, 59–66.
Viechtbauer, W., 2010. Conducting meta-Analyses in r with the metafor package. J. Stat. Softw. 36, 1–48.
Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.
Wang, Y., Zhang, Y., Ji, W., Yu, P., Wang, B., Li, J., Han, M., Xu, X., Wang, Z., 2016. Cultivar mixture cropping increased water use efficiency in winter wheat under limited irrigation conditions. PLoS One 11, 1–15.
Wiebe, N., Vandermeer, B., Platt, R.W., Klassen, T.P., Mohere, D., Barrowman, N.J., 2006. A systematic review identifies a lack of standardization in methods for handling missing variance data. J. Clin. Epidemiol. 59, 342–353.
Wolfe, M.S., Brändle, U., Koller, B., Limpert, E., McDermott, J.M., Müller, K., Schaffner, D., 1992. Barley mildew in Europe: population biology and host resistance. Euphytica 63, 125–139.
Wolfe, M.S., 1985. The current status and prospects of multiline cultivars and variety mixtures for disease resistance. Annu. Rev. Phytopathol. 23, 251–273.
Xu, X.-M., 2011. A simulation study on managing plant diseases by systematically altering spatial positions of cultivar mixture components between seasons. Plant Pathol. 60, 857–865.
Zhou, K.Q., Wang, G.D., Li, Y.H., Liu, X.B., Herbert, S.J., Hashemi, M., 2014. Assessing variety mixture of continuous spring wheat (Triticum aestivum L.) on grain yield and flour quality in Northeast China. Int. J. Plant Prod. 8, 91–105.
Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J., Fan, J., Yang, S., Hu, L., Leung, H., et al., 2000. Genetic diversity and disease control in rice. Nature 406, 718–722.
Zhu, Y.Y., Fang, H., Wang, Y.Y., Fan, J.X., Yang, S.S., Mew, T.W., Mundt, C.C., 2005. Panicle blast and canopy moisture in rice cultivar mixtures. Phytopathology 95, 433–438.
Zhu, J., van der Werf, W., Anten, N.P.R., Vos, J., Evers, J.B., 2015. The contribution of phenotypic plasticity to complementary light capture in plant mixtures. New Phytol. 207, 1213–1222.