

Baking quality of wheat variety mixtures: Describing the mechanisms for mixture effects

Amaury Beaugendre^{a,*}, Bruno Godin^b, Dominique Minget^c, Marjolein Visser^a

^a Université Libre de Bruxelles, Faculty of Sciences, Brussels School of Bioengineering, Agroecology Lab, Postal Address: Box 264/2, 50 Avenue Franklin Roosevelt, 1050, Brussels, Belgium

^b Walloon Agricultural Research Centre, Knowledge and Valorization of Agricultural Products Department, Valorization of Agricultural Products, Biomass and Wood Unit, Postal Address: 24 Chaussée de Namur, 5030, Gembloux, Belgium

^c Walloon Agricultural Research Centre, Life Sciences Department, Bioengineering Unit, Postal Address: 234 Chaussée de Charleroi, 5030, Gembloux, Belgium

ARTICLE INFO

Keywords:

Variety mixtures
Organic heterogeneous material
Baking quality
Wheat

ABSTRACT

The use of intra-crop diversity (e.g.: variety mixtures) in bread wheat cropping is getting popular in Europe, mostly for agronomic purposes. However, much less is known about the implications on baking quality.

In this paper, we formalized and tested a framework based on two hypothetical mechanisms for mixture effects as a result of plant interactions within mixtures: (i) *proportion shifts*, relating to changes in grain weight proportion of the varieties at harvest and (ii) *component alteration*, relating to changes in the baking quality of the component varieties. To test this framework, we measured several baking quality indicators on twelve variety mixtures and their component varieties in pure stands. By recording varietal proportions at harvest, we could measure the relative importance of both mechanisms in explaining observed mixture effects.

Our results showed that *proportion shifts* explained a large share of mixture effects on protein baking quality (Zélény sedimentation index and W baking strength) but failed to explain mixture effects on protein content in one year and Hagberg's falling number in both years. Our results also suggest *component alteration* on protein content resulting from altered nitrogen uptake in mixtures, and possibly on Hagberg's falling number resulting from lodging reduction in mixtures.

1. Introduction

At the turn of the 2020's, EU breeding regulations have seen sweeping evolutions aimed towards organic breeding. As of 2022, the new status of Organic Heterogeneous Material (OHM) is overturning decades of the strict DUS doctrine (Distinction, Uniformity, Stability) by allowing commercialization of seeds of germplasm that are "characterized by its high level of phenotypic and genetic diversity, and its dynamic nature to evolve and adapt to certain growing conditions". Besides, variety mixtures seem to be gaining in popularity among farmers. In France, the proportion of wheat area sown with variety mixtures evolved from 4.8% in 2017 (FranceAgriMer, 2017) to 19.5% in 2023, and these mixtures are aimed for breadmaking (Streff, 2023).

Agronomically-speaking, motivations for intra-crop diversity stem from three main advantages that are particularly relevant for organic farming systems (Wolfe et al., 2008): (i) compensation, (ii) complementarity and (iii) evolution (Barot et al., 2017; Beaugendre et al., 2022;

Döring et al., 2011). First, in the face of unpredictable events (weather, disease occurrence, ...), diversity brings stability through the presence of various resistance or tolerance profiles in the same field (compensation). Second, diversity can lead to facilitative interactions through the presence of complementary traits between genotypes (complementarity). Third, if part of the previous harvest is re-used as farm-saved seeds, the composition of a mixture can evolve along the years to gradually adapt to local conditions and farmer's practices through natural and/or mass selection (evolution).

These mechanisms bring forth entirely new logics for breeders. Instead of trying to accumulate a collection of desired traits within a single genotype, we can now think in terms of what does or does not work well together when mixing different genotypes of interest. Yet for now, few assembly rules guide this new breeding logic.

In the case of breadmaking, the prediction of baking quality indicators of flour blends on the basis of the known quality of their components is already well established (Cauvain, 2015; Posner, 2009).

* Corresponding author.

E-mail address: Amaury.beaugendre@ulb.be (A. Beaugendre).

<https://doi.org/10.1016/j.jcs.2024.103933>

Received 16 March 2024; Accepted 13 May 2024

Available online 15 May 2024

0733-5210/© 2024 Elsevier Ltd. All rights reserved, including those for text and data mining, AI training, and similar technologies.

Variety mixtures, however, may not be assumed to simply amount to a grain blend in terms of baking quality. For one, interactions between varieties in a mixture (competitive or facilitative) can affect their yield (as compared to the same varieties sown in pure stands) and hence impact the harvested proportions of the varieties within the mixture (Jackson and Wennig, 1997). We further refer to this anticipated mechanism as *proportion shift*. Besides, plant interactions could also affect baking quality of the component varieties individually, compared to pure stands of the same varieties. We further refer to this anticipated mechanism as *component alteration*.

Considering these two main mechanisms, mixture effects on baking quality can *a priori* theoretically go both ways. And indeed: there are only a few examples of the baking quality of variety mixtures being assessed in the literature – in most cases as an annex observation to an otherwise agronomic evaluation – and their results are equivocal. Authors either report a positive (Jackson and Wennig, 1997; Sarandon and Sarandon, 1995), an absence (Cowger and Weisz, 2008; Döring et al., 2015; Sammons and Baenziger, 1985; Walsh and Noonan, 1998) or, in some cases, a negative effect of mixtures (Cowger and Weisz, 2008) on baking quality. It is therefore relevant, for the sake of improving the baking quality of variety mixtures (or avoiding its degradation), to investigate the specific mechanisms underlying mixture effects on baking quality, which the previously cited papers seldom address.

This paper aims at contributing to this challenge. In organically-managed trials in Wallonia, Belgium, we have grown twelve variety mixtures as well as their component varieties in pure stands over two years. By comparing mixtures to their pure stand components, we first quantify mixture effects for several baking quality traits. Then, on a subset of these mixtures, we conduct a deeper analysis of the mechanisms underlying these mixture effects. On this basis, we seek to confirm (or inform) the two above-mentioned mechanisms for mixture effects (*proportion shifts* and *component alteration*), their respective importance in mixture effects, and the more specific mechanisms that underlie them.

2. Methodology

2.1. Plant material

Eight varieties were chosen to constitute a contrasted and diverse panel to be used in pure stands and mixtures. Their main characteristics are listed in Table 1. Four varieties were modern varieties: Claire, Renan, Soissons and Imperator. The first three were chosen because they are

parents of the YQ CCP, a Composite Cross Population developed in the UK in the early 2000's (Döring et al., 2015) which we studied in other trials of the same research project (data not shown). Imperator was chosen to include a more recent variety that is representative of the current organic varietal offer: it was registered in 2018 and is recommended for organic cropping in Wallonia, where we lead our trials. Claire is known to be a biscuit variety, while the other three are considered apt for breadmaking. Renan, in particular, is considered in France to be a “blé ameliorant” or “blé de force”, a category attributed to varieties with particularly high baking strength. The other four varieties were heritage varieties predating the Green Revolution and were chosen for their contrasted agronomic characteristics: Chiddam d'Automne à Epi Blanc, Japhet, Prince Albert, Rouge de St-Laud. Their baking quality was unknown at the time of sowing.

The twelve mixtures are different combinations of the eight varieties grown in pure stands. All mixtures were prepared anew each year with each variety in equal seed proportions (accounting for thousand kernel weight and germination rates). Nine of them are two-way mixtures, two are four-way mixtures, and one is the mixture of all eight varieties (see Table 1). The mixtures were designed to provide gradients of contrasts for two main agronomic traits: plant height and early cover. Focus was put on those traits due to their links with weed suppressiveness, light competition (including between varieties within mixtures) and lodging. Their agronomic evaluation is the subject of another research work (see Beaugendre, 2024).

2.2. Field trials

Field experiments were conducted on organically managed fields near Gembloux, Belgium during the growing seasons of 2021 and 2022 (harvest years). The first year of trials (harvest year 2021) took place in the “Coquelet” site (4.7222° N; 50.5612° E) in Gembloux. This plot used to be an apple orchard converted to organic agriculture in 2008. The orchard was dug up in 2011 and was replaced by a temporary meadow since then. Soil was characterized as loamy (clay content: 12–18%; sand content <15%). Soil mineral N content (up to 90 cm depth) was estimated to be 69.8 kg/ha on March 01, 2021. No fertilizer was applied. The second year of trials (harvest year 2022) took place in the “Penteville” site (4.6524° N; 50.5507° E) in Gembloux. The previous crop was winter barley – and a temporary meadow before that. Soil was again characterized as loamy. About 6 weeks prior to sowing, 30 t/ha of cow manure and 10 t/ha of sugar factory lime were applied. Mineral N

Table 1
Description of the plant material.

Germplasm name (acronym)	Type	Registration Year/Earliest known record	Baking-quality class (French classification – CTPS and ARVALIS)
Claire (C)	Modern	1996	Biscuit
Imperator (I)	Modern	2019	Superior breadmaking
Renan (R)	Modern	1989	Improver/strength
Soissons (S)	Modern	1996	Superior breadmaking
Chiddam d'automne à épi blanc (CH)	Heritage	1840	Unknown
Japhet (J)	Heritage	1892	Unknown
Prince Albert (PA)	Heritage	1851	Unknown
Rouge de St-Laud (RSL)	Heritage	<1880	Unknown
Mixture acronym	Component varieties	Variety Number	
C-I	Claire – Imperator	2	
CH-PA	Chiddam d'automne à épi blanc – Prince Albert	2	
J-C	Japhet – Claire	2	
J-PA	Japhet – Prince Albert	2	
J-RSL	Japhet- Rouge de St-Laud	2	
J-PA-RSL-C	Japhet – Prince Albert – Rouge de St-Laud – Claire	4	
PA-R	Prince Albert – Renan	2	
PA-RSL	Prince Albert – Rouge de St-Laud	2	
RSL-S	Rouge de St-Laud – Soissons	2	
S-R	Soissons – Renan	2	
PA-RSL-S-R	Prince Albert – Rouge de St-Laud – Soissons – Renan	4	
All	Claire, Chiddam d'automne à épi blanc, Imperator, Japhet, Prince Albert, Renan, Rouge de St-Laud, Soissons	8	

content (90 cm depth) was estimated to be 95.9 kg/ha on February 16, 2022. No other fertilization was applied.

The two growing seasons were remarkably contrasted in terms of weather conditions, especially the summer. The summer of 2021 was exceptionally wet and with numerous thunderstorms. In 2022, the summer was instead marked by drought and heat.

Trials were sown in a randomized complete block design with four replicates, at a sowing density of 100 seeds/m². Harvested plots measured 7.5 m² in 2021 and 10.5 m² in 2022. Trials were respectively sown on October 9, 2020 and October 18, 2021. Mechanical weeding was performed with a tine-harrow once in spring each year, plus once at the end of autumn 2020. In 2021, harvest was delayed until August 15, 2021 as a result of near-daily rainfall but could take place under fairly dry conditions. In 2022, harvest could take place on time and in ideal conditions on July 28, 2022.

2.3. Agronomic data

2.3.1. Plot level data

A lodging resistance score (LRS) was given to each plot according to [van Waes \(2006\)](#) after each major lodging event (i.e. events after which lodging was clearly visible in the field) using equation (1):

$$\text{Lodging Resistance Score} = 9 - E \frac{(9 - I)}{100} \quad (1)$$

where E is the percentage of lodged area within the plot, and I is the lodging intensity (where 1 corresponds to stems fully lying on the ground and 9 to stems perfectly straight and vertical). In both years there were two main lodging events that occurred at similar stages: a first approximately two weeks after heading (LRS_{Early}), and a second approximately one month after heading (LRS_{Late}). Grain yield (GY) was measured in each plot from the combine-harvested grain and was corrected at 15% moisture content.

2.3.2. Plant level data

We collected plant-level data on mixtures J-C, J-PA, J-RSL, PA-R, PA-RSL, RSL-S and S-R, in which component varieties were easily distinguishable thanks to strong phenotypic contrasts (ear color, awnedness, plant height, ...). In all plots of these mixtures, as well as in pure stand plots of their component varieties, we marked 12 plants from each variety separately at the heading stage. Just after heading, we measured the Nitrogen Balance Index (NBI) on the flag leaf of each marked plant using a DUALEX optical sensor (Pessl Instruments). The NBI gives an indication of the mass concentration of nitrogen in leaves based on measures of leaf chlorophyll and flavonoid contents ([Cervic et al., 2012](#)), and is a good indicator of plant nitrogen status ([Tremblay et al., 2009](#)). The same plants were collected just before harvest. Their ears were threshed in the lab, and their grains weighed separately (Plant yield). Since we did not detect differences in emergence between varieties (data not shown) and since varieties were sown in equal proportions in each mixture, we used this average plant yield, measured for each component variety within the mixtures, to estimate their grain weight proportions at harvest. \widehat{p}_{ij} , the estimated grain weight proportion of variety i in mixture j at harvest, was calculated as follows:

$$\widehat{p}_{ij} = \frac{\overline{\text{Plant yield}}_{ij}}{\sum_{i=1}^n \overline{\text{Plant yield}}_{ij}}$$

where $\overline{\text{Plant yield}}_{ij}$ is the mean plant yield of variety i in mixture j .

2.4. Quality assessment

All quality analyses were performed at the Valorization of agricultural products, biomass and wood Unit of the CRA-W. Plot replicates

were pooled in equal weight proportion prior to analysis, hence there was one grain sample per object (mixture or pure stand) per site-year. Focus was set on quality variables that are commonly used to evaluate grain lots.

2.4.1. Grain analysis and milling

Protein content (PRT; N*5.7) as well as test weight (TW) were measured on grain samples by near-infrared spectrometry with an Infratec NOVA (FOSS analytics, Denmark). For Hagberg's falling number and Zélény's sedimentation index, we used flour obtained through their specific milling instruments, respectively the Lab Mill (Pertin Instruments, Sweden; on 300 g of grains) and the Sedimat mill (Brabender, Germany; on 100 g of grains). White flour (T550 = 0.55 % dry matter ash content) used for alveograph analyses was obtained by milling the grains using a CD1 mill (Chopin technologies, France), following ISO 27971 (2015). All weights were normalized to a 15 % moisture content, taking into consideration the respective water content of each sample.

2.4.2. Flour analyses

Hagberg falling number (HFN) was determined according to ISO 3093:2009, using a Falling Number 1310 (PerkinElmer, USA) with 2 repetitions of 7 g of flour per sample. Zélény sedimentation index (ZEL) was measured according to ISO 5529:2007 using Sedimat apparatus (Brabender, Germany; 2 repetitions with 3.2 g of flour per sample). Baking strength (W) was measured using the Alveograph NG (Chopin technologies, France; constant hydration method) with 5 repetitions of 50 g of dough per sample, following ISO 27971:2015.

2.5. Data analyses

2.5.1. Principal component analysis

In order to get a general overview of the characteristics of our varieties, mixtures and site-years, we started by applying a principal component analysis on our dataset. The PCA included all baking quality variables as well as grain yield (GY) and lodging resistance scores (LRS). GY and LRS were averaged across replicate plots in each year. In order to visualize the effects of both environment, germplasm as well as their interaction, this PCA was conducted on the whole data set instead of averaging over the two site-years.

2.5.2. Testing for baking quality mixture effects

To quantify mixture effects on baking quality, we compared measured mixture quality (Q_{mix}) to the expected mixture quality in the absence of any mixture effect (Q_{nil}). We remind the reader that for the baking quality indicators considered in this research, the literature ([Cauvain, 2015](#)) or the methods' international standards state that the baking value of a flour blend can be found by calculating the weighted arithmetic mean of its components' baking values:

$$Q_{blend} = \sum_{i=1}^n Q_i * p_i \quad (2)$$

where Q_{blend} is the baking value (for a given quality indicator) of the blend, Q_i is the baking value of the i th variety within that blend and p_i is the weight proportion of this variety in the blend. To get the expected HFN of a mixture, we must use the conversion to liquefaction number using the following formulae ([Cauvain, 2015](#)):

$$\text{Liquefaction Number (LN)} = \frac{6000}{\text{HFN} - 50} \quad (3)$$

$$\text{HFN}_{blend i} = 50 + \frac{6000}{\sum_{i=1}^n \text{LN}_i * p_i} \quad (4)$$

where i represents the varieties composing the blend.

Assuming the mixture had no effect whatsoever on its component varieties, their individual quality characteristics should remain unchanged, and their proportions at harvest should simply depend on their respective yield potentials in pure stands. We can thus estimate Q_{nil} , the expected quality of a nil-effect mixture of n varieties, using equation (2) and calculating p_i as follows:

$$p_i = \frac{Y_{i\ PS}}{\sum_{i=1}^n Y_{i\ PS}} \quad (5)$$

where $Y_{i\ PS}$ is the grain yield of variety i measured in a pure stand.

At this point, we would like to point out that harvested mixtures are grain blends rather than flour blends, which can introduce deviations from the above formula (Posner, 2009). Our samples were not large enough to measure Q_{nil} and Q_{prop} (see below) on grain blends reconstituted from pure stand grains for all mixtures, so we had to rely on estimations using equation (2). However, we made tests with several grain blends constituted from pure-stand samples to make sure that we were not introducing major biases, and found that the measured values satisfactorily matched the estimations based on equation (2) (data not shown).

After having calculated Q_{nil} for all mixtures in each year for all of our baking quality variables, we then calculated mixture relative performance (RP) as the ratio of mixture quality Q_{mix} (measured on the harvested mixture), over Q_{nil} :

$$RP = \frac{Q_{mix}}{Q_{nil}} = \frac{Q_{mix}}{\sum_{i=1}^n Q_i * \frac{Y_{i\ PS}}{\sum_{i=1}^n Y_{i\ PS}}} \quad (6)$$

Since we pooled the replicates, our data does not allow us to test the presence of a mixture effect ($RP \neq 1$) for each mixture individually. Instead, we checked, for each quality variable, whether mixture relative performance was significantly different from 1 on average for our whole mixture panel of 12 mixtures using one-sample t -tests with $\mu = 1$ (null hypothesis).

2.5.3. Investigating mixture effects' mechanisms

Following equation (2), differences between observed values (Q_{mix}) and Q_{nil} could be the result of (i) changes in p_i , the grain proportions of the component varieties in the harvested mixture – an effect which we call *proportion shift*, and which was already pointed out by Jackson and Wennig (1997); or (ii) changes in Q_i , the baking quality of the individual component varieties within the mixture – an effect which we call *component alteration*.

In order to evaluate the contribution of these two mechanisms to the observed mixture effects, we first calculated new estimations of our baking quality criteria, Q_{prop} , using \hat{p}_{ij} , the varietal proportions at harvest that we estimated with our plant samples (see 2.3.2). Q_{prop} estimations and all the analyses that follow were thus performed only on the seven mixtures in which we could sample individual plant data. To assess the role of proportion shift, we then calculated the R^2 and root-mean-square deviation (RMSD) of Q_{prop} as an estimation of Q_{mix} (the true value, measured on the harvested mixture), which we compared to the R^2 and RMSD for Q_{nil} as an estimation of Q_{mix} . Higher R^2 and lower RMSD for Q_{prop} than Q_{nil} would indicate a contribution of proportion shift to the observed mixture effects.

Considering that the residuals of Q_{prop} (i.e. the difference between Q_{mix} and Q_{prop}) represent the remaining mixture effects that could not be explained by proportion effects, we used these as a proxy variable to study component alteration. To try to identify causal mechanisms for component alteration, we checked for correlations between Q_{prop} residuals and two potential explanatory variables.

For protein-related baking quality traits (PRT, ZEL, W), we formulated the hypothesis that plant nitrogen uptake could have played a part in component alteration. To approach changes in plant nitrogen uptake between mixtures and pure stand, we calculated an index, ΔNBI_{mix} ,

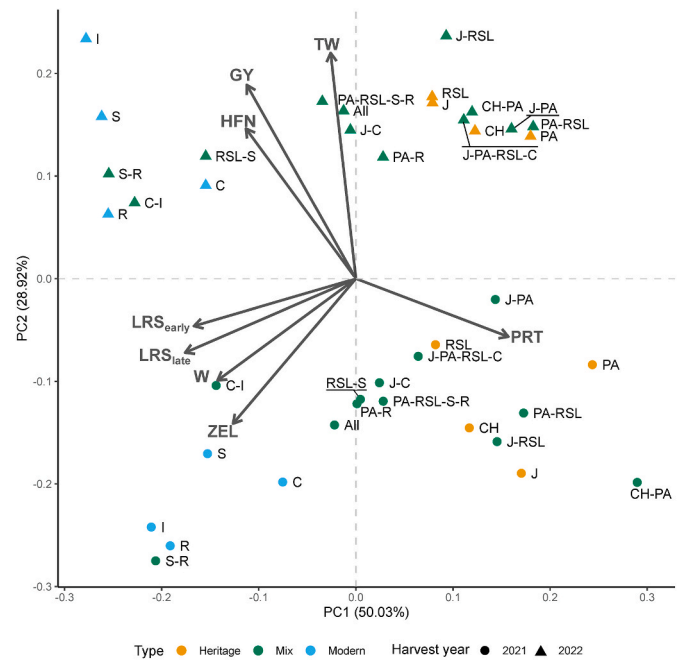


Fig. 1. Biplot for a Principal Component Analysis performed on 3 agronomic and 5 baking quality indicators for 8 pure-stand varieties (both modern and heritage/landraces) and 12 variety mixtures over the 2021 and 2022 harvest years. Objects are colored and shaped according to germplasm type and site-year, respectively. Germplasms are labeled with their acronyms (see Table 1). GY: grain yield; LRS: lodging resistance score; PRT: grain protein content; TW: test weight; ZEL: Zélény sedimentation index; W: baking strength; HFN: Hagberg's falling number.

based on NBI measures. This index is, for each mixture, the proportion-weighted mean of its component varieties' NBI relative change between mixture and pure stand:

$$\Delta NBI_{mix} = \sum_{i=1}^n \frac{(NBI_{i\ mix} - NBI_{i\ PS})}{NBI_{i\ PS}} \hat{p}_i \quad (7)$$

Where $NBI_{i\ mix}$ is the mean NBI of the mixtures' i th component variety measured within the mixture, $NBI_{i\ PS}$ is the mean NBI of the mixtures' i th component variety measured in pure stand, and \hat{p}_i is the grain proportion of the i th component variety in the mixture at harvest, estimated from our plant data. If, on (weighted) average, NBI was higher in the mixture than in its component varieties' pure stands, ΔNBI_{mix} will be positive (and vice-versa). A measure of relative rather than absolute change was chosen because there were large and consistent differences in NBI between some varieties, which may have introduced biases towards the varieties with higher NBI if an absolute change had been chosen.

For HFN and TW, we hypothesized an effect of lodging (Berry et al., 2004): lodging reduction (or increase) in mixtures compared to the pure stands could have improved (or degraded) HFN and TW. To quantify mixture effects on lodging, we calculated an index, ΔLRS_{mix} , accounting for differences in LRS between mixtures and pure stands of their component varieties, weighted by the varieties' proportions in the harvested mixtures:

$$\Delta LRS_{mix} = \sum_{i=1}^n (LRS_{mix} - LRS_i) \hat{p}_i \quad (8)$$

Where LRS_{mix} is the lodging resistance score of the mixture and LRS_i that of its i th component variety in pure stand, and \hat{p}_i is the grain proportion of the i th component variety in the mixture at harvest, estimated from our plant data. If, on (weighted) average, the mixture lodged less than its

Table 2

Mixture relative performance (RP) for PRT, TW, ZEL, W and HFN for all mixtures in both years of trial.

Observed values (Q_{mix}) and the expected values in the absence of mixture effects (Q_{nil}) are also displayed. One sample t-tests were performed to check whether relative performances were significantly different from 1 on average for both site-years separately, and then together. P-values of those t-tests are reported. Asterisks show which tests were significant ($\alpha = 0.05$).

	PRT (%)			TW (kg/hL)			ZEL (mL)			W (10^{-4} J)			HFN (s)		
	Q_{mix}	Q_{nil}	RP	Q_{mix}	Q_{nil}	RP	Q_{mix}	Q_{nil}	RP	Q_{mix}	Q_{nil}	RP	Q_{mix}	Q_{nil}	RP
2021 (Coquelet)															
All	12.01	12.56	0.96	72.91	71.70	1.02	22	28	0.80	113	142	0.79	164	118	1.39
C-I	10.53	12.14	0.87	71.76	69.10	1.04	29	35	0.82	96	163	0.59	329	324	1.02
CH-PA	14.86	13.37	1.11	70.19	72.61	0.97	18	18	1.02	62	69	0.90	75	74	1.02
J-C	13.28	13.17	1.01	72.60	68.69	1.06	24	26	0.93	138	114	1.21	275	219	1.26
J-PA	13.42	14.65	0.92	74.69	72.32	1.03	16	21	0.75	97	105	0.93	258	163	1.58
J-PA-RSL-C	12.99	13.35	0.97	73.40	70.98	1.03	16	19	0.85	78	85	0.92	217	162	1.34
J-RSL	13.25	13.13	1.01	71.38	72.34	0.99	18	18	1.03	93	85	1.10	104	133	0.78
PA-R	12.92	13.56	0.95	72.91	73.08	1.00	21	29	0.73	114	196	0.58	235	202	1.16
PA-RSL	13.05	13.53	0.96	70.88	73.20	0.97	10	12	0.82	41	56	0.73	99	134	0.74
PA-RSL-S-R	12.88	12.63	1.02	72.64	73.12	0.99	19	25	0.76	101	149	0.68	189	171	1.11
RSL-S	12.04	11.84	1.02	72.72	73.15	0.99	15	22	0.69	101	109	0.93	135	153	0.88
S-R	12.49	11.80	1.06	73.14	73.05	1.00	44	37	1.19	305	235	1.30	296	253	1.17
Mean			0.99			1.01			0.87			0.89			1.12
p-value			0.522			0.397			0.010 *			0.116			0.125
2022 (Penteville)															
All	12.10	11.60	1.04	78.80	77.44	1.02	16	22	0.72	79	121	0.65	277	324	0.85
C-I	10.60	10.28	1.03	76.10	76.30	1.00	27	25	1.09	166	105	1.57	356	350	1.02
CH-PA	13.50	13.85	0.97	77.90	77.43	1.01	10	13	0.79	51	53	0.97	275	287	0.96
J-C	12.03	10.27	1.17	76.74	74.01	1.04	13	11	1.17	80	65	1.24	364	319	1.14
J-PA	13.60	13.90	0.98	78.20	77.34	1.01	13	13	1.01	51	66	0.77	314	317	0.99
J-PA-RSL-C	13.10	12.19	1.07	77.70	75.69	1.03	10	12	0.85	50	51	0.98	301	290	1.04
J-RSL	12.60	12.00	1.05	79.80	77.89	1.02	11	12	0.92	38	57	0.67	341	275	1.24
PA-R	13.16	12.41	1.06	75.82	77.86	0.97	14	22	0.63	73	158	0.46	358	348	1.03
PA-RSL	13.80	13.05	1.06	77.10	77.66	0.99	9	9	0.95	11	38	0.29	283	256	1.11
PA-RSL-S-R	11.81	11.68	1.01	77.70	78.40	0.99	12	21	0.58	70	146	0.48	334	321	1.04
RSL-S	10.85	11.09	0.98	77.90	78.83	0.99	14	19	0.73	187	135	1.38	327	303	1.08
S-R	11.00	11.29	0.97	78.70	78.30	1.01	31	31	0.99	198	217	0.91	396	370	1.07
Mean			1.03			1.01			0.87			0.87			1.05
p-value			0.065			0.288			0.032 *			0.256			0.118
Total mean			1.01			1.01			0.87			0.88			1.08
p-value			0.419			0.182			$6 \times 10^{-4} *$			0.065			0.042 *

component varieties in pure stands, then ΔLRS_{mix} is positive (and vice-versa). Contrarily to ΔNBI_{mix} , an absolute difference was more adequate than a relative difference because LRS ranges very close to 0 (scores go from 1 to 9), so using relative differences would have introduced major biases.

ΔNBI_{mix} and ΔLRS_{mix} were calculated for each of the seven mixtures within which we could sample individual plant data (see 2.3.2) in each year. To test our hypotheses, we calculated Spearman correlation coefficients of ΔNBI_{mix} and ΔLRS_{mix} with the residuals of Q_{prop} , and tested these correlations for statistical significance ($\alpha = 0.05$).

All data analyses were performed on R programming language using RStudio (R Core Team, 2023).

3. Results and discussion

3.1. Principal component analysis

Before delving into the analyses of baking quality mixture effects, we give a global overview of our data. In order to get insight into how our baking value variables are structured by object and growing season contrasts, we conducted a PCA on our dataset including both site-years without aggregation (see Fig. 1). The first two principal components respectively captured 50.03 and 28.92 % of variance and thus allow to have a good view on this variable structuring.

The PCA very clearly displays the distinction between both site-years: 2021 is clearly characterized by lower GY, TW and HFN. This very likely reflects the contrasted meteorological conditions between 2021 and 2022. The summer of 2021 was exceptionally wet, and the

near-daily rainfall postponed harvest by at least two weeks, conditions which are known to be detrimental to TW and HFN in particular (Dorrian et al., 2023; Farrer et al., 2006). See (Beaugendre, 2024) for more detailed results on lodging and grain yield in these trials. In much lesser proportions, protein content (PRT) and quality (ZEL and W) were a little higher in 2021 than in 2022. Here, the higher PRT may be associated to the lower grain yield (PRT and GY are negatively correlated, likely due to a dilution effect).

The other apparent contrast of our PCA lies between modern and heritage varieties. Modern varieties had lower PRT, higher ZEL and W, were much more lodging-resistant, and had slightly higher HFN and GY than the heritage varieties. Nothing surprising in these observations, which match previous research (Løes et al., 2020): modern breeding has considerably reduced plant height including the introduction of semi-dwarf alleles) to reduce lodging, increased average yield (Gooding, 2009) and has selected for baking quality improvements, particularly aiming at enhanced gluten quality rather than simply targeting higher protein content (Osman et al., 2012), which may also explain the lower PRT in these varieties (that is also likely attributable to a dilution effect). Although it is not particularly striking in this biplot, Claire slightly stood out from other modern varieties, which reflects its classification as a biscuit variety: its TW, ZEL and W were lower than other modern varieties (Table A1).

Last but not least, mixtures are positioned rather coherently across the PCA biplots: modern-only mixtures (C-I and S-R) are clustered together with modern varieties, mixed-age mixtures are situated between modern and heritage varieties, and heritage-only mixtures are clustered together with the heritage varieties. Mixture effects are,

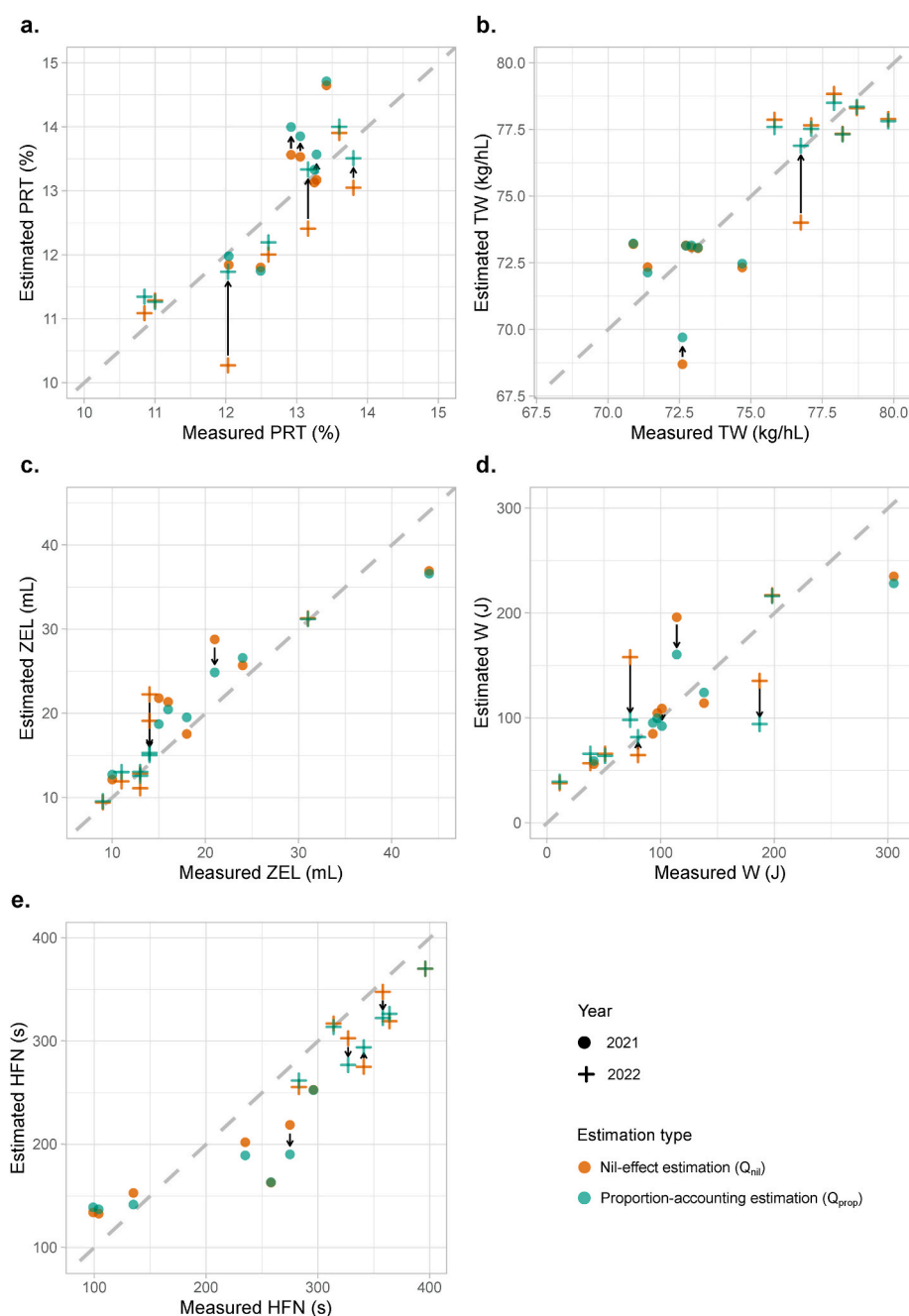


Fig. 2. Graphical representation of the accuracy of nil-effect and proportion-accounting estimations. Estimated values are plotted against observed values. In each plot, datapoint color indicates the estimation type and datapoint shape indicates the year. The grey dotted line represents the perfect fit. Black arrows help visualize the differences between the nil-effect and proportion-accounting estimations. The data presented here concerns a subset of 7 mixtures (out of 12) for which individual plant data could be collected to measure grain weight varietal proportion in the harvested mixture. PRT: grain protein content; TW: test weight; ZEL: Zélény sedimentation index; W: baking strength; HFN: Hagberg's falling number. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

however, somewhat hinted at on this PCA: overall, mixtures are rarely positioned at midpoint between their component varieties; and, more strikingly, mixed-age mixtures tend to cluster closer to the heritage varieties than to the modern, the only exception being RSL-S in 2022 which rather clusters together with the modern varieties.

3.2. Mixture effects

3.2.1. Testing for baking quality mixture effects

Assuming that mixtures, in the absence of mixture effect of any kind, should fall exactly in the middle between their component varieties in

the PCA can only hold true when the harvested mixture contains an equal grain proportion of each variety. However, even in the absence of mixture effects, this scenario would rarely occur because our varieties typically vary in their yield potentials, and the higher yielder should thus be overrepresented in the harvested mixture. To clear this up, we calculated mixtures' relative performances (RP), which compare mixtures' measured baking quality (Q_{mix}) to their expected quality in a nil-effect configuration (Q_{nil}), which accounts for differences in yield potential between varieties. Results are shown in Table 2.

For PRT, we found relative performances ranging from 0.87 to 1.17 depending on the mixture, with no clear average mixture effect.

Table 3

R-squared (R^2) and Root-Mean-Square Deviations (RMSD) for nil-effect and proportion-accounting estimations of baking quality parameters.

As a reminder, R^2 is a unitless measure that estimates how much of the initial variability within observed values (Q_{mix}) has been accounted for by the estimations. A value of 1 (the maximum) means that the estimations perfectly match Q_{mix} . A negative value (rarely encountered for R^2 but mathematically valid) indicates that the estimations did worse than simply using the mean of Q_{mix} as the sole estimation for all measures. RMSD is a measure of deviation and must thus be interpreted with respect to the variable's scale. The closer the RMSD is to 0, the better the estimations. This data was calculated from a subset of 7 mixtures (out of 12) for which plant data could be collected to estimate grain weight varietal proportions in the harvested mixtures.

Year	Quality variable	Nil-effect estimation (Q_{nil})		Proportion-accounting estimation (Q_{prop})	
		R^2	RMSD	R^2	RMSD
2021	PRT (%)	−0.431	0.62	−1.187	0.77
	TW (kg/hL)	0.506	1.98	0.645	1.68
	ZEL (mL)	0.756	5.3	0.849	4.1
	W (J)	0.715	42	0.805	35
	HFN (s)	0.774	50	0.705	57
2022	PRT (%)	0.461	0.83	0.906	0.35
	TW (kg/hL)	0.693	1.58	0.849	1.11
	ZEL (mL)	0.741	3.8	0.980	1.0
	W (J)	0.655	41	0.668	40
	HFN (s)	0.801	35	0.800	35
Both	PRT (%)	0.306	0.73	0.541	0.59
	TW (kg/hL)	0.600	1.79	0.748	1.42
	ZEL (mL)	0.751	4.6	0.892	3.0
	W (J)	0.689	42	0.746	38
	HFN (s)	0.784	43	0.739	47

Likewise, there was no average mixture effect on TW, for which RP ranged from 0.97 to 1.06. For ZEL, we found more contrasting relative performances, ranging from 0.58 to 1.19, with an overall significant negative effect on both site-years. For W, we found even more contrasting values, ranging from 0.29 to 1.57, also with an average negative mixture effect which was nearly significant when taking both site-years together. Finally, we found a positive effect of mixtures on HFN, ranging from 0.74 to 1.58, which was only significant when taking both years together.

These results confirm the presence of baking quality mixture effects, and point out that, on average, our mixture set tended towards decreased ZEL (and W) and enhanced HFN. Although we could not test mixtures individually, the wide ranges of RP we found for most variables (including ZEL and HFN) in the same site-years seem to confirm that

mixture composition (and their interaction with the environment) can be a major determinant of mixture effects.

3.2.2. Investigating mixture effects' mechanisms

Once that mixture effects have been identified, farmers and breeders need some understanding of their underlying mechanisms to inform mixture composition. In a subset of 7 mixtures, we could collect more precise data in order to disentangle the roles of proportion shifts and component alteration in the observed mixture effects. To examine the contribution of proportion shifts, we made quality estimations (Q_{prop}) that account for the measured varietal proportions in the harvested mixtures, and we checked whether they matched the true mixture quality (Q_{mix}) better than Q_{nil} (see Fig. 2 and Table 3). Then, we used the residuals of Q_{prop} relative to Q_{mix} (i.e.: the share of mixture effects that was not explained by proportion shifts) as a proxy for component alteration: we tested these residuals for correlations with variables which we hypothesized to be involved in component alteration (Table 4).

In several mixtures, the measured varietal proportions in the harvested grain substantially differed from those expected from the component varieties' yield in pure stands (Figure A1), which sometimes resulted in quite noticeable differences between Q_{prop} and Q_{nil} (Fig. 2). The underlying mechanisms for these proportion changes is the object of another research (see Beaugendre, 2024), in which we show them to mainly result from competition. For most quality variables, proportion shifts appeared to explain a substantial part of the mixture effects (see Fig. 2 and Table 3), with Q_{prop} improving R^2 and RMSD compared to Q_{nil} for nearly all variables: the only exceptions were PRT in 2021 and HFN in both years, for which R^2 and RMSD actually degraded.

PRT was the only variable with marked differences in this regard between seasons. In 2021, mixture effects on PRT appeared to be very poorly explained by proportion shifts (R^2 and RMSD degraded from Q_{nil} to Q_{prop}), but the contrary is observed for 2022. Correspondingly, component alteration seems to better explain mixture effects for PRT in 2021: Q_{prop} residuals were significantly positively correlated to ΔNBI_{mix} in 2021 (and not in 2022; see Table 4). ΔNBI_{mix} reflects differences in plant nitrogen accumulation between mixtures and pure stands and should thus indeed affect grain protein content. We however note that the very low predictive accuracies of Q_{prop} and Q_{nil} in 2021 (negative R^2) may partly be an artifact of a low spread of measured PRT values in this year (12.0–13.4%, while the range of PRT in 2022 was 10.8–13.8%). In support of this affirmation, we can also see that RMSD for Q_{nil} was actually lower in 2021 than in 2022. These results should thus be interpreted with some caution.

TW did not seem to be majorly affected by mixture effects, as already seen in 3.2.1. As already mentioned in 3.1, there was a strong year to year variation for this variable (Fig. 2b), with much lower TW in 2021,

Table 4

Spearman's rank correlation coefficients (ρ) and their associated p-values for Q_{prop} residuals against explanatory variables.

Q_{prop} residuals are the residuals of the proportion-accounting estimations of baking quality against the measured values in mixtures, representing the share of mixture effects which are not explained by changes in varietal proportion in the mixtures. ΔNBI_{mix} and ΔLRS_{mix} represent differences in, respectively, plant nitrogen status and lodging, between mixtures and their component varieties in pure stands. This data was calculated from a subset of 7 mixtures (out of 12) for which plant data could be collected to measure NBI and varietal proportion in the mixture.

Explanatory variable	Quality variable (Q_{prop} residuals)	2021		2022		Both	
		ρ	p-value	ρ	p-value	ρ	p-value
ΔNBI_{mix}	PRT	0.857	0.024	0.429	0.354	0.710	0.006
	ZEL	0.821	0.034	0.000	1.000	0.574	0.035
	W	0.714	0.088	0.214	0.662	0.218	0.454
ΔLRS_{mix} Early lodging	TW	0.464	0.302	−0.321	0.498	0.066	0.823
	HFN	0.607	0.167	0.607	0.167	0.506	0.065
ΔLRS_{mix} Late lodging	TW	0.250	0.595	0.036	0.963	0.029	0.928
	HFN	0.536	0.236	0.500	0.267	0.358	0.209

yet low within-year variation. Q_{prop} estimations for TW did not markedly differ from Q_{nil} (Fig. 2b), except for one particular mixture in each year, J-C (see Table A2), which explains the overall R^2 and RMSD improvements (Table 3). Claire indeed stood out as a variety producing smaller grains (and TW) than all other varieties of our trials, explaining why proportion shifts in a mixture containing Claire can strongly affect its TW. In any case, correlations of Q_{prop} residuals with ΔLRS_{mix} were very low (Table 4), suggesting that lodging had little influence in these mixture effects.

Proportion shifts appeared to be a major contributing factor to mixture effects for ZEL (see Table 3 and Fig. 2c), which makes sense: ZEL is strongly genetically determined (Branlard et al., 1992, 2001) and is thus not expected to be very sensitive to component alteration. As a result, ZEL can indeed be expected to be more sensitive to proportion shifts, if there are proportion shifts and if component varieties are contrasted for ZEL. This was the case for several of our mixtures (particularly PA-R or RSL-S), which had very contrasted protein qualities and were subject to substantial proportion shifts. These mixtures indeed explain most of Q_{prop} 's R^2 improvements in ZEL. In most cases, it was the variety with the lowest ZEL that saw its proportion increase, which explains why RP was inferior to 1 on average for this quality criterion (see Table 2). Protein content, on which growing conditions have a larger influence, can also affect ZEL, although to a much lesser extent than genetics (Branlard et al., 2001). Component alteration in PRT can thus be expected to lead to component alteration for ZEL. Our results match these assumptions, as component alteration in PRT indeed appears to match component alteration in ZEL: In 2021, we found component alteration to be the major contributor to PRT mixture effects, which appeared to be explained by plant nitrogen accumulation (ΔNBI_{mix} , see Table 4); in the same year,

Q_{prop} did not explain all of ZEL mixture effects ($R^2 = 0.849$) and its residuals were also significantly correlated with ΔNBI_{mix} ($\rho = 0.821$ and $p\text{-value} = 0.034$, Table 4). In 2022 we did not find component alteration in PRT, whose mixture effects were instead mainly explained by proportion shifts, and accordingly Q_{prop} nearly perfectly estimated ZEL in 2022 ($R^2 = 0.980$, see Table 3).

Results for W were similar to those for ZEL, but tamer – especially in 2022. Q_{prop} tended to improve R^2 and RMSD (see Table 3 and Fig. 2d), and there was a strong, near-significant positive correlation of Q_{prop} residuals with ΔNBI_{mix} in 2021 (see Table 4). The similarities between these variables were expected, since they have similar genetic and environmental (through protein content) determinants (Branlard et al., 2001). The weaker R^2 , higher RMSD and lower correlation coefficients in W than in ZEL may be related to the lower heritability of this trait, or to the more complex nature of this measure which can also be affected by starch damage or water absorption (Carson and Edwards, 2009).

We found that proportion shifts did not explain HFN mixture effects at all: Q_{prop} actually reduced R^2 and increased RMSD compared to Q_{nil} (see Table 3 and Fig. 2e). This suggests that the significant average positive mixture effect on HFN instead mainly resulted from component alteration. Since our mixtures generally lodged less, and later, than their most sensitive component varieties, we had hypothesized that it could have led to component alteration. Indeed, although genotype also plays a role in its determination (Lunn et al., 2001), HFN is much tributary to environmental factors such as lodging, weather conditions or delayed harvest (Berry et al., 2004; Farrer et al., 2006), which our trials were particularly exposed to (lodging in both years; wet summer and delayed harvest in 2021). Correlations of Q_{prop} residuals with ΔLRS_{mix} were positive and nearly significant for early lodging ($p\text{-value} = 0.065$ when taking both years, Table 4), which gives credit to our hypothesis. Other effects could however also be at play and potentially explain these weak correlations, perhaps related to grain maturity or humidity trapped in the canopy of height-contrasted mixtures. In any case, this appears to be a prime example of a complementarity effect in mixtures.

4. Conclusion

The scientific literature reports very little research investigating the baking quality of wheat variety mixtures, even though their popularity in the field is increasing. Although mixture effects have sometimes been reported, their underlying mechanisms were never investigated properly. With this paper, we formalize a simple framework for understanding mixture effects on baking quality by describing two general mechanisms: *proportion shifts*, relating to changes in varietal proportions within harvested mixtures that result from intervarietal interactions (competition and/or facilitation), and *component alteration*, relating to changes in the baking quality of a mixture's component varieties resulting from how they grow and interact in the mixture. With our trials, we could demonstrate the applicability of this framework, as we showed substantial evidence for the role of proportion shifts, and circumstantial evidence of component alteration in explaining observed mixture effects.

In a first application of this framework, our results could show that quality traits with strong genetic determinism (e.g. protein quality as measured by ZEL and W) are more likely to be subject to the effects of proportion shifts rather than component alteration, since the environmental specificities of the mixture (compared to a pure stand) should have little impact on those traits at the component-variety-level. When designing a mixture, farmers or breeders should thus pay particular attention to the yield potential (which will contribute to determine varietal proportions at harvest) and competitiveness of the component varieties, and put these factors in perspective with their baking quality traits. Indeed, our results illustrated how the dominance of a low-quality variety in a mixture can drastically reduce mixture quality.

Further applications of this framework should aim to better characterize component alteration. Here, we had to rely on indirect measures of component alteration on a relatively low number of mixtures, so we could not deeply address these mechanisms. We could show that positive mixture effects on lodging probably positively affected the Hagberg falling number in mixtures; or that mixture effects on nitrogen accumulation in crop plants could also lead to component alteration for protein content and quality, but these mechanisms need to be confirmed and detailed. Ideally, grains of each component variety of a mixture should be separated at harvest and their baking quality measured individually in order to quantify these effects. Direct quantification of component alteration would then allow better identification of their underlying causes. Identification of component alteration mechanisms could then contribute to mixture assembly guidelines for improved baking quality.

Funding

This work was supported by a “Research Fellow – ASP” doctoral grant by the F.R.S.-FNRS (grant no. 34844751). It was also financially supported by the David et Alice Van Buuren fund from the Jaumotte-Demoulin foundation.

CRediT authorship contribution statement

Amaury Beaugendre: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Bruno Godin:** Data curation, Methodology, Resources, Supervision, Writing – review & editing. **Dominique Mingeot:** Conceptualization, Supervision, Writing – review & editing. **Marjolein Visser:** Conceptualization, Supervision, Writing – review & editing.

Declaration of competing interest

None.

Data availability

Data will be made available on request.

Acknowledgments

We warmly thank Léon Calonne, Fabre Dehon, Benoît Lambert, David Mathy, Jean-Marc Molenberg, Yordan Muhovski, Xavier Seffer, Benoît Vervaeren and Luc Watelet for their technical assistance with field trials. We are also grateful to Marion Chartier, Fabre Dehon and Sévrine Goffin for their technical assistance in grain and flour analyses.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jcs.2024.103933>.

References

- 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 (2), 13. <https://doi.org/10.1007/s13593-017-0418-x>.
- Beaugendre, A., 2024. Looking for balance in organic heterogeneous wheat crops: effects of trait contrasts and sowing density on plant interactions, and their consequences on yield and quality. Université libre de Bruxelles.
- Beaugendre, A., Mingeot, D., Visser, M., 2022. Complex plant interactions in heterogeneous material require the ecological rethinking of sowing density recommendations for bread wheat. A review. *Agron. Sustain. Dev.* 42 (9) <https://doi.org/10.1007/s13593-021-00735-7>.
- Berry, P.M., Sterling, M., Spink, J.H., Baker, C.J., Sylvester-Bradley, R., Mooney, S.J., Tams, A.R., Ennos, A.R., 2004. Understanding and reducing lodging in cereals. *Adv. Agron.* 84, 217–271. [https://doi.org/10.1016/S0065-2113\(04\)84005-7](https://doi.org/10.1016/S0065-2113(04)84005-7).
- Branlard, G., Dardevet, M., Saccomano, R., Lagoutte, F., Gourdon, J., 2001. Genetic diversity of wheat storage proteins and bread wheat quality. *Euphytica* 119, 59–67. https://doi.org/10.1007/978-94-017-3674-9_18.
- Branlard, G., Pierre, J., Rousset, M., 1992. Selection indices for quality evaluation in wheat breeding. *Theor. Appl. Genet.* 84 (1–2), 57–64. <https://doi.org/10.1007/BF00223981>.
- Carson, G.R., Edwards, N.M., 2009. Chapter 4: criteria of wheat and flour quality. In: Khan, K., Shewry, P.R. (Eds.), *Wheat: Chemistry and Technology*, fourth ed. AACC International Press, pp. 97–118 <https://www.cerealsgrains.org/Pages/default.aspx>.
- Cauvain, S., 2015. *Technology of Breadmaking*, third ed. Springer International Publishing. <https://doi.org/10.1007/978-3-319-14687-4>.
- Cerovic, Z.G., Masdoumier, G., Ghazlen, N.B., Latouche, G., 2012. A new optical leaf-clip meter for simultaneous non-destructive assessment of leaf chlorophyll and epidermal flavonoids. *Physiol. Plantarum* 146 (3), 251–260. <https://doi.org/10.1111/j.1399-3054.2012.01639.x>.
- Cowger, C., Weisz, R., 2008. Winter wheat blends (mixtures) produce a yield advantage in North Carolina. *Agron. J.* 100 (1), 169–177. <https://doi.org/10.2134/agronj2007.0128>.
- Döring, T.F., Annicchiarico, P., Clarke, S., Haigh, Z., Jones, H.E., Pearce, H., Snape, J., Zhan, J., Wolfe, M.S., 2015. Comparative analysis of performance and stability among composite cross populations, variety mixtures and pure lines of winter wheat in organic and conventional cropping systems. *Field Crops Res.* 183, 235–245. <https://doi.org/10.1016/j.fcr.2015.08.009>.
- Döring, T.F., Knapp, S., Kovacs, G., Murphy, K., Wolfe, M.S., 2011. Evolutionary plant breeding in cereals—into a new era. *Sustainability* 3 (10), 1944–1971. <https://doi.org/10.3390/su3101944>.
- Dorrian, K., Mkhabela, M., Sapirstein, H., Bullock, P., 2023. Effects of delayed harvest on wheat quality, gluten strength, and protein composition of hard red spring wheat. *Cereal Chem.* 100 (1), 196–212. <https://doi.org/10.1002/cche.10637>.
- Farrer, D., Weisz, R., Heiniger, R., Murphy, J.P., Pate, M.H., 2006. Delayed harvest effect on soft red winter wheat in the southeastern USA. *Agron. J.* 98 (3), 588–595. <https://doi.org/10.2134/agronj2005.0211>.
- FranceAgriMer, 2017. *Variétés des céréales à paille - Récolte 2017* (Les Etudes Céréales). <https://www.franceagrimer.fr/fam/content/download/53655/document/04++Enqu%C3%AAtes++Vari%C3%A9t%C3%A9s+c%C3%A9r%C3%A9ales+%C3%A0+paille+2017.pdf?version=8>.
- Gooding, M.J., 2009. Chapter 2 - the wheat crop. In: Khan, K., Shewry, P.R. (Eds.), *Wheat: Chemistry and Technology*, fourth ed. AACC International Press, pp. 19–49. <https://doi.org/10.1016/B978-1-891127-55-7.50009-4>.
- 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 (3), 261–269. [https://doi.org/10.1016/S0378-4290\(97\)00007-5](https://doi.org/10.1016/S0378-4290(97)00007-5).
- Løes, A.-K., Frøseth, R.B., Dieseth, J.A., Skaret, J., Lindö, C., 2020. What should organic farmers grow: heritage or modern spring wheat cultivars? *Organic Agriculture* 10 (1), 93–108. <https://doi.org/10.1007/s13165-020-00301-7>.
- Lunn, Major, B.J., Kettlewell, P.S., Scott, R.K., 2001. Mechanisms leading to excess alpha-amylase activity in wheat (*Triticum aestivum*, L) grain in the U.K. *J. Cereal. Sci.* 33 (3), 313–329. <https://doi.org/10.1006/jcrs.2001.0369>.
- Osman, A.M., Struik, P.C., Lammerts van Bueren, E.T., 2012. Perspectives to breed for improved baking quality wheat varieties adapted to organic growing conditions. *J. Sci. Food Agric.* 92 (2), 207–215. <https://doi.org/10.1002/jsfa.4710>.
- Posner, E.S., 2009. Chapter 5: wheat flour milling. In: Khan, K., Shewry, P.R. (Eds.), *Wheat: Chemistry and Technology*, fourth ed. AACC International Press, pp. 119–152.
- R Core Team, 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.
- Sammons, D.J., Baenziger, P.S., 1985. Performance of four winter wheat cultivars in blended populations. *Field Crops Res.* 10, 135–142. [https://doi.org/10.1016/0378-4290\(85\)90021-8](https://doi.org/10.1016/0378-4290(85)90021-8).
- Sarandon, S.J., 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 (2), 288–294. <https://doi.org/10.2307/2405096>.
- Streff, A., 2023. *Enquête V@riétés Céréales 2023*. ARVALIS.
- Tremblay, N., Wang, Z., Bélec, C., 2009. Performance of dualax in spring wheat for crop nitrogen status assessment, yield prediction and estimation of soil nitrate content. *J. Plant Nutr.* 33 (1), 57–70. <https://doi.org/10.1080/01904160903391081>.
- van Waes, J., 2006. Evaluation of lodging. In: Donner, D., Osman, A. (Eds.), *Handbook "Cereal Variety Testing for Organic and Low Input Agriculture"*. COST860 – SUSVAR, Chair Hanne Østergård.
- Walsh, E.J., Noonan, M.G., 1998. Agronomic and quality performance of variety mixtures in spring wheat (*Triticum aestivum* L.) under Irish conditions. *Cereal Res. Commun.* 26 (4), 427–432. <https://doi.org/10.1007/BF03543521>.
- Wolfe, M.S., Baresel, J.P., Desclaux, D., Goldringer, I., Hoad, S., Kovacs, G., Löschenberger, F., Miedaner, T., Østergård, H., Lammerts van Bueren, E.T., 2008. Developments in breeding cereals for organic agriculture. *Euphytica* 163 (3), 323–346. <https://doi.org/10.1007/s10681-008-9690-9>.

Glossary

- HFN: Hagberg Falling Number
 LN: Liquefaction Number
 LRS: Lodging Resistance Score
 NBI: Nitrogen Balance Index
 PRT: grain protein content
 RP: Relative Performance (quality)
 TW: Test Weight
 W: baking strength (Chopin Alveograph)
 ZEL: Zelený sedimentation index