



Performance of elite and heritage germplasm in barley genotype mixtures: effects on yield and disease under diverse management scenarios

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Abstract

Genotype mixtures are multiple crop lines grown together to improve yield, stability, and disease control by utilizing different genetic and morphological traits. Incorporating heritage germplasm may enable exploitation of low input adaptation traits while retaining the high yield of elite modern cultivars. However, the effects of nutrient application, sowing density, and disease management on competition/facilitation dynamics in genotype mixtures with diverse germplasms, such as landraces, remain largely unknown. A set of complimentary plot experiments, undertaken in the arable cropping area of the east of Scotland, assessed genotype mixtures using heritage lines and/or elite cultivars of both spring and winter barley. The experimental systems manipulated the sowing densities, mixture composition, nitrogen application, and fungal disease pressure across three different field seasons. Here we show that the advantages of genotype mixtures were highly dependent on the genotypic makeup of the mixture and the environmental conditions in which they are grown, demonstrating complex genotype mixture × environment interactions. Genotype mixture performance in barley is highly dependent on the interaction of genetic composition and management factors. This paper revealed, for the first time, that small amounts of heritage germplasm enhanced yield stability, though overall yields rarely match those of the elite monocultures and no consistent disease reduction was observed. Although barley gains limited benefits from mixing genotypes, our study is able to highlight complex trends in mixture composition and environment that are relevant for crops with greater genotype mixture yield benefits.

Keywords Barley · Landrace · Intracropping · Cultivar mixtures · Fungal disease · Cropping systems

1 Introduction

1.1 Genotype mixture benefits

The cultivation of two or more genotypes of the same crop in the same field during the same season, in an inter-genotype manner, is known as intracropping (Omolo and Ogango 2001) but is also more generically as cultivar, variety, or genotype mixtures, and as blends amongst growers (Newton et al. 2009). There are many reports illustrating

how genotype mixtures result in increased yield and reduced disease in various crop plants (Finckh et al. 2000; Kiær et al. 2009; Newton et al. 2009; Tschurr et al. 2023). Mixture benefit is based on the assumption that the diverse genotypes buffer against environmental stress when grown together (Zhu et al. 2000). This occurs through a combination of processes, namely compensation/competition, complementation, and facilitation (Wolfe 1985).

Cereal genotype mixtures commonly increase yield compared to the mean of their monocultures grown separately. The amount of extra yield is generally positively correlated with the diversity and complexity of the mixture (Newton et al. 2010). However, numerous reports have showcased no significant increase in yield (Finckh et al. 2000; Paynter and Hills 2008; Newton et al. 2009) highlighting the complexities of these interactions that could be explained by response differences to agronomic treatments, such as fertilizer (Reiss and Drinkwater 2018) and fungicide (Kristoffersen et al. 2020). While there is evidence that increased diversity and

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complexity generally have a positive effect on yield (Ajal et al. 2022), the factors that increase or decrease this interaction response are not well established, and thus, the situations in which genotype mixtures might provide agricultural advantage cannot be clearly defined.

In essence, efficiency in agricultural systems is largely about competition for and utilization of resources, whether deriving from the soil, such as nutrients and water, or from above ground, mainly light. Genotype mixture trials are typically designed using mixtures of established cultivars, with the selection of constituent cultivars having a potentially large effect on the mixture yield response due to differences in compensation/competition for these resources. The selection of constituent cultivars with complementary traits affecting uptake and utilization of these resources will result in greater efficiency. Therefore, manipulation of the availability of such resources and the degree of interaction between the mixture components may help identify the cultivars or trait combinations needed to best exploit different resources available.

1.2 Potential benefits of using landrace or heritage germplasm

In recent decades, cereal cultivars have been bred for high input agronomy, particularly fertilizers, pesticides, and soil tillage, producing cultivars that generate high yields in response to such agronomy on farm. Before the 1950s, and in earlier centuries, cereals were primarily landraces selected on-farm and re-grown locally (Newton et al. 2011). In Scotland, the spring barley landraces were commonly known as “Scots Bere” (Jarman 1996) and were grown as populations of heterogeneous rather than homogeneous monocultures (Southworth 2007). Landraces have been mainly confined to marginal agricultural environments, as they are unable to make the most efficient use of modern nitrogen input, in terms of output for human agricultural systems, and will frequently lodge, which is problematic for harvest (Martin et al. 2010; Rajala et al. 2017). However, landraces, such as Scots Bere, are adapted to reduced self-competition under low-level nutrient environments and have shown to harbor resistances to biotic stresses (Cope et al. 2021) as well as tolerances to abiotic stresses (Cope et al. 2020, 2022) that could, when sown in mixtures, provide yield benefits and stability. Established landraces are often referred to as “heritage” varieties, lines, or germplasm.

Mixing genotypes within and between two different germplasm groups, such as landraces and elite cultivars, may result in greater resource use efficiency and subsequently greater yield. However, the effects of their different environmental origins on their interaction in mixtures and, in turn,

the way this will be affected by both resource availability and level of competition are generally unknown.

1.3 Genotype mixtures with landraces in practice

In this series of trials, we tested mixtures of elite cultivars and landrace barley lines, both within and across genetic groups, over several plot experiments in Scotland over a number of years, under a range of nitrogen resource conditions and competition pressures. These treatments allowed for the manipulation of different key factors, modifying the levels of competition vs facilitation. For instance, resource amount can be manipulated in an agricultural system through fertilizer application, thus likely influencing the impact of competition. The diversity of components within the system may be altered through specific design strategies, which would influence facilitation, with complementary trait variation being an important aspect of the design. Competition for resources could be further manipulated by adjusting the sowing densities of the mixtures overall but could also scale the way in which plants facilitate each other, thus being especially informative when in conjunction with nutrient application. Furthermore, the interplay between competition and facilitation can be explored by varying disease presence—this disease presence may be manipulated by the application of different agricultural practices, including fungicide usage, exacerbating or alleviating the stress element.

The plot experiments were designed to determine how inherent differences in resource competition traits between the genepools affect their interaction and yield outcome and discuss how this might be translated into recommended practices. Our hypotheses were as follows: (H1) landrace or heritage lines mixed with elite germplasm, with the increased crop genetic and morphological differences, will have a broader diversity in interactions with the environment and thus provide increased yield resilience through complementarity, (H2) the yield resilience will vary with management practices—such as nitrogen application, fungal pathogen management strategies, and sowing density—factors that will influence the balance of competition vs facilitation.

2 Materials and methods

The study is comprised of three separate trials sown over the course of 3 years in the same region, using spring barley in the first two trials (Trial 1, 2015; Trial 2, 2018) and winter barley in the last (Trial 3, 2021). Trial fields all had at least 2 years of conventional cropping beforehand to ensure soil health and evenness for subsequent trial use. All trials were

Table 1 The list of different elite cultivars and heritage/landrace lines used in the three experiments, with the 722 code referring to the mixtures outlined in Table 2, the season being the growing season, and the ticks (✓) indicating 723 what experimental year they were used in.

Genotype name	Code	Genotype type	Season	2015	2018	2021
Optic	A	Elite cultivar	Spring	✓		
KWS-Irina	B	Elite cultivar	Spring	✓		
KWS Sassy	C	Elite cultivar	Spring		✓	
Fairing	D	Elite cultivar	Spring		✓	
Propino	E	Elite cultivar	Spring		✓	
RGT Planet	F	Elite cultivar	Spring		✓	
Laureate	G	Elite cultivar	Spring		✓	
KWS Orwell	H	Elite cultivar	Winter			✓
Bazooka	I	Elite cultivar	Winter			✓
LG Mountain	J	Elite cultivar	Winter			✓
KWS Hawking	K	Elite cultivar	Winter			✓
KWS Cassia	L	Elite cultivar	Winter			✓
Bere 125	M	Heritage	Spring	✓		
Bere 113	N	Heritage	Spring	✓		
Bere 116	O	Heritage	Spring	✓		
Bere 121	P	Heritage	Spring	✓		
Bere 122	Q	Heritage	Spring	✓		
Bere m08	R	Heritage	Spring	✓		
Bere 119	S	Heritage	Spring	✓		
Bere 223	T	Heritage	Spring	✓		
Bere 112	U	Heritage	Spring	✓		
Scotch Annat 200	V	Heritage	Spring	✓	✓	
Craigs Triumph (SSRPB)–135	W	Heritage	Spring	✓	✓	
Morayshire Gold-180	X	Heritage	Spring	✓	✓	
Common-218	Y	Heritage	Spring	✓	✓	
Bere-118	Z	Heritage	Spring	✓	✓	
Hatif de Grignon	Ä	Heritage	Winter			✓
Dea	Å	Heritage	Winter			✓
Pioneer	Æ	Heritage	Winter			✓
Dura	Ö	Heritage	Winter			✓
Herfordia	Ø	Heritage	Winter			✓

sown with the same Hege 8-row plot drill following cultivation and harrowing.

2.1 Trial 1—2015

This trial was conducted over two locations, with both the fungicide treated and non-fungicide treated grown at Balruldery, Scotland, UK (56°28'50.0"N 3°06'45.3"W), and the continuous fungal treatment site located 5 km away at Mylnfield farm (56°27'19.6"N 3°04'08.0"W), the first following a winter wheat crop and the second a spring barley crop. The soil on both sites was a sandy loam and the weather (Supplementary Figure 1) and soil (Supplementary Figure 2) monitoring data were recorded at Balruldery through a COSMOS field station (Smith et al. 2024).

This trial compared monocultures against mixtures of a cultivar and a heritage line, in 50:50 and 90:10 ratios (based on proportion of seed number needed for final density;

Table 1). The heritage lines consist of both heritage varieties, that undertook formal breeding in the early twentieth century, and landrace lines, that were genetically fixed through single seed descent to produce homozygous lines from landrace populations—that have not undergone formal breeding.

Both sites were arranged in a randomized split-plot design, grouped by fertilizer treatment, in plots of 4.8 × 1.55 m sown at the common Scottish farm standard of 360 seed/m². The full fertilizer (1.0×) treatment for each site was optimized for spring malting barley and tailored to the specific site with an application of 300 kg/ha 22-4-14 NPK (+7.5 SO₃) in early April and then 200 kg/ha in May. These applications were applied at 1.0× and 0.0× (none).

The standard herbicide treatment for spring barley was applied for all plots—Traton SX (active ingredients met-sulfuron-methyl 111 g/kg and tribenuron-methy 222 g/kg; 45g/ha) and charge (active ingredient polyether-poly-methyl siloxane-copolymer 1000 g/l; 1l/ha). The fungicide

treatment consisted of three different levels: *fungicide*—consisting of Siltra Xpro (active ingredients Bixafen 60 g/l and prothioconazol 200 g/l; 0.6 l/ha) + Bravo (active ingredient chlorothalonil 720 g/l; 1.0 l/ha) + Vegas (active ingredient cyflufenamid 50 g/l; 0.3 l/ha) at GS30-32 (Tottman 1987) (commonly known as T1) and Siltra Xpro (0.5 l/ha) + Bravo (1.0 l/ha) at GS 39 (T2), *untreated*—grown on the same site as the fungicide treatment but without chemical application, and *continuous*—grown on a site that had continuous barley and no fungicide in the previous 13 years.

Harvest was undertaken with a Wintersteiger plot combine, collecting the grain from the whole plot which was consequently dried to constant moisture of approximately 14% before plot yields were recorded.

2.2 Trial 2—2018

This spring barley trial was conducted at Balruddery Farm, Scotland, UK (56°28'52.0"N 3°07'58.0"W), following a spring barley crop (Figure 1). The soil was a sandy loam and the weather (Supplementary Figure 1) and soil (Supplementary Figure 2) monitoring data were recorded at Balruddery through a COSMOS field station (Smith et al. 2024). The trial compared monocultures against two-component and four-component mixtures for different cultivars or heritage lines of spring barley (Table 2).

The trial was arranged in a randomized split-plot design, grouped by both fertilizer treatments and genotype category. The plot size was 2 × 1.55 m and sown at a low (100 seed/m²) and the common Scottish farm standard (360 seed/m²) density. The full fertilizer (1.0×) treatment for each site was optimized for spring malting barley and tailored to the specific site, with two applications of 250 kg/ha 22-4-14 NPK (+7.5 SO₃) in early April and May. These applications were applied at 1.5×, 1.0×, 0.5×, and 0.0× (none). This trial was conducted during an exceptionally dry period (Supplementary Figure 1), and thus, additional irrigation of 25 mm was applied on two occasions as evenly as possible across the whole trial using a Briggs gun irrigator. The standard herbicide treatment for spring barley was applied for all plots, as in trial 1—Traton SX (45g/ha) and charge (1l/ha).

Powdery mildew was assessed when it rose above trace levels. It was scored on a 1–9 scale where 1 represented no disease through 9 when 100% diseased or fully senescent (Newton and Hackett 1994; AHDB 2015), with scores of 2 representing 3 colonies per tiller (0.1%), 3 representing 5 colonies per leaf (1%), 4 representing ¼ infection of the lower leaves (5%), and scaling in line with disease progression.

Harvest was undertaken with a Wintersteiger plot combine, collecting the grain from the whole plot which was then dried to constant moisture of 14% before plot yields were recorded. Samples of the yield were acquired from

Table 2 The list of different elite cultivar/cultivars and heritage/landrace line mixtures used in the three experimental years, with the code referring to the mix of genotypes outlined in Table 1, the mixture type indicating the what germplasm the mixture is made from, and the ticks (✓) indicating what ratios they were used in.

Year	Mix code	Mix type	90:10	50:50	25:25:25:25
2015	BP	Cultivar:heritage mix	✓	✓	
2015	BZ	Cultivar:heritage mix	✓	✓	
2015	AT	Cultivar:heritage mix	✓	✓	
2015	AR	Cultivar:heritage mix	✓	✓	
2015	BS	Cultivar:heritage mix	✓	✓	
2015	BU	Cultivar:heritage mix	✓	✓	
2015	AZ	Cultivar:heritage mix	✓	✓	
2015	BT	Cultivar:heritage mix	✓	✓	
2015	BQ	Cultivar:heritage mix	✓	✓	
2015	AQ	Cultivar:heritage mix	✓	✓	
2015	BR	Cultivar:heritage mix	✓	✓	
2015	BO	Cultivar:heritage mix	✓	✓	
2015	AO	Cultivar:heritage mix	✓	✓	
2015	AS	Cultivar:heritage mix	✓	✓	
2015	AP	Cultivar:heritage mix	✓	✓	
2015	AU	Cultivar:heritage mix	✓	✓	
2018	FE	Cultivar mix		✓	
2018	CD	Cultivar mix		✓	
2018	GC	Cultivar mix		✓	
2018	GD	Cultivar mix		✓	
2018	GE	Cultivar mix		✓	
2018	FD	Cultivar mix		✓	
2018	CE	Cultivar mix		✓	
2018	FGDE	Cultivar mix			✓
2018	FGCD	Cultivar mix			✓
2018	FG	Cultivar mix		✓	
2018	FGCE	Cultivar mix			✓
2018	FC	Cultivar mix		✓	
2018	DE	Cultivar mix		✓	
2018	GCDE	Cultivar mix			✓
2018	FCDE	Cultivar mix			✓
2018	WXYZ	Heritage mix			✓
2018	VZ	Heritage mix		✓	
2018	XY	Heritage mix		✓	
2018	WX	Heritage mix		✓	
2018	WY	Heritage mix		✓	
2018	WZ	Heritage mix		✓	
2018	VY	Heritage mix		✓	
2018	XZ	Heritage mix		✓	
2018	VWYZ	Heritage mix			✓
2018	VWXY	Heritage mix			✓
2018	VW	Heritage mix		✓	
2018	VWXZ	Heritage mix			✓
2018	VX	Heritage mix		✓	
2018	YZ	Heritage mix		✓	
2018	VXYZ	Heritage mix			✓

Table 2 (continued)

Year	Mix code	Mix type	90:10	50:50	25:25:25:25
2021	HJKL	Cultivar mix			✓
2021	HIKL	Cultivar mix			✓
2021	HIJK	Cultivar mix			✓
2021	HIJL	Cultivar mix			✓
2021	IJKL	Cultivar mix			✓
2021	ÄÖÄÖ	Heritage mix			✓
2021	ÄÆÄÖ	Heritage mix			✓
2021	ÄÆÖÄ	Heritage mix			✓
2021	ÄÆÖÖ	Heritage mix			✓
2021	ÆÖÄÖ	Heritage mix			✓

the dried material and analyzed for the nitrogen level using an Infratec nitrogen analyzer using Near-Infrared (NIR) Spectroscopy.

2.3 Trial 3—2021

This winter barley trial was conducted at Balruddery, Scotland, UK (56°29'02.3"N 3°08'02.9"W), following a winter wheat crop. The soil was a sandy loam and the weather (Supplementary Figure 1) and soil (Supplementary Figure 2) monitoring data were recorded at Balruddery through a COSMOS field station (Smith et al. 2024). The trial compared monocultures against four-component mixtures for different cultivars or heritage lines of winter barley (Table 2).

The trial was arranged in a randomized split-plot design, grouped by fertilizer treatments, and grouped by genotype category. The plot size was 2 × 1.55 m and sown at a low (100 seed/m²) and the common Scottish farm standard (360 seed/m²) density. The full fertilizer (1.0×) treatment for each site was optimized for winter malting barley and tailored

to the specific site; 350 kg/ha 0-20-30 NPK was applied at sowing and then two applications of 310 kg/ha of Extran S 29N (+15 SO₃) were applied in the spring. These applications were applied at 1.5×, 1.0×, 0.5×, and 0.0× (none). The standard herbicide treatment for winter barley was applied for all plots—Liberator (active ingredients diflufenican 100 g/l and flufenacet 100 g/l; 0.6l/ha) and Zypar (active ingredients Arylex 6 g/l and florasulam 5 g/l; 1l/ha).

Disease progress was scored as outlined in Trial 2, but for multiple pathogens at multiple times: powdery mildew (3 times), *Rhynchosporium* (twice), and brown rust (once). Scores with more than one time point had the area under the disease progress curve (AUDPC) calculated to estimate the overall impact of the disease.

Harvest was undertaken with a Wintersteiger plot combine, with the whole plot yield harvested, calculated, and recorded by the combine. Additionally, the plots were assessed for growth stage—using the guide outlined in Zadoks et al. (1974), heading date, and lodging percentage—as outlined in Kiær et al. (2020).

2.4 Statistical analysis

Each trial was analyzed independently using a mixed-effects model, with the statistical program (R Core Team 2013), via packages lme4 (Bates et al. 2015), lmerTest (Kuznetsova et al. 2017), pbkrtest (Halekoh and Højsgaard 2014), and emmeans (Lenth 2022). The fixed-effects factors were nitrogen fertilizer, mixture type (“Cultivar mono” and “Heritage mono” in all, “Cultivar heavy mix” and “Equal mix” in trial 1, and “Cultivar mix” and “Heritage mix” in trials 2 and 3), and either fungal treatment (trial 1) or sowing density (trials 2 and 3). The structural factor was the column. Mixtures had a predicted value based on the constituent monocrop plots in the same treatment and assessed if significantly different

Figure 1 An image of the 2018 field trial showcasing the different agricultural practices of reduced nitrogen and reduced seeding density in cultivars and heritage material. Source: taken by co-author ACN.



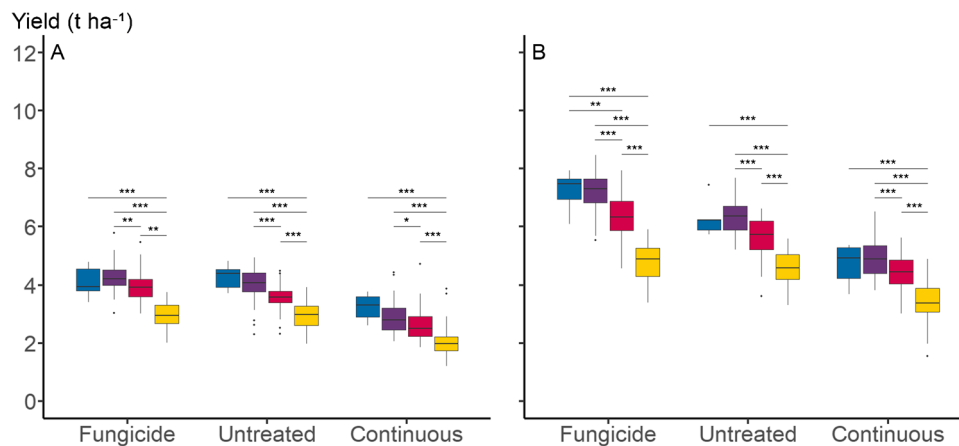


Figure 2 Yield from a 2015 plot experiment comparing different mixture levels of heritage lines and modern cultivars of spring barley (blue, cultivar monoculture; yellow, heritage line monoculture; purple, 90:10 mix of cultivar and heritage lines; and pink, equal mix of cultivars and heritage lines) with different fungal pressures (low to high; fungicide—standard field site with fungicide applied,

untreated—standard field site with no fungicide applied, and continuous—field where continuous barley growth had occurred and disease was heavily present with no fungicide applied). Significant differences are only shown within the same fungal and nitrogen treatment; the denotations are “*” for $P < 0.05$, “**” for $P < 0.01$, and “***” for $P < 0.001$.

from the recorded value using the `emmeans::contrast` function (Lenth 2022). Additionally, for each year, each treatment, and each mixture type, the coefficient of variation (CV) was calculated—defined as the ratio of the standard deviation to the mean yield, expressed as a percentage.

Data visualization was performed using “R” packages `ggplot2` (Wickham 2016), `ggpubr` (Kassambara 2023), and `rmisc` (Hope 2013). Weather and soil monitoring data was arranged using the “R” package `lubridate` (Grolemund and Wickham 2011) and visualized with a locally estimated scatterplot smoothing (LOESS).

3 Results and discussion

Our study sought to explore the effects of mixing heritage germplasm (including both bred heritage varieties and homozygous lines made from non-bred landrace populations) and elite cultivars to enhance yield in barley. Our findings suggest that while germplasm diversity has the potential to enhance yield resilience, this effect was not consistently observed across all experimental conditions. In a few specific circumstances, mixing germplasm types showed beneficial effects. However, these instances were not sufficient to support the broader hypothesis of genotype mixtures providing a yield benefit.

3.1 Germplasm mixture performance

Hypothesis 1, which proposed that mixing heritage germplasm and elite cultivars would enhance yield resilience through complementary effects, was only partially

supported. While certain mixtures showed yield advantages, these effects were inconsistent and highly context-dependent. The diverse genetic backgrounds of landrace lines did not universally enhance the performance of elite material nor did they provide a significant resilience advantage under varying conditions. As Allard and Adams (1969) demonstrated, long-term natural selection in heterogeneous populations can foster stable multigenotypic associations. However, once populations are fixed, as with the heritage lines in our study, these cooperative dynamics are likely diminished, potentially restricting their ability to enhance performance when mixed with dominating elite cultivars. Figure 2 illustrates that all mixtures, composed of heritage lines, cultivars, and different mixture levels of the two, produced higher yields than the heritage monoculture, with a significant difference between mixture types ($P < 0.001$) in the 2015 trial. Additionally, the cultivar-heavy mixture significantly outperformed the equal mixture ($P < 0.001$), suggesting that the proportion of elite germplasm plays a key role in yield outcomes. However, no significant difference is observed between the cultivar monoculture and the equal mixture, despite large differences, due to the large standard errors.

Moreover, when factoring in the different nitrogen treatments, there is a significant difference between the nitrogen and no-nitrogen treatments ($P < 0.001$), with the no-nitrogen treatment having an average of 62% of the with nitrogen yield. Additionally, there is a significant difference in how the mixture types respond to the different nitrogen treatments ($P < 0.001$), with the cultivar mono maintaining slightly more of its yield in zero nitrogen while the heavy

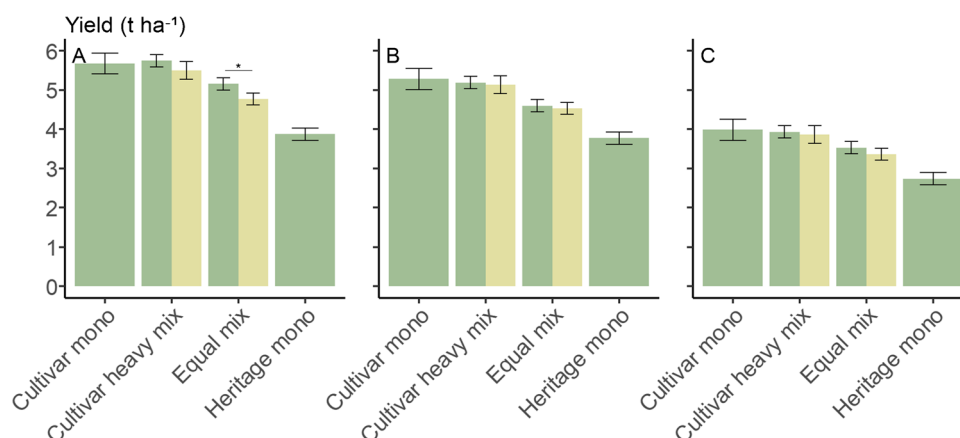


Figure 3 Yield from a 2015 plot experiment with different mixture levels of heritage lines and modern cultivars of spring barley (Table 1) with different fungal pressures, low to high; fungicide—standard field site with fungicide applied **A**, untreated—standard field site with no fungicide applied **B**, and continuous—field where continuous barley growth had occurred and disease was heavily present with no fungicide applied **C**—averaging the different nitrogen

treatments. The predicted yield (light) for each mixture is estimated using `emmeans::contrast` based on the proportional contributions of the constituent monoculture with the same treatment; recorded values (dark) are those recorded from the field experiment. Significant differences are only shown between recorded and prediction results; the denotations are “*” for $P < 0.05$, “**” for $P < 0.01$, and “***” for $P < 0.001$.

mix maintains slightly less compared to the average of its components.

The yield of the mixtures, when compared to the expected performance (i.e., the mean of the proportional constituent parts), showed no significant difference in 2015, with the exception of the fungicide-treated plots. In these plots, regardless of nitrogen levels, the equal mixture yielded more than expected (Figure 3).

This lack of consistent benefit was particularly evident in this comparison of mixed germplasm treatments to monocultures, especially under standard agricultural practices. The coefficient of variation for yield showed more stability in cultivars compared to heritage lines across all nitrogen levels and fungal treatment strategies (Figure 4A–C), with higher nitrogen applications generally increasing stability. The mixtures had yield stabilities similar to the heritage lines when grown in low nitrogen. However, nitrogen applications caused increases in stability to a much greater extent in the mixtures, bringing the stability closer to that observed in the cultivars, a trend much more pronounced with lower disease control (the continuous barley site).

3.2 Genotype mixtures of heritage lines vs elite cultivars in different management practices

While significant differences in yield were identified in the spring barley 2018 trial between the different nitrogen treatments, density levels, and their interactions ($P < 0.001$), there was no significant difference between the mixtures and their respective monocultures overall. Similarly, in the 2021 winter barley trial, despite differences in nitrogen levels (P

$= 0.004$), density, mixture class, and their respective interactions ($P < 0.001$ and $P = 0.004$ for the density*mixture class interaction), no significant difference was found overall between the mixtures and monocultures.

In the spring barley, significant differences in yield were seen between mixture treatments. When broken down by level (mono, 2-comp, and 4-comp) and class (heritage and cultivar), significant differences were only found in the latter (Supplementary Figure 3). The lack of differences in the levels was seen in both the cultivar and heritage material, suggesting that the mixing at these levels is not diverse enough to recreate any population effect seen in the landrace populations (from which the majority of the heritage lines derive).

A few studies, such as Paynter and Hills (2008), have reported no positive interactions for grain yield in similar systems. This is an important point, particularly given the potential under-reporting of non-significant results. The occasional lack of interaction, or even a negative interaction for yield or a yield component, is not unexpected and may stem from several factors. In the context of the winter barley cultivars used by Paynter and Hills (2008), the lack of diversity in yield-critical traits could explain the absence of positive interactions. However, trait interactions are highly dependent on environmental factors, and these interactions can shift in positive or negative directions depending on the specific conditions. Thus, the final yield response is the cumulative result of these dynamic interactions.

This complexity is further illustrated by species interactions, where even large trait diversity may not guarantee consistently positive outcomes. For example, the land equivalent ratio (LER) may be negative, neutral, or

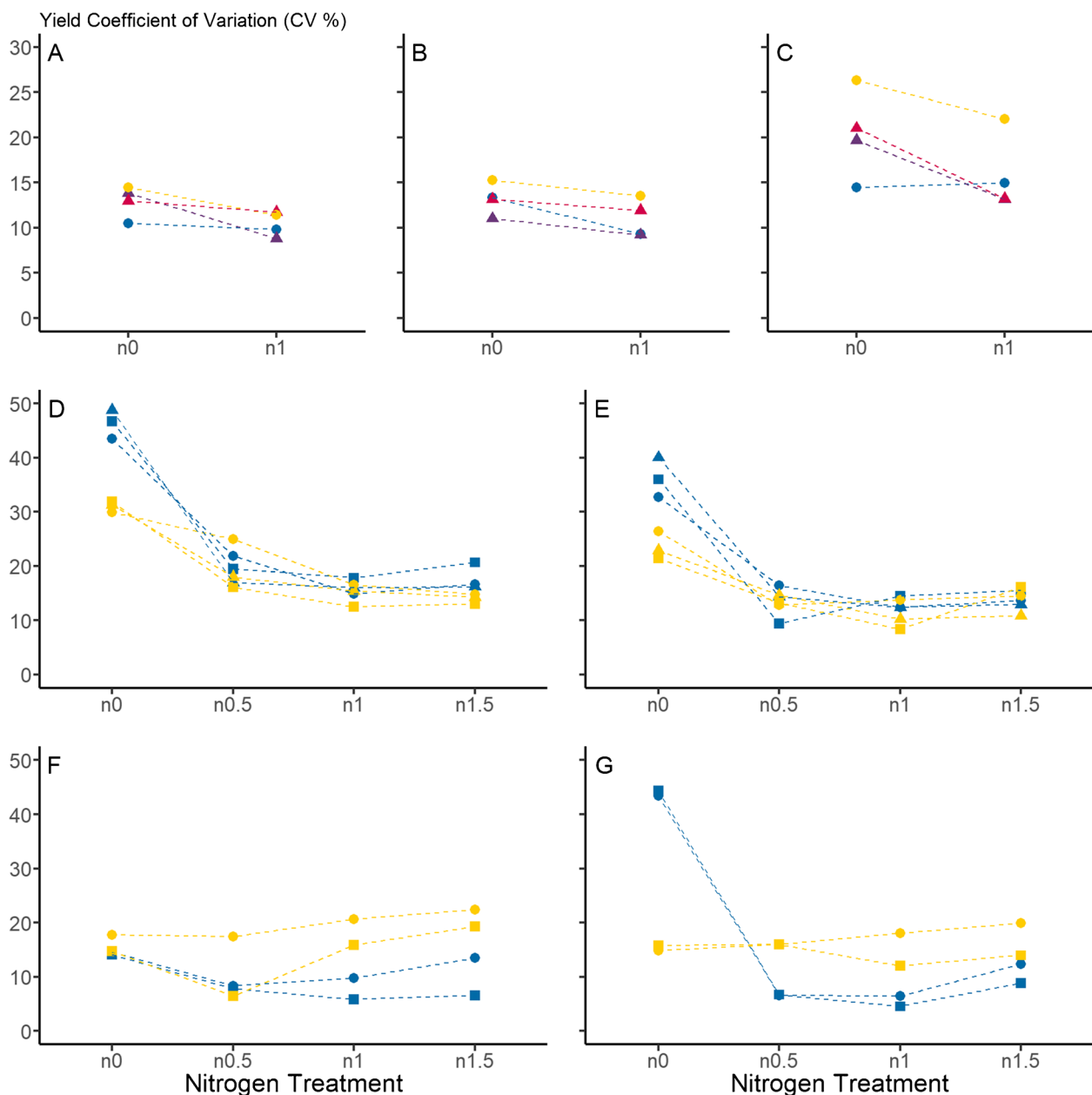


Figure 4 Coefficient of variation for the yield under differing nitrogen treatments from plot experiments undertaken in 2015 with different mixture levels of heritage lines and modern cultivars of spring barley (Table 1) with different fungal pressures—low to high; fungicide—standard field site with fungicide applied **A**, untreated—standard field site with no fungicide applied **B**, and continuous—field where continuous barley growth had occurred and disease was heavily present with no fungicide applied **C**; 2018 with different two- and four-component mixtures of either heritage lines or modern cultivars of spring barley (Table 1) under different sowing densities—100

D and 360 seeds/m² **E**; and 2021 with different four-component mixtures of either heritage lines or modern cultivars of winter barley (Table 1) under different sowing densities—100 **F** and 360 seeds/m² **G**. Data is colored by material type (blue, cultivar monoculture; yellow, heritage line monoculture; purple, 90:10 mix of cultivar and heritage lines; and pink, equal mix of cultivars and heritage lines), with the shapes representing the number of different components it is made up from (circle, monoculture; triangle, two components; and square, four components). Error bars (obscured by data points) are calculated from standard deviation.

positive, with positive outcomes more commonly observed in natural systems (Brooker et al. 2024). Our study, which assessed mixtures of lines with a broad range of functional traits—from elite material to diverse European landrace

lines—under different agricultural practices, further supports this notion. The relatively low number of mixture \times environment (G2 \times E) combinations that delivered higher-than-expected yields underscores the importance of

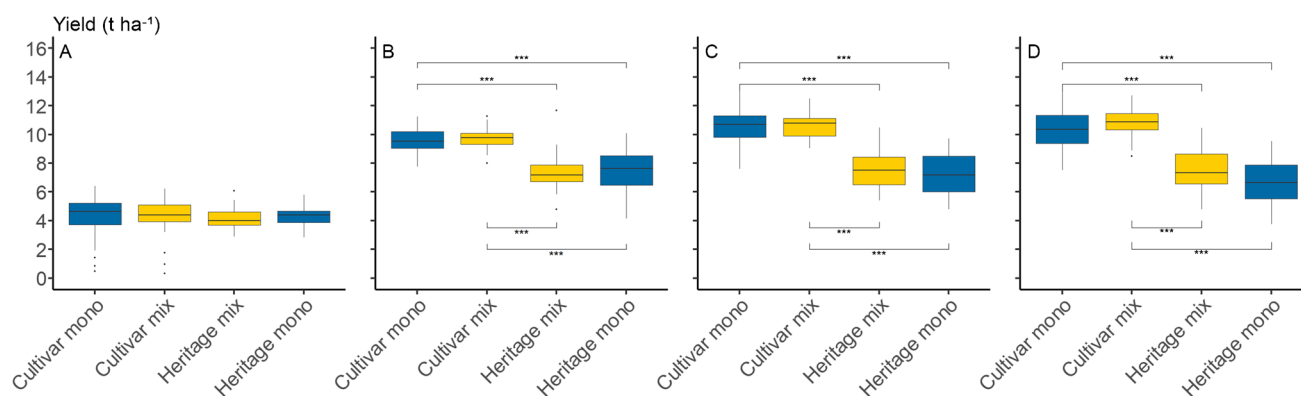


Figure 5 Yield from a 2021 plot experiment with the average of different four-component mixtures (yellow) or monocultures (blue) of winter barley (using either heritage lines or modern cultivars), split based on the nitrogen application—0% **A**, 50% **B**, 100% **C**, or 150%

D of the standard nitrogen application for the region. Significant differences are only shown within facet; the denotations are “*” for $P < 0.05$, “**” for $P < 0.01$, and “***” for $P < 0.001$.

selecting the correct mixture components for the specific environmental context, both natural and agricultural, to achieve the most beneficial interactions.

The likely bias in scientific publication against reporting non-significant interactions may contribute to the underestimation of neutral plant-plant and plant-plant-microbe interactions. This is concerning because such interactions are often summarized as cumulative or mean effects, which can obscure the occurrence of both positive and negative interactions that cancel each other out. Moreover, it may skew the findings of meta-analyses, such as those by Huang et al. (2024) and Reiss and Drinkwater (2018), which investigate the effects of intercropping.

The likely bias of reporting of genotype mixture data could thus be obscuring the importance of the components of the genotype mixture. Diverse mixtures, incorporated in genotype mixtures, promote competition, complementation, and facilitation; thus, the right complementation of phenotypic traits is needed to shift this to promoting wider stress protections and resource accumulation strategies—developing a more beneficial system as a whole (Wolfe 1985; Zhu et al. 2000). Mixtures of germplasm that are not complementary are unlikely to display the positive associations that have been reported in other studies (Finckh et al. 2000; Kiær et al. 2009; Newton et al. 2009; Tschurr et al. 2023). Our results show that the general trends in genotype mixtures were primarily driven by a few key combinations. In winter barley, significant effects of genotype mixtures generally resulted in higher yields; this trend was not identified in the spring barley.

3.2.1 Nitrogen and density

The differences between the mixture classes show increased winter barley yield in the cultivars in all nitrogen

levels except with zero input, where there was no difference between cultivar and heritage lines (Figure 5). This was the same across all sowing densities and did not change when in a genotype mixture or a monoculture. Similar results are seen in the lodging, with only the zero nitrogen input showing no difference in lodging between the heritage and the cultivars ($P < 0.001$) while the heritage lines lodged with any nitrogen input, and cultivars had low levels in all treatment levels.

When comparing the expected performance to the recorded results of the individual mixtures of spring barley, only mixtures of cultivars showed any difference. Some mixtures exhibited increased performance when in low N concentrations, while other mixtures exhibited reduced performance in the higher nitrogen levels (Supplementary Figure 4). Unlike the spring barley, the mixtures of winter barley with higher than predicted yields were seen in both heritage lines and cultivars (Figure 6) and only showed increased yields with the higher nitrogen levels; this is observed in a total of six mixtures (with a seventh showing a decrease). No mixtures showed any difference from the expected performance in the treatment levels below standard nitrogen.

Density was the only factor that affected the heading date in winter barley, with plants sown at lower densities heading an average of 3 days later than those sown at higher densities. Lower density sowing also resulted in higher seed nitrogen levels, with heritage seed showing higher nitrogen content regardless of whether it was part of a mixture or a monoculture (Supplementary Figure 5).

This supports Hypothesis 2, which posited that management practices influence the balance of competition and facilitation in intercropping systems, was more strongly supported. We observed varied performance across different mixture compositions when exposed to different nitrogen

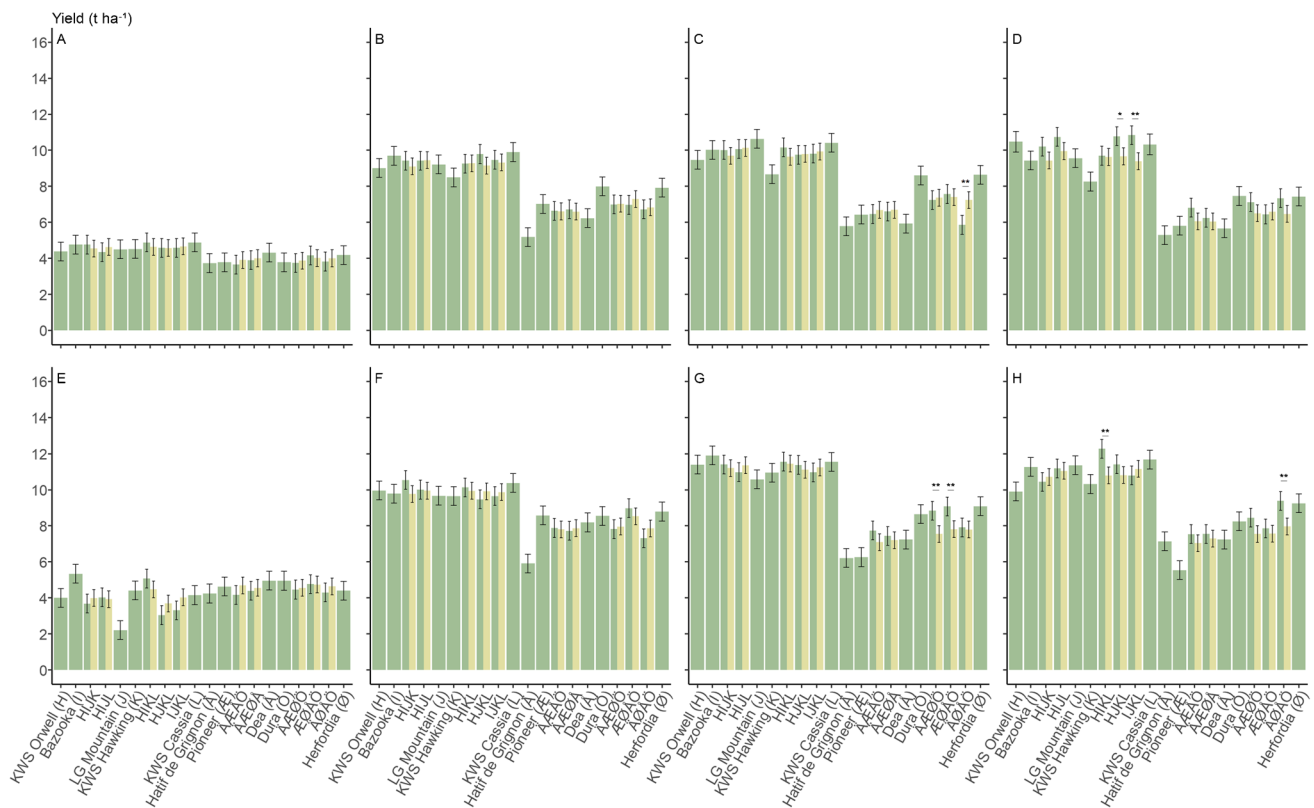


Figure 6 Yield from a 2021 plot experiment with different four-component mixtures of either heritage lines or modern cultivars of winter barley (Table 1), split based on the nitrogen application—0% **A** and **E**, 50% **B** and **F**, 100% **C** and **G**, or 150% **D** and **H** of the standard nitrogen application for the region—and the seeding density—the standard 360 **E–H**, and a low 100 seeds/m² **A–D**. The predicted yield

(light) for each mixture is estimated using emmeans::contrast based on the proportional contributions of the constituent monoculture with the same treatment. Recorded values (dark) are those recorded from the field experiment. Significant differences are only shown between recorded and prediction results; the denotations are “*” for $P < 0.05$, “**” for $P < 0.01$, and “***” for $P < 0.001$.

and planting density conditions. The clearest differences emerged under zero-nitrogen conditions compared to applied nitrogen levels and in continuous barley cropping systems compared to other sites. However, it was evident that the proportion of elite or heritage germplasm had a far larger impact on yield than the interactions between the germplasm types, which were rarely significant.

Moreover, the success of the mixture compositions was heavily influenced by the surrounding agricultural environment. Our results suggest that the performance of barley germplasm mixtures is highly dependent on factors such as nitrogen availability and planting density. For instance, winter barley mixtures performed better under higher nitrogen conditions, while spring barley mixtures thrived in low-nitrogen environments. This environmental sensitivity emphasizes the importance of selecting the appropriate germplasm for specific agricultural conditions to optimize yield outcomes.

While the choice of mixture components is crucial in determining whether intercropping leads to increased yields, it does not act in isolation. As our results indicate,

the surrounding agricultural environment also crucially influences how germplasm interacts to impact yield, as found in intercropping studies (Weih et al. 2021; Ma et al. 2022). In our study, no individual mixtures showed a significant yield increase in more than one seed density and nutrient treatment combination. This suggests that the mixtures in barley are highly dependent on the environment in which they are sown. If the mixture of components increases yield by making best use of the environmental conditions, changing these conditions will thus alter the suitability of any mixture. With increased testing of mixtures, we can identify components that will benefit different scenarios. This context-dependent performance echoes earlier findings that natural selection tends to preserve synergistically interacting genotypes, potentially leading to stable multigenotypic associations (Allard and Adams 1969). In these results, we identified that mixtures containing winter barley components KWS Hawking and KWS Cassia show an increased yield under above-average nitrogen conditions, while spring barley components of Fairing and Laureate show decreased yields.

Difference in how the nitrogen affected the genotype mixtures is mainly evident between spring and winter barley. Our experiments show that genotype mixtures of winter barley predominantly get positive effects in the high N conditions (100–150% of standard), while mixtures of spring barley have more positive effects in the low N conditions (0–50% of standard). This is confirmed in strip intercropping, with some species benefiting from high N yet others not (Ayisi et al. 1997), with the caveat that comparisons with intercropping under low N conditions are difficult as most include nitrogen-fixing crops (Toker et al. 2024). These environmental factors, particularly nitrogen levels, not only influenced yield outcomes but also shaped other key agronomic traits, including disease resistance. Comprehending how these environmental variables interact with barley germplasm to affect disease dynamics is critical for improving barley production systems.

3.2.2 Stability

The variation in the 2018 spring barley yield revealed a trend that differed from the mixed germplasm 2015 trial. Specifically, heritage lines showed more stability, while cultivars experienced a more significant drop in stability when grown under zero nitrogen (Figure 4A–E). In general, there are no differences in the yield stability between the different amounts of applied nitrogen, but a large difference between those with and those without any additional nitrogen, with the latter showing a considerably lower stability. Additionally, the lower seeding density results in a decrease in the yield stability.

Yield stability in the winter lines exhibited similar yet distinct trends in contrast to the spring barley. In both sowing densities, the heritage lines presented reduced yield stability vs the cultivars (Figure 4F–G). Unlike the spring crop, the monocultures showed clear signs of reduced yield stability compared to the four component mixtures; this difference is reduced with reducing levels of nitrogen treatment. Additionally, the prominent reduction in yield stability with zero nitrogen in the spring crops is only observed in the winter cultivars, with a small reduction in low (100 seeds m⁻²) seeding densities and a large reduction in standard seeding densities (360 seeds m⁻²). Heritage winter lines did not exhibit any reduction in yield stability under zero nitrogen.

Some mixtures in this study produced yields significantly higher than expected under a no-interaction model. However, no mixture outperformed the highest-yielding monoculture. Thus, the use of low yielding heritage material as individual lines cannot provide the necessary yield boost to offset the reduction in yield from its use as a significant portion of the sowing material. In contrast, unlike the elite material that has been bred for use in monocultures (Bourke et al. 2021), the heritage material had all but

one mixture-treatment combination give higher or equal yields. This suggests that heritage material, like landraces, is naturally suited to growing in a diverse genetic environment (Villa et al. 2005)—a concept supported by Allard and Adams (1969), who found that genotypes surviving multiple generations of mutual selection exhibited significantly higher synergistic interactions compared to modern cultivars. That being said, while heritage material may contribute to stability, it does not appear to provide a yield advantage over elite monocultures. This distinction is crucial for agricultural strategies that seek to optimize both yield and resilience.

Differences in yield stability have been identified as a benefit of genotype mixtures, providing a buffer over changes between years, with mixtures showing a lower average coefficient of variation over time (Reiss and Drinkwater 2018). The mixtures in this study were compared in the same site and time, monitoring the variation within groups of germplasm, heritage, and modern. Winter wheat under standard conditions showed lower coefficients of variance, similar to the findings in Reiss and Drinkwater (2018). In contrast, spring genotypes showed less consistency in this pattern. In the elite-heritage mixtures reported here, under standard nitrogen treatments, the addition of a small portion of heritage material into the modern material produced greater stability without sacrificing yield.

4 Fungal disease mitigation and occurrence

4.1 Disease pressure

The 2015 trial included three different fungal disease management strategies to provide differing levels of fungal inoculum pressure. Significant differences were seen between the fungal treatments ($P < 0.001$), as well as in the interaction of treatment*nitrogen and treatment*mixture ($P < 0.001$), along with their respective three-way interaction ($P = 0.03$). This three-way interaction manifests as a smaller yield reduction between the heritage lines and the cultivars when grown with increased fungal inoculum pressure (Figure 2). This difference is further decreased under low nitrogen conditions.

While the heritage material (mostly landrace lines) has been proven to provide resistance to specific diseases (Cope et al. 2021), this resistance is usually as a result of the environment it developed on and thus is a resistance to a specific disease (Newton et al. 2011), leaving it susceptible to others. This and the results generated here suggest that any yield benefit conveyed to the elite cultivars through mixing is offset by the increase in diseases such as powdery mildew. Thus, the application of fungicide

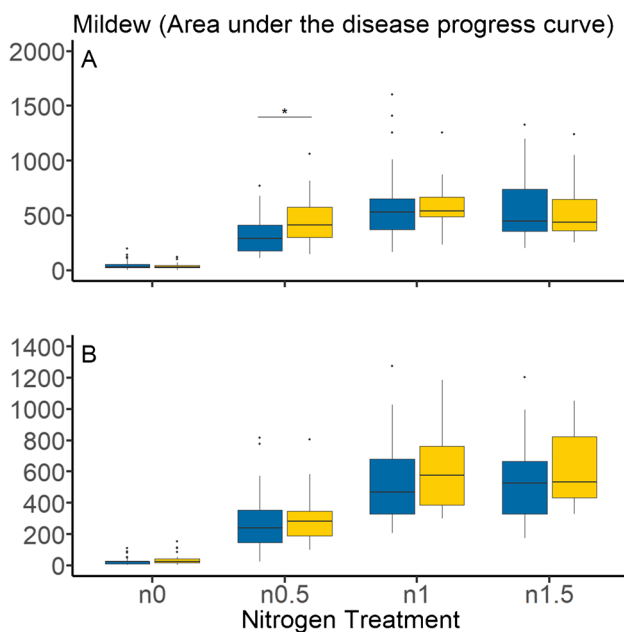


Figure 7 The area under the disease progress curve for measurements of powdery mildew over the course of a 2021 plot experiment, with different four-component mixtures (yellow) or monocultures (blue) of winter barley (using either heritage lines or modern cultivars), split based on the nitrogen application (as a percentage of the standard for the crop) and the seeding density—the standard 360 **B**, and a low 100 seeds/m² **A**. Significant differences are only shown between the mixture types with the same nitrogen and density treatment; the denotations are “*” for $P < 0.05$, “**” for $P < 0.01$, and “***” for $P < 0.001$.

allows for other benefits from the heritage germplasm to increase yield.

4.1.1 Disease occurrence

The assessment of powdery mildew (*Blumeria graminis* f.sp. *hordei*) severity on the spring barley crop showed no significant difference in the mixture levels, yet with significant differences in the density and mixture class ($P < 0.001$), with additional interactions between nitrogen-density ($P = 0.016$), density-mixture class ($P < 0.001$), and the three-way interaction ($P = 0.016$). The powdery mildew levels significantly increase in the heritage lines, both in mixed and monoculture, when sown at a lower density. This is seen in all nitrogen levels except in the monoculture grown at standard nitrogen levels (Supplementary Figure 6). In the winter barley, the powdery mildew was tracked over multiple time points and was also indicated to increase with lower sowing densities ($P = 0.032$), but with no difference between the mixture classes. However, there was a significant difference in the interaction of nitrogen to density to mixture level ($P = 0.01$), manifesting as a significant increase in powdery

mildew detected in the mixture, compared to the monoculture when in low seeding density under 50% nitrogen conditions (Figure 7). Additionally, a significant difference in powdery mildew levels can be identified between nitrogen treatments ($P = 0.003$), with the increasing nitrogen levels causing an increase in powdery mildew.

Similarly to the powdery mildew scoring over time, the *Rhynchosporium* (or scald, *Rhynchosporium commune*) disease severity scoring over time (AUDPC) in winter barley showed significant increases with reduced sowing densities ($P = 0.006$) and with increased nitrogen levels ($P < 0.001$). Differences in the mixture types were only observed in the standard agricultural applications of sowing density and nitrogen, where the cultivar monoculture had increases of *Rhynchosporium* vs the heritage lines and the cultivar mixture (Supplementary Figure 7; $P < 0.001$).

Brown rust (*Puccinia hordei*) severity in winter barley also showed significant increases at lower sowing densities ($P = 0.008$), but the levels of disease showed different patterns with nitrogen treatments ($P < 0.001$), resulting in increases in brown rust the closer to the standard fertilizer treatments, with only n1 and n1.5 being significantly different from no-nitrogen input. Mixture class was also significantly different ($P < 0.001$), showing an increase in disease in the cultivar material. There is a significant difference in how the density interacts with the mixture class ($P = 0.043$). This is shown as a much larger increase in disease in the cultivar when grown at low seeding density (Figure 8A). Similarly, the interaction of mixture class and nitrogen is also significantly different ($P = 0.003$), with only the higher two nitrogen treatments being significant, and the standard nitrogen exhibiting a much larger increase in disease in the cultivars compared to the heritage lines than in the 150% nitrogen treatment (Figure 8B).

In general, the levels of foliar fungal diseases in this experiment fluctuated more with environment than with germplasm. A low sowing density and higher nitrogen level tended to increase the level of disease of the three assessed—powdery mildew, *Rhynchosporium*, and brown rust. The increase with lower sowing densities could be due to the allocation of biomass resources, as Hecht et al. (2016) have found that the lower the sowing density the lower the biomass allocation to the stem fraction, thus reducing the physical barriers and allowing pathogen spread. The increase in disease with higher fertilizer levels has been noted before (Veresoglou et al. 2013). Dordas (2008) noted that obligate pathogens (such as those causing powdery mildew and brown rust) would increase with increased N, but facultative pathogens would not, indicating that *Rhynchosporium*, a hemi-biotroph, should likely show a more variable response depending on its infection stage.

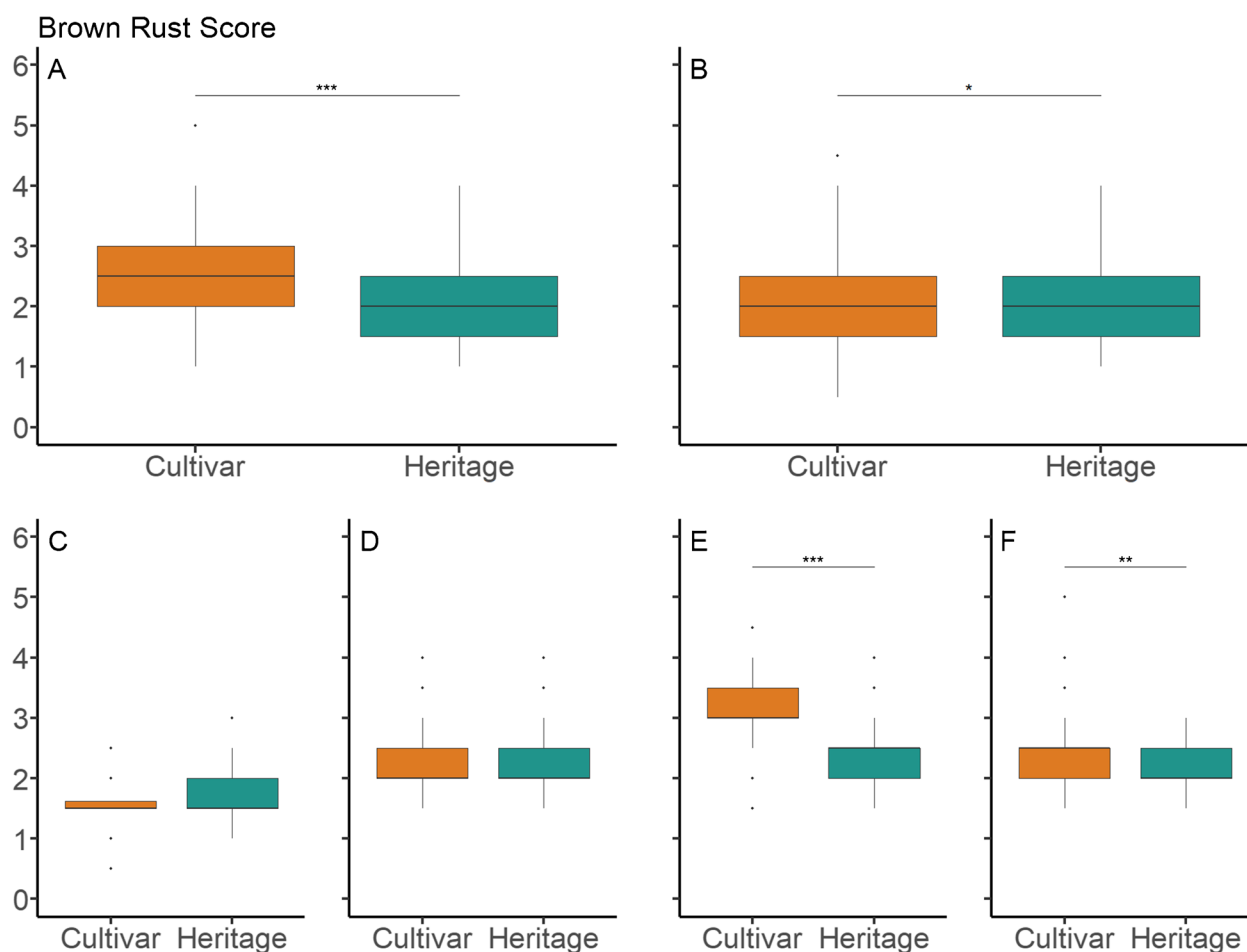


Figure 8 The score for brown rust disease (caused by *Puccinia hordei*) during the course of a 2021 plot experiment, with different four-component mixtures or monocultures of either heritage lines (teal) or modern cultivars (orange) of winter barley. The data has split based on either the seeding density - standard 360 **B**, or low 100

seeds/m² **A**, or the nitrogen application - 0% **C**, 50% **D**, 100% **E**, or 150% **F** of the standard nitrogen application for the region; with the other treatments averaged. Significant differences are only shown within facet; the denotations are “*” for $P < 0.05$, “**” for $P < 0.01$, and “***” for $P < 0.001$.

5 Conclusions

This study aimed to assess whether barley genotype mixtures combining elite cultivars and heritage germplasm (including landraces and heritage varieties) could enhance yield and disease resilience under variable management conditions. The results from this study demonstrate that the performance of barley genotype mixtures is highly context-dependent, regardless of whether the germplasm is new (elite cultivars) or old (heritage cultivars and landraces). Due to the small changes in yield, we can identify that the management factors, such as nitrogen levels and sowing densities, have critical roles in determining which mixture components will aid in the improvement of yield. This supports H2, which proposed that management practices influence the balance between competition and facilitation in genotype mixtures. Despite some early signs of disease resistance in the heritage material, our results showed no consistent reduction in

disease levels in genotype mixtures compared to monocultures, suggesting that genotype mixing does not necessarily mitigate disease pressure.

As hypothesized in H1, we expected that combining heritage lines with elite cultivars would increase yield resilience via complementary effects. This hypothesis was only partially supported, as benefits were limited and context-dependent. Although genotype mixtures of barley show promise, they do not necessarily surpass the yields of the highest-yielding monocultures in any particular year or location in our trial. This statement is especially evident when mixing with the lower-yielding heritage germplasm. Nevertheless, mixtures using a small amount of heritage germplasm were shown to improve yield stability without significantly reducing yield, showing an increased consistency across different environmental conditions. Moreover, mixtures made from solely heritage germplasm showed more benefit from genotype mixtures in terms of yield

stability, likely due to their background, and thus, they gain more benefit from being grown as a population, as is convention, as opposed to populations made from elite germplasm. The use of heritage lines, rather than populations in this study, allows for the comparison between genotype mixing different germplasm sources, though it should be noted that this eliminated much of the diversity held within the landrace populations to be consistent with the cultivar material. One key aspect that this study did not look into is whether the quality traits were improved or more consistent—an aspect that could offer a clear benefit of economic gain as the yields are mostly consistent with the monocultures.

While barley showed limited benefits from growing in genotype mixtures, our study has been able to identify complex trends about the importance of mixture composition and environment that may be overlooked in, but still relevant for, crops with greater genotype mixture yield benefits such as rice, maize, and wheat. This is the first study to show that small proportions of heritage germplasm can improve yield stability in elite barley mixtures under specific environmental conditions, providing new insights into genotype mixture \times environment ($G^2 \times E$) interactions. Future research should be focused on refining mixture design over all crops by exploring the interactions between plant trait space and their environment. Better understanding genotype \times environment interactions, as demonstrated in our study with nitrogen and sowing density, researchers can develop more refined genotype mixture and intercropping scenarios in varying agricultural settings, ensuring their potential benefits are fully actualized.

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Authors' contributions JC: formal analysis, investigation, writing—original draft, writing—review and editing, visualization. AN: conceptualization, methodology, investigation, writing—original draft, writing—review and editing, project administration, funding acquisition.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability The R code that was used to statistically analyze and present the findings of this study is available from the corresponding author upon reasonable request.

Declarations

Ethics approval The authors declare that no ethics approval was necessary to conduct or publish this work.

Consent to participate The authors declare that no consent to participate was necessary to conduct or publish this work, due to the absence of human subjects.

Consent for publication The authors declare that no consent for publication was necessary to conduct or publish this work, due to the absence of human subjects. The authors involved consent for this work to be published.

Conflict of interest The authors declare no competing interests.

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