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ORIGINAL ARTICLE

Mixing things up! Identifying early diversity benefits and facilitating the development of improved variety mixtures with high throughput field phenotyping

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Abstract

Crop diversification is a potential strategy to increase the stability and productivity of crops, while reducing pathogen pressures and pesticide requirements. Crop variety mixtures provide some of these diversification benefits and their cultivation is fully compatible with current mechanized agronomic practices. However, the development of optimal variety mixtures is a long, labour-intense process requiring extensive field trials. High throughput field phenotyping (HTFP) methods provide promising applications in field testing because they allow for precise, repeatable, and rapid measurements of crop properties. Here, we evaluated the use of HTFP for developing high-performing oat (*Avena sativa*) variety mixtures by testing its suitability to predict diversity yield benefits from repeated canopy measurements across the growing season. Analyzing 26 mixtures of five varieties, we found significant overyielding at harvest, that is, mixtures were on average more productive than expected based on component pure stands. This grain yield overyielding was well predicted from deviations between mixture and pure stand canopy cover estimations, derived from HTFP mid-way through the growing season. This shows that (i) positive interactions between oat varieties occur already at an early stage, (ii) such interactions lead to increased potential for light interception, (iii) HTFP offers rapid, scalable methods to screen for performant variety mixtures.

1 | INTRODUCTION

Increasing climate uncertainty and a still-growing human population call for an increase in the stability and productivity of agriculture (Seneviratne et al., 2021; Tilman et al., 2011). At the same time, there is an increasing urge to reduce the environmental impact of crop production, and new regulations are limiting the use of pesticides to control pests. This means that crops have to be grown more efficiently, and yield gaps, the differences between potential and actual yields, must be closed (Senapati et al., 2022). However, this is hampered by increased climatic variability; a problem that is likely to worsen in the future (Keating et al., 2014; Tschurr et al., 2020). Breeding more robust and productive varieties or improving crop management are seen as key elements in addressing some of these mentioned challenges. However, both breeding as well as new management practices typically come with trade-offs, for example, amongst different breeding goals such as quantity and quality of products, or the trade-off between ecological management, by using less inputs, and yield in agricultural systems (Kanter et al., 2018; Sukumaran et al., 2018).

Crop diversification is a known means to render production more resilient to climate and weather-related variability (Kopp et al., 2023; Renard & Tilman, 2019). Increased diversity in agriculture can be exploited through spatial and temporal variation (e.g., crop rotations) or at different scales (e.g., strip cropping), benefiting farmers or the environment or both (Brooker et al., 2015). In both natural and agricultural systems, diversity has been shown to contribute to resilience and productivity (Lin, 2011). At the crop level, intercropping (more than one species) or variety mixtures (more than one variety or genotype) can be used to increase within-field diversity (Brooker et al., 2015). Intercropping offers greater potential for plant architectural and trait diversity compared to intracropping, as varieties are more similar to each other. Species-rich natural plant or crop communities are known to often be more productive and stable than less diverse systems (Gross et al., 2014; Ives & Carpenter, 2007). However, crop-level diversification by intercropping multiple species is often perceived as incompatible with modern mechanized agricultural practices (Brooker et al., 2015). Mixtures of varieties offer an interesting middle ground between pure and mixed cultures because they allow to increase within-field genetic and trait diversity, but are similar to pure stands in terms of processing (Barot et al., 2017; Finckh et al., 2000; Mundt, 2002; Newton et al., 2009).

Meta-analyses of the benefits of variety mixtures have indeed shown that (i) variety mixtures often have higher yields than their respective pure stands (overyielding), albeit average benefits are relatively minor, for example, approximately 2% –4% in wheat; (ii) mixtures are effective in suppressing disease epidemics, and overyielding strongly increases under high disease pressure, and (iii) yield stability is often slightly higher in variety mixtures (Borg et al., 2018; Kristoffersen et al., 2020; Kiær et al., 2009; Reiss & Drinkwater, 2018; Smithson & Lenné, 1996). Furthermore, mixtures may buffer effects from environmental influences and tend to show a higher resilience (McAlvay et al., 2022). Importantly, these identified benefits can be expected to occur on average in any random mixture, and even without prior knowledge of the potential drivers of positive mixture effects. For example, diversity-mediated disease suppression has been shown to occur in experimental apple cultivar mixtures (reduction of apple scab incidence [*Venturia inaequalis*]) or in commercial wheat variety mixtures (reducing Septoria tritici blotch [*Zymoseptoria tritici*]) that were not deliberately designed to do so (Kristoffersen et al., 2020; Kellerhals et al., 2003). It has been speculated that crop variety mixtures could potentially provide even greater benefits once varietal combinations with optimal trait complementarity (e.g., different disease resistances, different resource requirements, different

Core Ideas

- Overyielding effects in crop variety mixtures with different numbers of mixture partners were evaluated.
- Grain yield overyielding was found to be correlated with early measurable traits, that is, canopy cover overyielding.
- High throughput field phenotyping can be used at early vegetative stages to predict the potential of crop variety mixtures.

environmental optima, and so on) can be identified (Barot et al., 2017; Wuest et al., 2021). For example, deploying such variety mixtures specifically to suppress the spread of pathogens and at very large scales has been associated with remarkable effects in the past, whereby diseases effectively disappeared from diversified regions (Finckh et al., 2000; Mundt, 2002; Wolfe et al., 1992; Zhu et al., 2000). Overall, it is therefore conceivable that screening for particularly good variety combinations and their wider use can lead to substantial improvements in crop yields. However, the development of well-performing mixtures currently creates several challenges. On the one hand, there are agronomic constraints on the trait differences that exist between the varieties to be combined within the field. For example, large divergence in phenology between mixture components is undesirable, as this has a strong influence on the optimal harvest time point or other agronomic management decisions. At the same time, some phenological differences may also be beneficial to minimize risks, exemplifying the conflict between maximizing trait diversity for beneficial interactions and minimizing trait diversity for ease of management (Litrico & Violle, 2015). Unfortunately, little is currently known about the drivers of overyielding or improved crop stability in variety mixtures. This impedes their targeted design based on simple predictors for increased diversity benefits. Currently, developing variety mixtures relies on empirical testing, and involving a potentially large number of combinations of different genotypes (Wuest et al., 2021). The reason for this is that the "combinatorial universe" of possible mixtures (including two-way, three-way, four-way, and so on combinations) grows exponentially with an increase in the number of varieties available. Especially in field trials, data collection and phenotypic evaluation of mixtures can therefore become a bottleneck, particularly if the data collection is done by breeders or other human evaluators. Here, we present a technical approach that increases screening throughput, reduces the space and labor requirements for field experiments, and therefore exhibits the potential to facilitate the development of variety mixtures.

In plant breeding, high throughput field phenotyping (HTFP) shows large potential to gather vast amounts of data in a standardized and repeatable manner (Atkinson et al., 2018; Araus et al., 2018; Reynolds & Langridge, 2016). For HTFP, we consider a wide range of technologies that rely on automated data acquisition workflows in order to analyze and evaluate plant traits (Jangra et al., 2021). In our work, we have used image-based HTFP methods, meaning automatically collected images by the field phenotyping platform (FIP) (Kirchgessner et al., 2017), which are then further processed with deep learning models (Zenkl et al., 2022). This allows the extraction of plant traits, such as canopy cover (CC), which is represented by the green leaf fraction in an image. A major advantage of HTFP over manual ratings as performed by humans is that it is more objective and avoids the rating variability associated with different raters and rater bias (Jiang et al., 2020). Using automated measurement methods allows to conduct time-resolved measurements of plant growth and identify mechanisms that improve crop performance (Walter et al., 2015). To investigate how HTFP methods could be used to evaluate optimal mixture partners, preferably at an early stage of plant growth, we conducted a field experiment with 108 plots. Variety mixtures of oat (*Avena sativa*) were used for this experiment, as oat is less susceptible to pests compared to other crops, such as wheat (*Triticum aestivum*), making it of particular interest for organic farming. Though there is no clearly defined trait for early vigor of plants (Grieder et al., 2015), we used early CC as a trait describing the early plant development (Tschurr et al., 2023). CC describes the percentage of plant area covered within a region of interest, in this study a plot of the field trial (Roth et al., 2022), from nadir view. The CC values can therefore range between 0 and 100%. The experiment took place at the research site for plant science of ETH Zurich in Eschikon, Lindau, where the FIP is located (Kirchgessner et al., 2017). The FIP is a rope suspended camera system that allows to take precise and automated images. During the whole vegetation period, RGB images of different variety mixtures were taken using the FIP, in order to investigate the performance of different genotypes in combination. By measuring CC and yield on a plot level basis over different mixture levels, this study aimed to (i) use HTFP as a method to identify well-performing mixture partners, and at an early stage; (ii) improve the throughput for a potential practical application, allowing to scale up the evaluation of multiple mixtures, and (iii) deliver a method to reduce time-consuming and labour-intensive measurements that can reveal potential drivers of end-of-season benefits of mixtures.

2 | MATERIAL AND METHODS

2.1 | Plant material and measurements

Field experiments were conducted at the ETH Research Station for Plant Sciences Lindau-Eschikon, Switzerland (47.449 N, 8.682E, 520 m a.s.l.) below the FIP in the year 2022 (Kirchgessner et al., 2017). The typical climate shows relatively cold winters, warm and precipitation rich summers over the past 30 years (see Supplemental Figure A.1). The soil of the experimental field is a gleyic cambisol with 21% clay, 21% silt, and 3.5% organic matter (Kirchgessner et al., 2017). In this study we examined a set of five summer oat varieties that are recommended in Switzerland, namely: Canyon (Can), Delfin (Del), Husky (Hus), Lion (Lio), and Zorro (Zor) (see Table A.1). The varieties were grown in pure stands and in two-way (10), three-way (10), four-way (5), and five-way (1) mixtures, leading to 26 different mixture compositions. The proportions of each variety in a mixture were calculated as follows: two way: 50% of the number of sown seeds for each variety, three way: 33.3% of each variety, four way: 25% of each variety, five way: 20% of each variety. With this, not only various varieties were investigated but also multiple mixture levels. Pure stands were grown at higher replication levels (six replications) than mixtures because their yield is used repeatedly in the estimation of mixture overyielding. Specifically, experimental plots were grown with a size of 1.25 × 6 m, and arranged in a randomized complete block design with 3 replications, each containing all 26 mixtures and 2 × 5 pure stands. All plots were sown on March 10, 2022 with 9 rows per plot and a seed density of 385 seeds per square meter. The plots were harvested with a combine thresher on July 15, 2022 (127 days of growing season). Yield data was measured after harvesting of the whole plots, using a small combine harvester constructed for field experiments, for each individual plot, no differentiation within plots for the specific varieties was done.

An RGB 21 Mega Pixel full frame digital single-lens reflex (DSLR) camera (EOS 5D Mark II, 35 mm lens (Canon Inc., Tokyo, Japan) attached to the FIP was used for the measurements which delivers a ground sampling distance of ~0.3 mm, by carrying the camera approximately 2.5 m above canopy in nadir view. The measurements were conducted according to feasible weather conditions, about two times a week. This resulted in 34 measurements over the entire growing season, 20 of which were taken before canopy closure, when differences between mixtures in CC can be assumed.

2.2 | Data processing

The FIP images cover a larger area than one experimental plot. The region of interest was therefore defined as the plot within an intended boundary to reduce border effects. This was done by detecting the sowing rows, according to the method used in Anderegg et al. (2023).

From the region of interest, the canopy cover (CC) was calculated by using the deep learning network trained and tested in Zenkl et al. (2022). This approach uses a pixel-based segmentation, meaning that a deep learning algorithm with a convolutional neural network is able to label each pixel as soil or as plant. With this so-called "soil-plant mask," it is possible to calculate the ratio between soil and plant pixels in an experimental plot, which results in canopy cover. To reduce the spatial heterogeneity effects within the experimental field site we applied the SpATS package developed by Rodríguez-Álvarez et al. (2018) to the CC values for each individual measurement time point, as well as for the end-of-season yield. After fitting the SpATS model, the spatial corrected best linear unbiased prediction (BLUP) values were extracted. As they describe the best predicted overall value for each mixture (or pure stand) we used these values for further analysis. In this study we refer to it as "spatially corrected values." The expected yield was calculated as described in the following equations with the BLUPs.

Expected yield (EY) is calculated as the sum of the values (i.e., CC and yield individually) from their respective pure stands (*Mono*), by the relative proportion of each mixture partner (n) (Equation 1).

$$EY_{\text{mixture } 1:n} = \sum_{i=1}^{n} \frac{Mono_i}{n} \tag{1}$$

Overyielding grain yield ($\mathrm{OY}_{\text{grain yield}}$) and Overyielding canopy cover ($\mathrm{OY}_{\text{canopy cover}}$) were calculated as the differences between the measured value (*Measurement*) and the EY (Equation 2)

$$OY_{\text{mixture } 1:n} = Measurement_{\text{mixture } 1:n} - EY_{\text{mixture } 1:n} \tag{2}$$

Overyielding (OY) was calculated for yield ($\mathrm{OY}_{\text{grain yield}}$) and canopy cover ($\mathrm{OY}_{\text{canopy cover}}$) (Equation 2) and these results were used for further statistical analysis. For comparison, the OY values have been scaled as percentage of the measured values.

In a first step, mixture yields have been modeled according to the spatial corrected values of the grain yields deriving from the pure stands and the according EY within a linear model. The yield was considered as a function of the EY yield in the linear model ANOVA.

In a next step, a one-sided, paired t-test between the expected values (EY) and the measured values was performed. Then, a robust linear model was fitted by using the robustbase library (Maechler et al., 2021) in R (R Core Team, 2018). The linear model was fitted with the $\mathrm{OY}_{\text{grain yield}}$ as a function of $\mathrm{OY}_{\text{canopy cover}}$ for each CC measurement time point until canopy closure was reached (first 20 measurement time points have been integrated to the analysis). Also a Pearson correlation between $\mathrm{OY}_{\text{grain yield}}$ and each $\mathrm{OY}_{\text{canopy cover}}$ measurement was calculated.

3 | RESULTS

The 26 different (two-way, three-way, four-way, and five-way mixtures) were harvested 127 days after sowing (DAS) to determine end-of-season grain yield. Final yield averaged 6.8 kg/plot which corresponds to approximately 7.5 tons/ha. This a relatively high yield level for Switzerland (average commercial yield approximately 5 tons/ha; IP-Suisse, 2020). We then determined mixture yields and patterns of overyielding, that is, the observed yield deviations of a mixture from the spatially corrected average pure stand yields of its components. Mixture yields were found to be predictable from the average pure stand yields (spatially corrected) of components, that is, combinations of varieties with higher estimated pure stand yields also resulted in higher-yielding mixtures (linear model ANOVA $F_{1,24} = 9.6$, $p < 0.01$; but with moderate $R^2 = 0.29$; Supplemental Figure A.2).

At the same time, we estimated a significant average $\mathrm{OY}_{\text{grain yield}}$ of 2.3 % (Figure 2; t-test for overyielding >0%: $t_{25} = 4.35$, $p < 0.001$), equivalent to an average mixture yield benefit of 150 g per plot (~ 166 kg per hectare). $\mathrm{OY}_{\text{grain yield}}$ was highest in two-way mixtures but decreased linearly with the number of components (ANOVA $F_{1,24} = 6.02$, $p = 0.022$; see Supplemental Table A.2). For example, $\mathrm{OY}_{\text{grain yield}}$ was estimated to be positive in all two-way mixtures, whereas only 60% of the four-way mixtures exhibited positive $\mathrm{OY}_{\text{grain yield}}$ estimates.

We next examined if mixture benefits had already been evident in crop stand development throughout the season. For this, we had used repeated HTFP measurements (34 time points in total) to estimate CC from the resulting images. Overall, CC estimates increased up to about 67 DAS and remained constant thereafter (Figure 1). Therefore, for further CC analysis the first 20 measurement time points were used until the canopy was closed and the constant phase started. After spatial correction to reduce the effects of field heterogeneity at the plot level, $\mathrm{OY}_{\text{canopy cover}}$ was calculated for each mixture composition and each time point. In this case, the $\mathrm{OY}_{\text{canopy cover}}$ refers to deviations of mixture CC from expectations derived from the average of component pure stand CC. $\mathrm{OY}_{\text{canopy cover}}$ was calculated for each time point, and overyielding estimates were also overall positive and peaked around 50 days after sowing (DAS) (Figure 3).

As with the grain yield data, the two-way mixtures exhibited highest $\mathrm{OY}_{\text{canopy cover}}$, higher than the three-way and four-way mixtures. Maximal differences in $\mathrm{OY}_{\text{canopy cover}}$ between the different mixture levels were observed during the phase of maximal growth of the canopy (Figure 3). Given that patterns of overyielding in mid-season canopy cover measurements were similar to those of final grain yield measurements, we next determined correlation between these two entities (Figure 4A).

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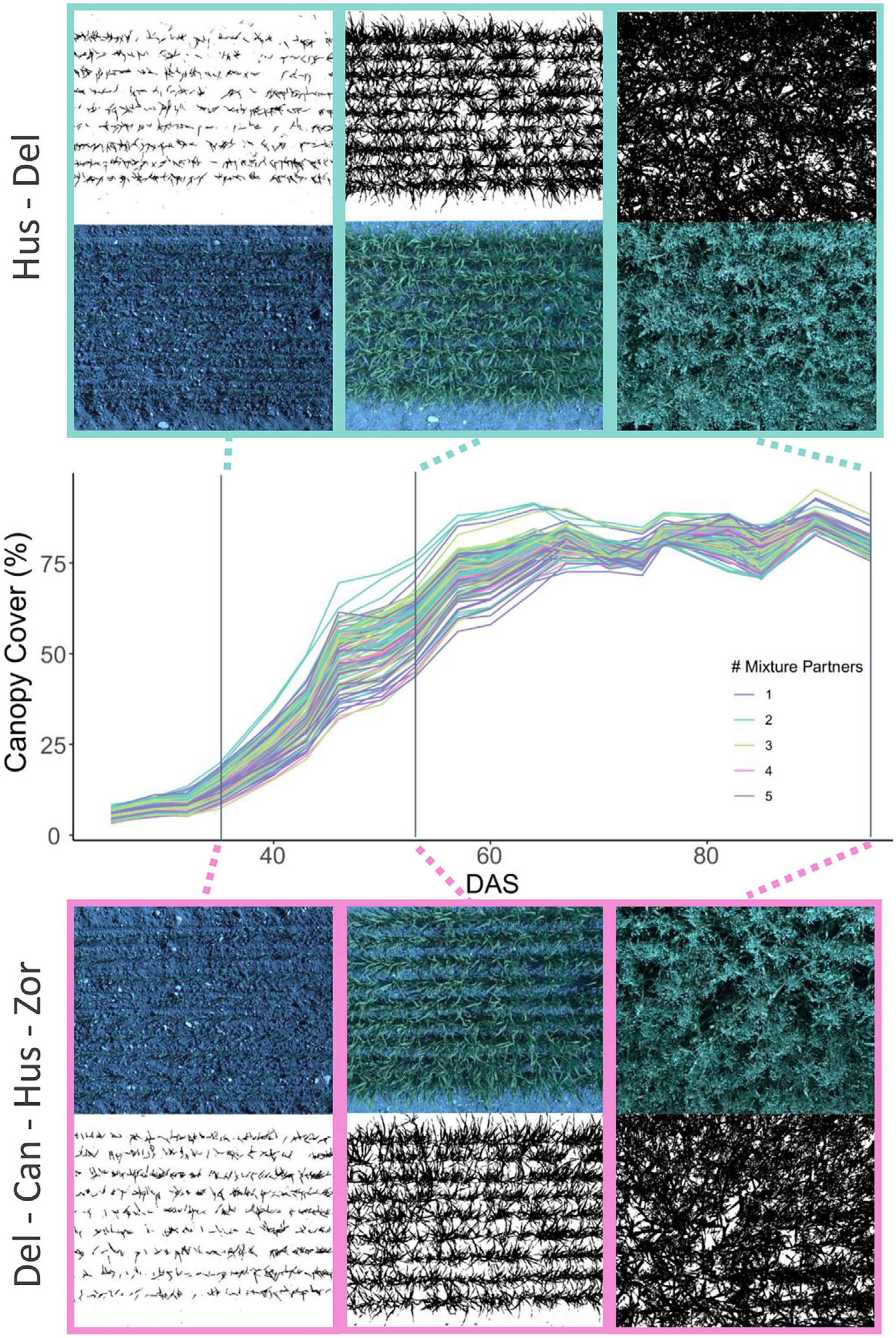

FIGURE 1 Overview of the canopy cover development. Middle: Development of canopy cover (spatially corrected values), shown in percent over time (in days after sowing [DAS]) on plot level. The colors indicate the different mixture levels (pure stand to five-way mixtures). Top and bottom: Images of two plots that were taken at three time points, indicated by vertical lines (at 32, 53, and 95 DAS). Examples were chosen to show a two-way mixture (top; Hus-Lio) and a four-way mixture (bottom; Del-Can-Hus-Zor). For each plot the Red-Green-Blue color space (RGB) image and the corresponding segmented image in plant and soil fraction are shown (black represents plant pixels).

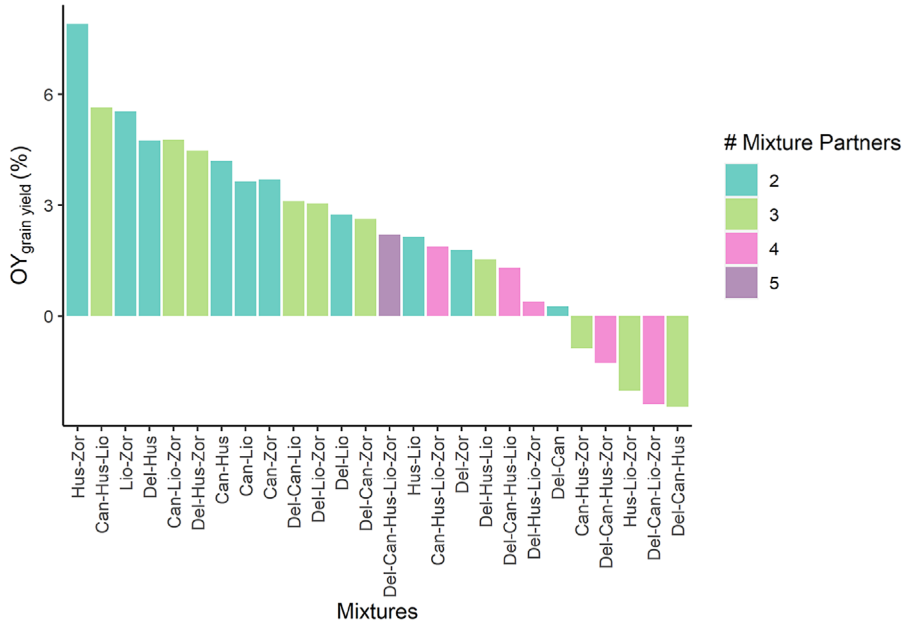

FIGURE 2 Grain yield overyielding estimates ($OY_{grain\ yield}$) per mixture composition are displayed in percent (y-axis). The different mixtures (x-axis) are sorted according to the highest (left) to the lowest estimates (right). Positive values indicate overyielding, negative values indicate underyielding. The colors indicate different mixture levels (number of partners in a mixture). Further data are shown in Supplemental Figure A.2.

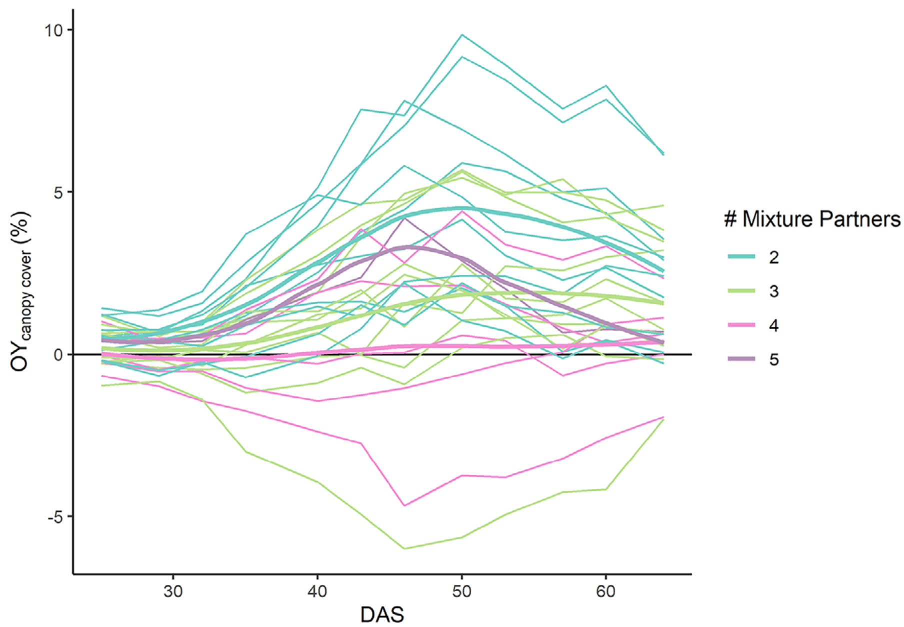

FIGURE 3 The overyielding of canopy cover ($OY_{canopy\ cover}$) per plot (spatially corrected) is displayed in percent over time. Positive values show an overyielding, negative values an underyielding effect. The colors indicate different mixture levels (number of partners in a mixture). The bold lines in corresponding colors represents the average of the different mixture levels.

The Pearson correlation coefficient between the end-of-season $OY_{grain\ yield}$ and the $OY_{canopy\ cover}$ at each measurement time point increased over time up to 50 DAS, remained high until 60 DAS and then decreased (Figure 4). At its maximum at 50 DAS, the Pearson correlation coefficient between the two entities was 0.48 (Figure 5). In related terms, we assessed the potential of $OY_{canopy\ cover}$ to predict $OY_{grain\ yield}$ using a simple linear model ($OY_{grain\ yield}$ as a function of $OY_{canopy\ cover}$). As shown in Figure 4B, the p-value from the linear models were minimal at 50 DAS. Significant p-values values were obtained between DAS 40 and 64 (p-value below 0.05; grey line Figure 4B). In other words, predicting $OY_{grain\ yield}$ from $OY_{canopy\ cover}$ was effective over an extended time period, around the time of maximal growth.

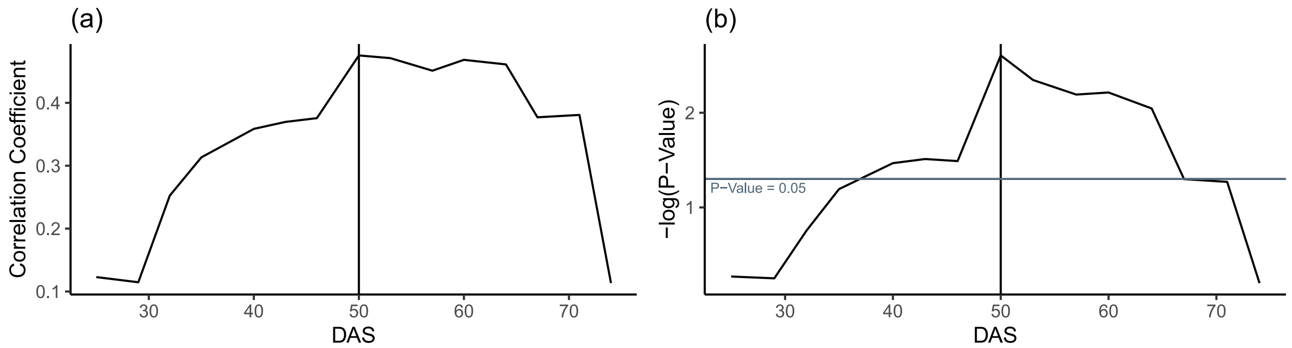

FIGURE 4 Panel A shows the correlation and -log(p-value) of the linear model which compares $OY_{canopy\ cover}$ on each day (until DAS 75) to final $OY_{grain\ yield}$ for each mixture (spatially corrected) in percent. The highest correlation (in panel A) and the smallest p-value (in panel B) was found at 50 DAS (vertical lines). The grey line in panel B represents a p-value of 0.05 below which an effect was considered as significant.

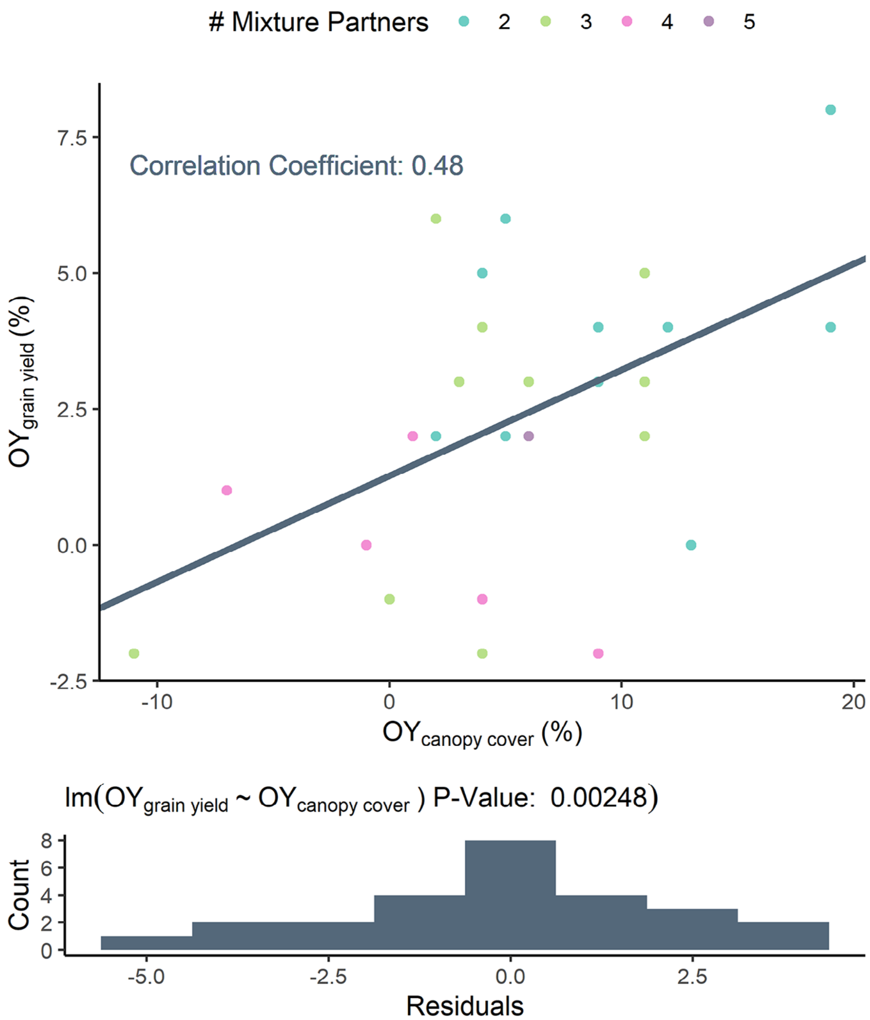

FIGURE 5 Top panel: The correlation between $OY_{grain\ yield}$ at 50 DAS in percent and $OY_{canopy\ cover}$ in percent is shown with a correlation coefficient of 0.48. The colors indicate different mixture levels (number of partners in a mixture). The grey line represents the fit of the linear model. Lower panel: The distribution of the residuals from the linear model is shown, where $OY_{grain\ yield}$ was modeled as a function of the $OY_{canopy\ cover}$, with a p-value of 0.0025 and normal distributed residuals (see Supplemental Table A.3).

4 | DISCUSSION

In our experiment with five different oat varieties, combined into mixtures with different complexity levels (two way to five way), we found that mixture performance could be predicted from component pure stand yields, though only with moderate accuracy. This result is consistent with findings from a large wheat variety mixture experiment (Forst et al., 2019), and lends support to the notion that "good mixtures require good components." At the same time, we estimated significant end-of-season overyielding in mixtures, with an average of 2.3% across all mixtures and estimates ranging from -2.5% (underyielding) to +7.9% (overyielding). These values are also well in line with various previous experimental studies with cereal mixtures (Borg et al., 2018; Kristoffersen et al., 2020; Locmele et al., 2017; Manthey & Fehrmann, 1993; Reiss & Drinkwater, 2018). At the same time, and contrary to expectations, overyielding estimates were highest for two-way mixtures and decreased with increasing number of components. This contradicts the more common result from ecological experiments, where more varieties or species most often show higher yield (Caldeira et al., 2005; Tilman et al., 2001). Increased diversity often has positive outcomes in ecosystems, however, these may not always be adaptable to an agricultural setting (Barry et al., 2020; Chacón-Labella et al., 2019). This observation is difficult to reconcile with ecological theories and observations and would need further testing to be generalized. Potential explanations of such a pattern might be sought by examining patterns of competition and complementarity amongst varieties in mixtures (Justes et al., 2021; MacLaren et al., 2023), and by quantifying the relative gains of different genotypes in the mixtures by the additive partitioning method used to analyze biodiversity experiments (Loreau & Hector, 2001; Li et al., 2020). However, this would require designs that allow for the identification of individual genotypes in mixtures, which is challenging. In any case and regardless of the underlying drivers of overyielding, the presented method shows potential for simplifying the search for "optimal" variety combinations from a larger set of possible mixing partners.

When using HTFP to dynamically monitor crop stand development throughout the season, patterns of overyielding were found to be similar for final yield and for canopy cover estimates at multiple time points and already during earlier stand development. During the period of maximal crop growth, $OY_{\text{canopy cover}}$ estimates were significantly positive, highest for two-way mixtures, and decreased with increasing mixture complexity. Finally, mixture $OY_{\text{canopy cover}}$ estimates during this period were correlated well with end-of-season $OY_{\text{grain yield}}$, and could in principle be used to predict the latter. This has several implications: (i) It suggests that, at least to some extent, positive interactions amongst mixture components occur already at an early stage and positively influence the establishment of a denser canopy, which (ii) likely improves the interception of light during full stand establishment and growth, leading to higher resource use during the season and higher yield at the end of the season. Since HTFP could be used to dynamically measure a larger variety of traits over time (Araus et al., 2018; Kronenberg et al., 2017; Roth et al., 2021), such approaches could therefore strongly improve our understanding of the processes through which diversity benefits are mediated. Though not relevant in our experiment, which was managed so that the crop had exhibited only very limited weed pressure, an increased canopy cover during stand establishment could also increase the weed suppressive potential of mixtures, a property that has been of central interest in previous cereal mixture experiments (Kiær et al., 2009). Finally, (iii) HTFP offers rapid and scalable methods to screen for and develop high-performing variety mixtures, as discussed below.

Developing high-performing mixtures is typically concerned with the difficult problem of finding specific combinations of varieties that bring an added diversity value, for example, increased yield or yield stability as driven by positive plant–plant interactions. Without predictive methods, this "combinatorial problem" quickly escalates in terms of complexity: it often requires prohibitively large experimental designs, because the number of possible mixtures grows exponentially with the number of available components (e.g., $n \times (n-1)/2$ possible mixtures for two-way combinations sampled from n possible varieties). Here, HTFP could simplify the search for particularly good compositions, by allowing a rapid and scalable screening for positive interactions during early stand development. In this paper, we have described a significant relation between the canopy cover overyielding ($OY_{\text{canopy cover}}$) and grain yield overyielding ($OY_{\text{grain yield}}$). Canopy cover of evaluation plots (as described here) or even single rows (for upscaling, see below) can typically be assessed relatively easily using HTFP, facilitating screening for beneficial interactions between combined varieties. However, there may also be some caveats. According to our results, measurements at 50 DAS best predicted end-of-season overyielding, although correlations between the two entities were also high at different measurement time points. In other cases, optimal time points for measurement may differ between years or field sites, which would require the production of separate calibration datasets. Defining an optimal time in relation to the physiological stage of the crop (e.g., between booting and shooting) may alleviate this problem. Once such issues are solved, variety mixture screening methods could be implemented in efficient and economic ways (since the crop would not need to be grown to full maturity), for example, by growing multiple generations per season, or even by performing screens in between two crops as an alternative to a cover crop. Furthermore, in order to gain representative data, plot size could be varied according to the respective trait (Rebetzke et al., 2014). Estimation of yield is usually done in relatively large plots (1.25 × 6 m) while other traits such as canopy cover, plant height or plant indices can be readily measured in micro-plots (e.g., 1.25 × 1.75 m) or even single rows (Anderegg et al., 2020, 2021; Kronenberg et al., 2021; Roth et al., 2023). Using micro-plots or single rows, the number of evaluation units on a specific area can be a multiple (e.g., 3–4x) compared to a situation where yield plots are the measurement units. Finally, the duration of this experiment was 127 days, while summer oat in Switzerland usually grows around 5–6 months (~150–180 days), from February until August. Theoretically, two to three generations for an experiment could take place within this time span, in case an early measurement of CC at 50 DAS is found to be generally informative. Together with increases in plot numbers (due to smaller plots), this could increase the screening throughput even further.

In our study, two-way compositions most consistently exhibited overyielding, though the generality of such a pattern for oat variety mixtures will require testing across multiple environments and years. Restricting the focus on identifying optimal two-way mixtures (e.g., optimal in terms of yield and overyielding) would further simplify the development of predictive tools or rapid evaluation methods to determine mixture benefits. For example, assembling 20 varieties into all possible combinations, and considering pure stand and two-way up to five-way mixtures, would result in 21,699 compositions, of which only 190 are two-way mixtures. Mixture development may also be facilitated by using HTFP to rapidly monitor other traits, for example, plant height, senescence dynamics or color-based indices, or by predicting other mixture benefits from such data, such as yield stability or disease suppression (Anderegg et al., 2019). Finally, HTFP combined with additional multi-spectral imaging may ultimately achieve a high prediction accuracy of mixture benefits solely from traits measured in pure stands (Schweiger et al., 2021). Such approaches may be complemented by the development of further predictive tools, for example, based on crop models (Gu et al., 2022).

5 | CONCLUSION

This study demonstrates the potential of HTFP to investigate different partners and complexities of variety mixtures. Unlike higher-order mixtures, all two-way mixtures exhibited end-of-season overyielding, and independently of the respective varieties used. However, the generality of such a pattern for oat variety mixtures would require broader sampling and testing. A significant correlation between the $OY_{\text{grain yield}}$ and $OY_{\text{canopy cover}}$ at earlier crop development stages was found. This shows the potential of non-destructive measurement for canopy cover overyielding as an early predictive trait for beneficial mixture compositions. In this experiment, early measurements at 50 DAS appeared to be the optimal time point for such canopy cover measurements, that is, within the period in which the fastest increase in canopy cover occurred. Our work shows that HTFP provides a rapid and scalable tool to screen for and develop high-performing variety mixtures

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code are available upon reasonable request.

AUTHOR CONTRIBUTIONS

Flavian Tschurr: Conceptualization; methodology; software; formal analysis; visualisation; data acquisition; writing—original draft. **Corina Oppliger**: Conceptualization; methodology; formal analysis; visualisation; data acquisition; writing—original draft. **Samuel E. Wuest**: Supervision; methodology; formal analysis; visualisation; writing—original draft. **Norbert Kirchgessner**: Data acquisition; software; writing—review and editing. **Achim Walter**: Supervision; project administration; funding acquisition; writing—review and editing.

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