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RESEARCH ARTICLE

Wheat cultivar mixtures enhance the delivery of agroecosystem services compared to monocultures under contrasted tillage intensities and fertilization

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Abstract
Wheat cultivar mixtures provide a more complex and functional cropping system than monocultures. Their functionality may result in the delivery of agroecosystem services. However, research on cultivar mixture performance has mainly been done in controlled environments. Greenhouses and laboratory experiments do not account for environmental or agronomic factors that may influence the polyculture's functionality. To fill this research gap, we set up a novel strip-split-block experimental design with three factors (wheat treatment, tillage, and fertilization) in a field long-term trial. We assessed the performance of the modern wheat cultivar Florence-Aurora and the traditional cultivars Xeixa (*Triticum aestivum* L. subsp. *aestivum*) and Forment (*Triticum turgidum* L. subsp. *durum*) monocultures and their mixture in providing aphid and weed control and promoting crop yield under contrasting tillage practices (moldboard ploughing vs. chisel ploughing) and fertilization (farmyard manure applied or not applied). We analyzed aphid abundance, number of aphids per tiller, parasitism rate, weed abundance and richness, and crop yield. Additionally, we examined wheat establishment, cover, phenology, and height for cultivar characterization. We observed that soil management practices affected some aspects of the cropping system. The wheat cultivars differed in their aphid susceptibility and weed suppression ability, with Florence-Aurora being less suppressant to weeds and more prone to aphid infestation. Most remarkably, our study shows for the first time that mixing wheat cultivars with distinguished traits enhances associational resistance for aphid and weed control. These benefits were specifically important under high weed infestations generated by reduced tillage. Moreover, the yield of Florence-Aurora monoculture and the mixture was found to be influenced by tillage and fertilization. Our study underscores how soil management practices impact the functionality of cultivar mixtures. This emphasizes the need for further field research to better understand the complexity of farming conditions that influence the delivery of agroecosystem services by cultivar mixtures.

Keywords Wheat cultivar mixtures · Soil management practices · Functionality · Yield stability · Aphid control · Weed control

1 Introduction

Establishing monocultures and substituting traditional cultivars for modern ones are still common practices for organic cereal crops of the Mediterranean basin (Di Bene et al. 2022; Serra et al. 2019). These modern cultivars, often selected for their high yield (Ficiciyan et al. 2018), demonstrate superior performance compared to traditional cultivars under optimal environmental conditions. However, they are more prone to pest infestation and are weaker competitors against weeds (Bonnet et al. 2021; Lazzaro et al. 2018; Serra et al. 2019). This agricultural framework has led to a simplification of the cropping system, resulting in a significant loss of agrobiodiversity and associated diversity, and an overall decline in agroecosystem functionality (Altieri and Rogé 2009; Dainese et al. 2019; Tilman et al. 2014).

In contrast, increasing agrobiodiversity in cereal crops enhances agroecosystem complexity and functionality while preserving natural biodiversity in the field

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(Altieri and Rogé 2009; Barot et al. 2017; Gaba et al.2015; Koricheva and Hayes 2018; Wezel et al. 2014). Following Serra-Gironella and Alvaro (2017), a cultivar mixture involves simultaneously sowing a high-yield cultivar and one or a few companion cultivars, which provide specific benefits to polyculture. Implementing mixtures of cereal cultivars can provide resistance against pests and parasites, increase competitiveness against weeds, and improve yield stability. These functions ultimately provide agroecosystem services (Costanzo and Bàrberi 2014; Gibson and Nguyen 2021; Tilman et al. 2014). In mixtures containing a small number of cultivars, it is crucial to evaluate cultivar traits linked to desired agroecosystem services to avoid functional redundancy and improve mixture performance (Gaba et al. 2015; Lazzaro et al. 2018).

Aphids are considered a potential pest in cereal crops (Dedryver et al. 2010) and serve as a model organism for the study of insect-plant interactions (Rodriguez-Saona and Stelinski 2009). Functional mixtures of cereal cultivars provide aphid control services through associational resistance. Resistant cultivars visually and olfactorily mask the susceptible cultivar from aphids (Barbosa et al. 2009). For instance, Shoffner and Tooker (2013) conducted a laboratory experiment that found lower aphid abundance when mixing six-line wheat cultivars with varying levels of aphid resistance compared to three-line cultivar mixtures or monocultures. Moreover, cereal cultivar mixtures also provide indirect aphid control by attracting natural enemies, such as parasitoid wasps and predatory arthropods (Glinwood et al. 2009; Koricheva and Hayes 2018; Ninkovic et al. 2011). When it comes to weed control services, different types of cereal cultivars have various traits that contribute to weed suppression. For instance, wheat cultivars differ in height, aboveground biomass, and tillering capacity. An increased diversity of wheat traits can create a more competitive environment by capturing more light and a broader spectrum of nutrient resources, ultimately contributing to weed control services (Lazzaro et al. 2018; Worthington et al. 2013). Finally, the combination of traditional and modern wheat cultivars improves resilience to variation in environmental conditions, thereby enhancing yield stability (Borg et al. 2018; Ficiciyan et al. 2018; Reiss and Drinkwater 2018).

However, most research on cultivar mixture functionality has been conducted within controlled environments, ignoring the complexity of actual farming conditions (Barot et al. 2017; Gaba et al. 2015). Soil management practices, such as tillage and soil fertilization, can alter the cropping system performance by modifying weed abundance and nitrogen availability (Tamburini et al. 2016). This, in turn, may influence the functionality of cultivar mixtures. Conventional tillage (e.g., moldboard ploughing) is commonly used to reduce weed infestations (Armengot et al. 2015; Sans et al. 2011). Weeds can affect crop growth and yield (Baldivieso-Freitas et al. 2018; Diacono et al. 2019; Tamburini et al. 2020), and conventional tillage can reduce weed species richness (Tamburini et al. 2016). On the other hand, nitrogen fertilization significantly improves crop yield in cereal crops (Baldivieso-Freitas et al. 2018; Tamburini et al. 2016). However, nitrogen-rich soil conditions can also encourage aphid infestation due to the crop's high-quality sap (Aqueel and Leather 2011; Chabert and Sarthou 2017; Nowak and Komor 2010) (Figure 1).

This study used a long-term organic arable field experiment to assess the influence of soil management practices, namely, contrasting tillage systems and fertilization, on the functionality of different wheat varieties. It aimed to look at their mixture in particular. It evaluated the performance of three wheat cultivar monocultures (one modern and two traditional) and how the resulting cultivar mixture provided aphid and weed control and crop yield stability under different tillage and fertilization practices. We hypothesized that (i) the three cultivars exhibit distinct functional traits associated with weed and aphid control, (ii) the cultivar mixture displays lower weed infestation compared to monocultures, (iii) the cultivar mixture offers aphid control by both associational resistance and increased parasitism rate, (iv) the cultivar mixture and traditional cultivar monocultures present more stable yields than modern cultivar monoculture, and (v) tillage practices and fertilization affect the functionality of the cultivar mixture.

Fig. 1 Three wheat cultivars selected for this study. **a** Modern cultivar Florence-Aurora (*Triticum aestivum* L. subsp. *aestivum*). **b** Traditional cultivar Forment (*Triticum turgidum* L. subsp. *durum* Desf. (Husn.)). **c** Traditional cultivar Xeixa (*Triticum aestivum* L. subsp. *aestivum*). (Photos: Alejandro Pérez Ferrer).

2 Materials and methods

2.1 Study site

This study was conducted over two cropping seasons (2018–2019 and 2020–2021) in the rural area of Gallecs, a peri-urban agricultural area spanning 755 hectares located 15 km north of Barcelona (41° 33′ 31.9″ N 2° 11′ 59.5″ E, Catalonia, Northeast Spain). The area experiences a Mediterranean climate characterized by hot, dry summers, and mild winters. The mean annual temperature is 14.6 °C, with a mean of 629.2 mm rainfall. During the two cropping seasons, from December to June, the mean temperature and accumulated precipitation were 13.7 °C and 132.5 mm in the 2018–2019 period and 13.2 °C and 83.8 mm in the 2020–2021 period, respectively (Table 1).

The study was conducted in a long-term trial established in 2011 that combined contrasting tillage and fertilization factors over a 2-year crop rotation of cereals and legumes. The vetch-oat mixture crop preceded the first sampling season, while the chickpea crop preceded the second sampling season. Since 2006, the field has been organically managed with no pesticide application.

In 2011, we analyzed the soil properties of the field. The soil was a loamy clay (Baldivieso-Freitas et al. 2018) with low soil organic matter (1.5 ± 0.1%) and a slightly alkaline nature (pH = 8.1 ± 0.1). In 2020, the total nitrogen soil content was assessed. The average values were 0.179 ± 0.006% in fertilized plots and 0.133 ± 0.006% in non-fertilized ones.

2.2 Selection of winter wheat cultivars

The three wheat cultivars used in the experiment were chosen in collaboration with local farmers. We selected a modern cultivar, Florence-Aurora (*Triticum aestivum* L. subsp. *aestivum*), which is the predominant cultivar sown in the organic fields of Gallecs. The others were two traditional cultivars, Xeixa (*Triticum aestivum* L. subsp. *aestivum*) and Forment (*Triticum turgidum* L. subsp. *durum* Desf. (Husn.)). The modern cultivar, Florence-Aurora, is widely known for its baking qualities, while the other two impart aroma to the bread. The flour of the three cultivars is mixed and used for bread manufacturing in mills.

Furthermore, the traditional cultivars have different functional traits compared to Florence-Aurora. The three cultivars exhibit an upright growth pattern during their early stages of growth. However, Xeixa and Forment can present lodging problems at the ripening stage (Serra and Álvaro 2017). In addition, Florence-Aurora is of semi-dwarf stature (70 cm total height at harvest time), whereas Forment and Xeixa are traditionally tall cultivars (115 cm total height at harvest time) (Serra and Álvaro 2017). Plant height is a trait highly associated with weed control (Lavorel and Garnier 2002). Concerning aphid susceptibility, laboratory studies on odor profiles have indicated that Florence-Aurora was more attractive to aphids than traditional winter wheat cultivars (Tous-Fandos et al. 2023). When considering flour strength, flour strength is 350 W, 43 W, and 43 W in Florence-Aurora, Xeixa, and Forment, respectively (Serra and Álvaro 2017). Aqueel and Leather (2011) demonstrated in a laboratory experiment that some aphid species (e.g., *Sitobion avenae* (Fabricius, 1775) and *Rhopalosiphum padi* (Linnaeus, 1758)) were healthier and more fertile when feeding on high flour strength cultivars. They could thus reach higher population densities on these cultivars. Finally, the average yields of the three monocultures in the area at a 200 kg/ha sowing rate are 1800 kg/ha for Florence-Aurora and 1400 kg/ha for Xeixa and Forment.

2.3 Experimental design

The experiment used a strip-split block with three factors: tillage (conventional tillage using moldboard (MB) versus reduced tillage employing chisel (C)), fertilization (application of composted farmyard manure (F) versus no fertilizer (NF)), and crop type (three monocultures: Florence-Aurora (FA), Xeixa (XE) and Forment (FO), and the mixture of the three cultivars (MIX)).

The tillage factor was arranged in eight vertical strips, alternating between conventional and reduced tillage (four tillage blocks). Each vertical strip consisted of two connecting plots. The fertilization factor was applied in two horizontal strips distributed randomly across each of the two

Table 1 Monthly mean temperature and precipitation from the nearest automatic weather station (Parets del Vallès, 41° 34′ 2.4″ N 2° 13′ 34.2″ E) for the wheat growing season in 2018–2019 and 2020–2021.

	2018–2019						
	DEC	JAN	FEB	MAR	APR	MAY	JUN
Temperature (°C)	16.1	6.3	9.4	12.0	13.5	16.1	22.6
Precipitation (mm)	4.8	12.9	0.8	1.9	30.0	68.8	13.3
	2020–2021						
	DEC	JAN	FEB	MAR	APR	MAY	JUN
Temperature (°C)	8.8	7.1	11.5	11.4	12.9	17.6	23.4
Precipitation (mm)	80.1	0.5	0.8	0.4	1.0	0.8	0.2

vertical strips (four fertilization blocks), giving 16 plots measuring 12 m × 26 m. The 16 plots were divided into four subplots, creating 64 6 m × 13 m subplots. Each subplot was sown with one of the four crop type treatments, taking into account the strip-split block design and agricultural machinery operability. Ultimately, we had four replicates for each combination of tillage, fertilization, and crop treatment (Figure SM 1).

We used a moldboard plough (EG 85–240-8, Kverneland) for the conventional tillage treatment, which turned the soil over at a depth of 25 cm. In contrast, we used a chisel plough (KCCC 1187 – A00, Kverneland) for the reduced tillage treatment, operated at the same depth but with no soil inversion. In both scenarios, a rotary harrow at a depth of 5 cm was utilized to prepare the seedbed. Fertilized plots received 140 kg N ha^{-1} of manure. Tillage and manure application were carried out every year between November and January before sowing. Plots labeled as “no fertilizer” had not been given any fertilizer since 2011.

The sowing rates of FA, XE, FO, and MIX were 220 kg ha^{-1} in both years. The sowing ratio for the MIX was 6:2:2, being 60% Florence-Aurora (FA), 20% Xeixa (XE), and 20% Forment (FO). Due to the greater yield capacity and higher thousand kernel weight (TKW) of the Florence-Aurora cultivar, we sowed 110 kg/ha of FA and 55 kg/ha each of XE and FO in the mixture to achieve the desired ratio. The ratio of cultivars was the same as the ratio of cultivar flour when combined for bread production. Local farmers provided organic seeds treated with copper to prevent fungal infestation. Seeds were planted in rows 12 cm apart.

2.4 Field sampling

2.4.1 Wheat cultivar growth and phenology

During the mid-February stem elongation stage in both years, we assessed wheat establishment by counting the number of wheat plants on both sides of two 50 cm linear samples aligned with the sowing lines. These samples were randomly placed in every subplot, 2 m from the edge of the subplot. Two weeks before the harvest, we evaluated the wheat cover. The wheat cover was estimated visually by well-trained samplers in a 1 m^2 quadrat randomly placed at least 2 m away from the edge in each subplot, following previous evaluations (Baldivieso-Freitas et al. 2018).

The height of wheat was analyzed as an important characteristic for weed suppression (Worthington et al. 2013). Phenology was assessed to determine if harvesting the three cultivars simultaneously in real farming conditions is feasible. Furthermore, rapidly growing cultivars have demonstrated strong weed suppression capabilities (Coleman et al. 2001).

In 2019, wheat height and phenology samplings were carried out weekly from early April to mid-June. We gathered and measured the height and phenology of ten wheat tillers evenly spaced along a 10 m transect located in the middle of the subplot. The height of the wheat was measured from the base to the top of the sheath of the topmost leaf. From the booting stage (Z41), the height was measured from the base to the flag leaf. Wheat phenology was assessed visually using Zadoks’ scale (Zadoks et al. 1974). In the cultivar mixture, wheat cultivars were distinguished. Therefore, the number of tillers collected for each cultivar corresponded to the initial sowing ratio. We calculated the mean and standard error for height and phenology stage for each wheat cultivar on specific dates.

2.4.2 Weed species richness and abundance

We estimated weed abundance by measuring the aboveground dry biomass of weeds during late June in both sampling seasons. The aboveground biomass was hand-harvested in two 0.25 m^2 quadrats randomly distributed per subplot, 2 m away from the edge to avoid edge effects. The collected samples of aboveground biomass were oven-dried for 48 h at 60 °C. Two weeks prior to the harvest, we identified and counted weeds to assess weed species richness by examining one 1 m^2 quadrat positioned at least 2 m away from the edge (Baldivieso-Freitas et al. 2018).

2.4.3 Aphid abundance and parasitism rate

The monitoring of cereal aphids and their parasitoids was conducted every 3 weeks from early April to mid-June over the two growing seasons. We counted aphids and parasitized aphids (mummies) on ten wheat tillers distributed along a 10 m transect in the center of the subplots, following the same methods used in previous research (Mansion-Vaquié et al. 2017). In the cultivar mixture subplots, we differentiated between wheat cultivars. We selected ten tillers according to the intended sowing ratio (six tillers of FA and two each of XE and FO), and aphids were counted separately by cultivar. The aphid species were identified in the field. In 2021, unhatched mummies were reared in vials until parasitoids emerged. Both the parasitoid adults and the aphid mummies were then preserved in 70% ethanol. We identified hatched parasitoids at the genus level.

In this experiment, we conducted an analysis of aphid abundance, the number of aphids per tiller, and the parasitism rate. Aphid abundance was determined by the total sum of aphids recorded per subplot during the sampling season. It expressed the overall aphid pressure in every treatment. The number of aphids per tiller was examined at the aphid population peak, which was early May in both years. It was defined as the number of aphids on a cultivar tiller grown in monoculture (FA, XE, or FO) or in the cultivar mixture (MIX). Hence, it allowed for the comparison of aphid infestation on the same cultivar when grown in different crop types. The number of aphids per tiller was used to indicate the effects of associational resistance on the preferred cultivar. Finally, the parasitism rate was calculated by dividing the cumulative number of mummies by the total number of non-mummified and mummified aphids per subplot. The parasitism rate was assessed and analyzed to test for cascading effects.

2.5 Crop yield

The total dry grain weight per subplot was collected by a plot combine harvester and weighed on-site with a crane scale at the end of June. In addition, grain aliquots (800 to 1000 g) were cleaned in the laboratory and then oven-dried for 48 h at 60 °C to determine the dry grain's weight.

The land equivalent ratio (LER) was used to calculate the yield advantage of the cultivar mixture compared to sole crops. LER can be defined as the total land area of sole crops required to achieve the same yield as polycultures (Willey and Rao 1980):

$$\mathrm{LER} = \frac{\mathrm{Y_{MIX}}}{\mathrm{Y_{FA}} \times \mathrm{Z_{FA}} + \mathrm{Y_{XE}} \times \mathrm{Z_{XE}} + \mathrm{Y_{FO}} \times \mathrm{Z_{FO}}}$$

where Y_{MIX}, Y_{FA}, Y_{XE}, and $\mathrm{Y_{FO}}$ are the yields of wheat in MIX and the sole crop, respectively; Z_{FA}, Z_{XE}, and Z_{FO} are the sowing ratios in the cultivar mixture. An LER larger than 1.0 indicates that cultivar mixtures benefit crop yield, while values less than 1.0 suggest that cultivar mixtures have a negative impact on wheat yield.

2.6 Statistical analysis

All statistical analyses were conducted using R, version 4.1.1 (R Core Team 2021). The variable wheat establishment, wheat cover, wheat height, weed abundance, weed richness, aphid abundance, number of aphids per tiller, total parasitism rate, and crop yield were analyzed with linear mixed-effects models (LMM) or generalized linear mixed-effects models (GLMM) using the *glmmTMB* package (Brooks et al. 2017).

We fitted fifteen models for each response variable, considering all potential interactions. These models included four fixed factors: tillage, fertilization, crop type, and year (2019 and 2021). Additionally, tillage and fertilization blocks were included as random factors to account for the blocking structure. Wheat cover was used as a covariate in weed biomass, aphid abundance, and yield models. After testing all possible combinations, the best model for each response variable was chosen based on its Akaike information criterion, which was corrected for small sample sizes (see Table 2). We addressed spatial dependence in the residuals by incorporating principal coordinates of neighbor matrices (PCNM) (Borcard et al. 1992) when needed.

The significance of fixed-effect factors and their interactions was determined with an *F*-test with Kenward-Roger approximation for degrees of freedom for LMMs or a likelihood ratio test (LRT) for GLMMs. Pairwise comparisons were carried out using Tukey-adjusted estimated marginal means from the *emmeans* package (Lenth 2019). Post hoc tests were performed independently for each year. The *simulateResiduals* function from the *DHARMa* package was used to examine overdispersion and residual distribution (Hartig 2022).

Wheat establishment, cover, and height were fitted in a Gaussian LMM without interactions. For statistical analysis, we only considered wheat height at harvest time. Weed richness was fitted in a Gaussian LMM model with crop × year interaction. Weed biomass was analyzed using a gamma GLMM with a logit link function. The best fitted model had a crop × tillage interaction. Aphid abundance was fitted in a negative binomial model with year × crop type interaction. To statistically analyze the number of aphids per tiller, each cultivar was analyzed independently. Hence, we categorized the crop type factor into two distinct levels: monoculture (FA, XE, or FO) and MIX. To equalize the number of tillers sampled between monocultures and mixtures, the mean number of aphids on Florence-Aurora, Xeixa, and Forment tiller grown in the MIX was adjusted by dividing them by 0.6, 0.2, and 0.2, respectively. Then, the number of aphids per tiller was fitted to a negative binomial GLMM model without interactions. The parasitism rate was analyzed using a binomial GLMM with a logit link function. The best-fitted model had a year × crop × fertilization triple interaction. Crop yield was assessed using a Gaussian LMM with a logarithmic link function. The best-fitted model presented a crop type × year × tillage interaction.

3 Results and discussion

3.1 Growth pattern and phenology of winter wheat cultivars

In this study, we combined the primary modern cultivar, Florence-Aurora, with two traditional cultivars that exhibited complementary traits for aphid control, including cultivar odor profile and flour strength (Serra and Álvaro 2017; Tous-Fandos et al. 2023). Furthermore, we evaluated plant establishment, height, and phenology as crucial characteristics for weed infestation management and yield services (Costanzo and Bàrberi 2014; Lazzaro et al. 2018).

The mean wheat establishment was higher in 2019 than in 2021 ($F_{1,11} = 224.87$, $P < 0.001$). The mean wheat establishment values (mean ± SE) were 59.5 ± 3.1 and 34.6 ±

Table 2 Results from generalized linear mixed models (GLMM) relating four factors: crop type (W), year (Y), tillage (T), and fertilization (F) and wheat cover as a covariable. The table includes only the interactions found in the best models. The significance of fixed effect factors and their interactions was determined using an *F*-test with Kenward-Roger approximation for LMMs or a likelihood ratio test (LRT). Tillage, cultivar, and fertilization blocks were introduced as nested random factors. Wheat cover was included as a covariate in weed biomass, aphid abundance, and crop yield models. Only the best model for each response variable is presented.

Response variable	Crop type (W)	Year (Y)	Tillage (T)	Fertilization (F)	Wheat cover	$W \times Y$	$W \times T$	$W \times T \times Y$
Wheat establishment	$F_{3,9} = 51.12$ $P < 0.01$	$F_{1,11} = 224.87$ $P < 0.001$	$F_{1,11} = 2.17$ $P = 0.14$	$F_{1,11} = 0.22$ $P = 0.63$	-	-	-	-
Wheat cover	$F_{3,61} = 228.99$ $P < 0.001$	$F_{1,63} = 2778.12$ $P < 0.001$	$F_{1,63} = 36.60$ $P < 0.05$	$F_{1,63} = 26.60$ $P < 0.05$	-	-	-	-
Wheat height	$F_{1,63} = 4.14$ $P < 0.05$	-	$F_{1,63} = 0.11$ $P = 0.72$	$F_{1,63} = 3.18$ $P = 0.07$	-	-	-	-
Weed biomass	$F_{3,9} = 17.26$ $P < 0.001$	$F_{1,11} = 15.52$ $P < 0.001$	$F_{1,11} = 42.30$ $P < 0.001$	$F_{1,11} = 3.53$ $P = 0.06$	$F_{1,11} = 6.23$ $P < 0.05$	-	$F_{3,9} = 8.46$ $P < 0.05$	-
Weed richness	$F_{3,9} = 5.12$ $P = 0.09$	$F_{1,11} = 129.36$ $P < 0.001$	$F_{1,11} = 19.20$ $P < 0.001$	$F_{1,11} = 3.15$ $P = 0.14$	-	$F_{3,9} = 4.08$ $P = 0.11$		-
Aphid abundance	$\chi_{3,10} = 238.81$ $P < 0.001$	$\chi_{1,12} = 13.75$ $P < 0.001$	$\chi_{1,12} = 6.82$ $P < 0.05$	$\chi_{1,12} = 2.41$ $P = 0.08$	$\chi_{1,12} = 2.69$ $P = 0.10$	$\chi_{3,10} = 60.46$ $P < 0.001$	-	-
Parasitism rate	$F_{3,16} = 60.75$ $P < 0.001$	$F_{1,18} = 368.58$ $P < 0.001$	$F_{1,18} = 0.18$ $P = 0.67$	$F_{1,18} = 5.60$ $P = 0.14$	-	$F_{3,16} = 310.04$ $P < 0.001$	-	$F_{1,18} = 7.20$ $P = 0.08$
Number of aphids per FA tiller	$\chi_{1,5} = 68.50$ $P < 0.001$	$\chi_{1,5} = 11.10$ $P < 0.001$	$\chi_{1,5} = 5.94$ $P = 0.07$	$\chi_{1,5} = 0.06$ $P = 0.80$	-	-	-	-
Number of aphids per XE tiller	$\chi_{1,5} = 0.07$ $P = 0.78$	$\chi_{1,5} = 2.20$ $P = 0.15$	$\chi_{1,5} = 0.55$ $P = 0.41$	$\chi_{1,5} = 0.11$ $P = 0.60$	-	-	-	-
Number of aphids per FO tiller	$\chi_{1,5} = 1.25$ $P = 0.26$	$\chi_{1,5} = 5.65$ $P = 0.07$	$\chi_{1,5} = 1.09$ $P = 0.33$	$\chi_{1,5} = 0.15$ $P = 0.70$	-	-	-	-
Crop yield	$F_{3,61} = 7.80$ $P = 0.13$	$F_{1,63} = 11.24$ $P < 0.01$	$F_{1,63} = 9.31$ $P < 0.05$	$F_{1,63} = 23.61$ $P < 0.001$	$F_{1,63} = 17.84$ $P < 0.001$	$F_{3,61} = 15.73$ $P < 0.01$	$F_{1,63} = 4.68$ $P = 0.19$	$F_{1,63} = 4.71$ $P = 0.17$

6.0 individuals/m, respectively. Wheat establishment varied depending on the type of crop ($F_{3,9} = 51.12$, $P < 0.01$). The establishment of wheat in 2019 was similar across all crop treatments. However, in 2021, the FA wheat establishment was 21.4% lower than the other crop treatments.

Although wheat establishment was similar among cultivars, the crops showed varying levels of wheat cover before harvest. Wheat cover values (mean % ± SE) were 39.5 ± 3.1 in FA, 47.9 ± 3.6 in XE, 49.2 ± 3.5 in MIX, and 56.5 ± 3.8 in FO, with Florence-Aurora cover being significantly lower than Forment in both years ($F_{3,61} = 228.99$, $P < 0.001$). Therefore, the development of the wheat canopy varied among the different crops. These differences in wheat cover may lead to variations in aphid and weed pressure, affecting the ability of crops to respond to these stressors. Furthermore, wheat cover was significantly lower in every treatment in 2021 ($F_{1,63} = 2778.12$, $P < 0.001$). Finally, conventional tillage practices and fertilized treatments exhibited significantly higher wheat cover ($F_{1,63} = 36.60$, $P < 0.05$ and $F_{1,63} = 26.60$, $P < 0.05$, respectively).

Wheat cultivars differed in plant height ($F_{1,63} = 4.14$, $P < 0.05$). Specifically, the Florence-Aurora height (53.4 ± 2.7 cm) was significantly shorter than the Forment height (81.4 ± 4.5 cm) at harvest. Xeixa presented an intermediate height (62.5 ± 3.1 cm) (Figure 2). The height of the cultivars did not vary between individuals grown in monoculture and those grown in a mixture. This pattern suggests little intraspecific competition for light and nutrient resources, which is favorable for attaining high yields (Lavorel and Garnier 2002). Interestingly, neither tillage nor fertilization influenced plant height. Our data may suggest that soil management practices might not directly affect mixture performance, as cultivar target traits such as plant height and establishment remained consistent.

The phenological analysis indicated that Florence-Aurora is the earliest cultivar to reach flowering and grain ripening, followed by Xeixa and then Forment. The lag between Florence-Aurora and the other two cultivars was approximately 3 to 4 weeks for both flowering (Z61) and milk development (Z71), while between Xeixa and Forment, it was just 1 week.

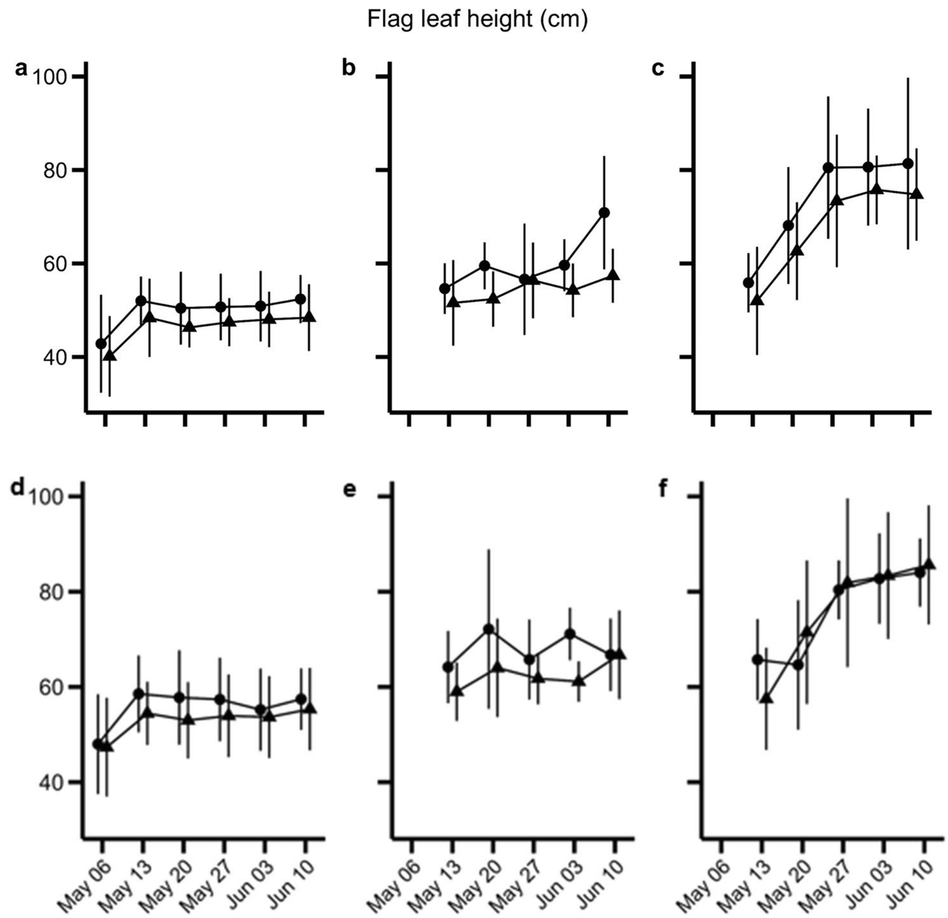

Fig. 2 Wheat cultivar flag leaf height (mean ± SE) from May to June 2019 compared between fertilization (fertilizer (F) and no fertilizer (NF)) and tillage (chisel (**a, b, c**) and moldboard (**d, e, f**)). Wheat cultivars: Florence-Aurora (**a, d**), Xeixa (**b, c**), and Forment (**c, f**).

All three cultivars reached ripeness, with grains hard and difficult to divide (Z91), within a week of each other (Figure SM 2). This synchronized ripening allows all three cultivars to be harvested simultaneously without complicating agricultural management (Di Bene et al. 2022).

3.2 Weed control service

In organic farming, controlling weeds is a significant concern for farmers. Reduced tillage practices help preserve biodiversity but can lead to weed infestations. Conversely, conventional tillage practices control weed infestations but threaten the diversity reservoir (Armengot et al. 2015; Baldivieso-Freitas et al. 2018). Moreover, we assessed the potential of the mixed wheat cultivar for weed management as an alternative to weed suppression while preserving weed species diversity.

The most common weed species identified throughout the two sampling seasons were as follows: *Chenopodium album* at 63.3%, *Fallopia convolvulus* at 17.2%, *Lolium rigidum* at 5.3%, *Polygonum aviculare* at 2.4%, and *Kickxia spuria* at 1.9% of the total plant abundance recorded. Weed species richness was significantly affected by year ($F_{1,11} = 129.36$, $P < 0.001$) and tillage ($F_{1,11} = 19.20$, $P < 0.001$) factors. Conventional tillage significantly reduced weed species richness in both years (4.8 ± 0.3 and 9.0 ± 0.3 species per sample in 2019 and 2021, respectively) in comparison to reduced tillage (7.0 ± 0.4 and 9.9 ± 0.4), emphasizing the importance of implementing reduced tillage practices to preserve weed diversity.

Weed abundance responded significantly to year ($F_{1,11}$= 15.52, $P < 0.001$), tillage ($F_{1,11} = 42.30$, $P < 0.001$), crop × tillage interaction ($F_{3,9} = 8.46$, $P < 0.05$), and wheat cover ($F_{1,11} = 6.23$, $P < 0.05$). In contrast, fertilization did not influence weed abundance ($F_{1,11} = 3.53$, $P = 0.06$). Weed abundance doubled in 2021. On the other hand, conventional tillage led to a 22.14% reduction in weed biomass in 2019 and a 19.89% reduction in 2021 compared to plots with reduced tillage. Weed abundance was similar across wheat monocultures and mixtures in 2019 but differed in 2021. Specifically, FA had a significantly higher weed abundance under reduced tillage than XE, FO, and MIX (Figure 3).

Soil management practices significantly impacted weed infestation, with tillage being the most influential factor. Previous studies have demonstrated that conventional tillage is efficient for weed control (Armengot et al. 2015; Baldivieso-Freitas et al. 2018; Sans et al. 2011). Furthermore, our findings indicate that soil nitrogen availability has a limited impact on weed control.

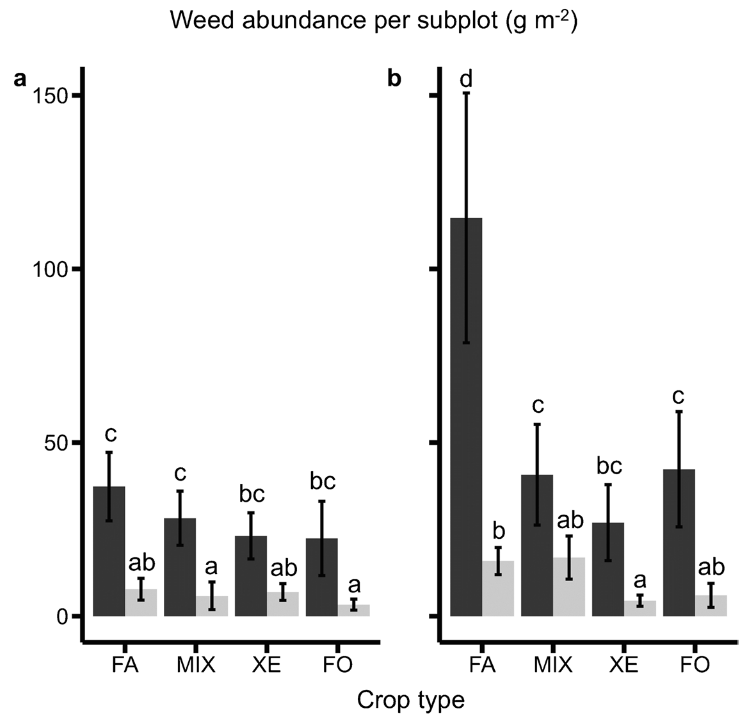

Fig. 3 Aboveground dry weed biomass per subplot (mean ± SE) at harvest time in 2019 (**a**) and 2021 (**b**) according to crop type (Florence-Aurora (FA), Xeixa (XE), and Forment (FO) monocultures and mixture (MIX)) and tillage (chisel (black bars) and moldboard (grey bars)) factors. Different letters above bars indicate statistically significant differences according to Tukey-adjusted pairwise EMMS comparisons ($P < 0.05$) within each year.

The provision of weed control by traditional cultivar monocultures or cultivar mixtures depended on tillage conditions. Crop type factor had a significant impact under higher weed infestation conditions caused by reduced tillage. Still, there were no differences between crop types under low weed infestation as caused by conventional tillage. Traditional taller cultivars presented greater wheat cover and were better at suppressing weeds than the modern and shorter Florence-Aurora cultivar, highlighting the importance of height as a plant trait for wheat cover and weed suppression (Lazzaro et al. 2018; Worthington et al. 2013). Moreover, this study represents the first time a three-cultivar wheat mixture has effectively controlled weeds in field conditions. Cultivar mixtures were more competitive against weeds than modern cultivar monoculture, likely due to the complementary heights and a more significant percentage of soil covered by wheat (Costanzo and Bàrberi 2014; Lazzaro et al. 2018). Contrary to Coleman et al.'s (2001) investigations, the early flowering Florence-Aurora did not provide weed-suppression benefits.

Our results were not consistent across sampling seasons. The wheat mixture effectively reduced weed infestation compared to the FA only during the 2020–2021 sampling season. In 2021, there were arid growing conditions, as the region experienced an approximately 80% reduction in rainfall. These conditions could account for the poorer crop establishment and wheat cover, especially in the case of the modern cultivar monoculture, leading to a higher weed infestation in FA plots. In this scenario, the combination of modern and traditional cultivars facilitates a stable wheat establishment and subsequent posterior wheat cover, which helps prevent high weed infestation.

3.3 Aphid control service

In this study, we also assessed the impact of soil management practices on aphid abundance and their possible influence on cultivar mixture efficacy for aphid control. During the two sampling seasons, we recorded a total of 39,275 aphid individuals on 3840 wheat tillers. The main aphid species were *Sitobion avenae* 83.67%, *Metopolophium dirhodum* 11.27%, and *Rhopalosiphum padi* 1.91%. Moreover, in the laboratory, we identified six parasitoid wasp genera, with *Aphidius* (48.34%) dominating as parasitoids and *Pachyneuron* (25.98%) and *Asaphes* (17.52%) genera as hyperparasitoids. The peak in aphid populations occurred in early May during both seasons, which coincided with the ear emergence phenology stage. This could be explained because the predominant aphid species, *Sitobion avenae*, generally colonizes cereal ears.

Aphid abundance showed significant differences according to year ($\chi_{1,12} = 13.75$, $P < 0.001$), crop ($\chi_{3,10} = 238.81$, $P < 0.001$), tillage factors ($\chi_{1,12} = 6.82$, $P < 0.05$), and crop × year interaction ($\chi_{3,10} = 60.46$, $P < 0.001$). Contrary to our expectations, neither fertilization ($\chi_{1,12} = 2.41$, $P = 0.08$) nor wheat cover ($\chi_{1,12} = 2.69$, $P = 0.10$) influenced aphid abundance. Aphid abundance was higher in 2021. Annual variation could be attributed to environmental stressors such as spring drought (see Table 1), which has also been found in similar field experiments (Mansion-Vaquié et al.

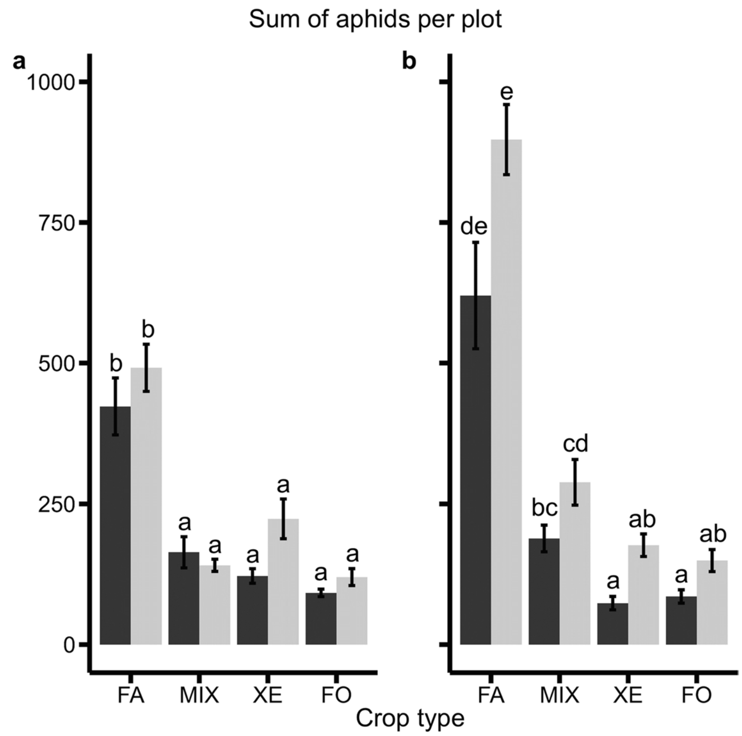

Fig. 4 Overall sum of aphids per subplot (mean ± SE) in 2019 (**a**) and 2021 (**b**) according to crop type (Florence-Aurora (FA), Xeixa (XE), and Forment (FO) monocultures and mixture (MIX)) and tillage (chisel (black bars) and moldboard (grey bars)) factors. Different letters above bars indicate significant differences according to Tukey-adjusted pairwise EMMS comparisons ($P < 0.05$) within each year.

2019). However, more importantly, FA exhibited a consistently greater aphid abundance when compared to XE, FO, or MIX in both sampling seasons. Furthermore, aphid abundance tended to increase with conventional tillage, although this trend was only significant in 2021 (Figure 4).

The number of aphids per tiller did not significantly impact tillage or fertilization. The number of aphids per tiller on Florence-Aurora tillers was significantly reduced in individuals grown in MIX ($\chi_{1,5}$= 68.50, $P < 0.001$), whereas the number of aphids per tiller of Xeixa and Forment tillers was not influenced by crop type ($\chi_{1,5} = 0.07$, $P = 0.78$ and $\chi_{1,5} = 1.25$, $P = 0.26$, respectively) (Figure 5).

The parasitism rate displayed significant differences between the 2 years ($F_{1,18} = 368.58$, $P < 0.001$), with a rate of 16.0 ± 1.2% in 2019 and 12.5 ± 0.7% in 2021. Moreover, crop type ($F_{3,16} = 60.75$, $P < 0.001$) and crop × year interaction ($F_{3,16} = 310.04$, $P < 0.001$) significantly affected the parasitism rate but did not show any pattern. For instance, in 2019, the FA parasitism rate was 22.4 ± 1.3% and MIX 19.2 ± 0.9% ($P < 0.001$), while in 2021, the rates were 9.0 ± 0.5% in FA and 11.3 ± 0.7% in MIX (P <0.01).

Our research indicates that soil management practices can affect the abundance of aphid populations. Higher aphid infestation in the conventional tillage treatment may be linked to the reduction in weed biomass and weed species diversity. This may lead to a reduction in within-field habitat quality for beneficial arthropods, such as aphid ground- and foliage-dwelling predators (Chabert and Sarthou 2020; Tamburini et al. 2016). Nonetheless, soil management practices did not influence the performance of traditional cultivar monocultures or cultivar mixtures concerning aphid control, as the cultivar mixture exhibited lower aphid populations compared to FA, irrespective of the tillage and fertilization.

The primary factor affecting aphid abundance was crop type (Costanzo and Bàrberi 2014; Tooker and Frank 2012). There was a notable difference in aphid susceptibility among cultivars, with the modern cultivar Florence-Aurora being more susceptible than the traditional cultivars Xeixa and Forment. Our research has shown that combining modern aphid-susceptible cultivars with aphid-resistant traditional cultivars can suppress aphids in the most susceptible cultivar (FA). However, in the other two cultivars, there was no effect. The number of aphids per tiller indicated that this control was likely achieved through associational resistance, as the Florence-Aurora plants grown in the mixture showed significantly lower infestations than the plants grown in monoculture. Associational resistance may have arisen because the selected cultivars had complementary functional traits, including distinct odor profiles that can attract or repel aphids (Tous-Fandos et al. 2023), as well as differences in height and plant nitrogen content (Ninkovic et al. 2016; Nowak and Komor 2010). Moreover, aphid-resistant cultivars, Forment and Xeixa, were taller than the susceptible cultivar, which may impede aphid host localization.

Finally, the inconsistency of the parasitism rate and the large variation between years suggests that crop type, fertilization, or tillage were not relevant to the parasitism rate. Also, contrary to our hypothesis, the decrease in aphid

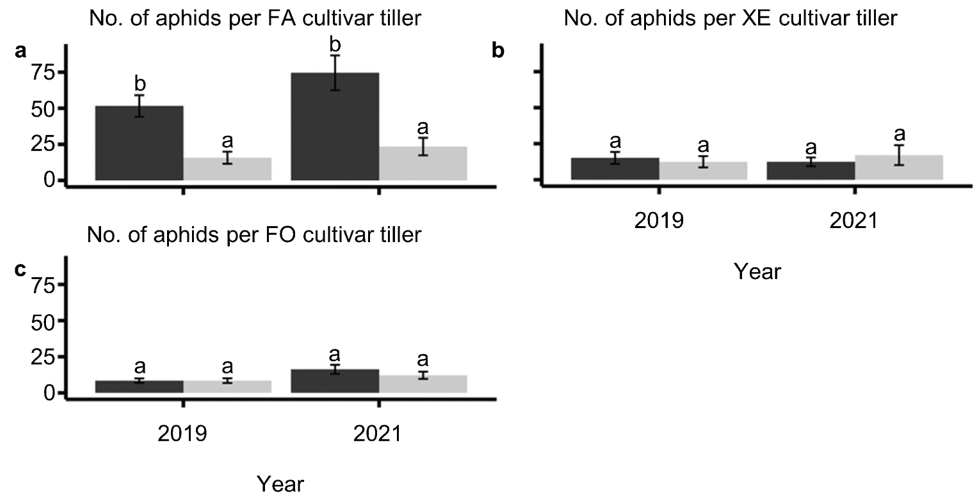

Fig. 5 Number of aphids per tiller (mean ± SE) at peak time on individual plants grown in monoculture (black bars) and cultivar mixture (grey bars) in 2019 and 2021. **a** Florence-Aurora cultivar, **b** Xeixa cultivar, and **c** Forment cultivar. Different letters above bars indicate statistically significant differences according to Tukey-adjusted pairwise EMMS comparisons ($P < 0.05$).

population in the cultivar mixture was not likely related to the parasitism rate. This supports the idea that associative resistance is the primary strategy for controlling aphids, as has been found in other systems (Koricheva and Hayes 2018).

3.4 Crop yield service

This paper examines the performance of modern and traditional wheat cultivar monocultures and wheat cultivar mixtures sown under different management practices in field conditions. Our objective was to develop practical and attractive cropping systems for farmers to implement in actual farming. To achieve this, we evaluated crop yield, as it is the most relevant variable for farmers when implementing diversity-related strategies. Moreover, we grouped together wheat cultivars that have similar crop husbandry needs and are used for similar commercial purposes. This area has been widely overlooked in relevant literature thus far, as suggested by Di Bene et al. (2022).

Similar to wheat establishment and wheat cover, crop yield was significantly lower in 2021 ($F_{1,63}$ = 11.24, $P <$ 0.01), most likely caused by differences in rainfall, which is known to be one of the main drivers of yield in the Mediterranean region (Basso et al. 2012; Gandía et al. 2021). Fertilization emerged as the primary factor affecting wheat yield ($F_{1,63}$ = 23.61, $P < 0.001$), resulting in a 9% difference in 2019 and a 29% difference in 2021 compared to nonfertilized plots. Conventional tillage increased wheat yield in both years, showing a significant impact in 2021 ($F_{1,63}$ = 9.31, $P < 0.05$). Predictably, wheat cover had a positive correlation with yield ($F_{1,63}$ = 17.84, $P < 0.001$). In general, the three monocultures and the mixture had similar yields ($F_{3,61}$ = 7.80, P = 0.13). However, traditional cultivar monocultures XE and FO exhibited significantly higher yields under nonfertilized and reduced tillage conditions compared to the modern cultivar FA. Furthermore, FA and MIX yields were affected by tillage and fertilization, leading to lower yields in non-fertilized and reduced tillage plots (Figure 6).

Soil management practices significantly affected crop yield. Supporting prior research, fertilization was a limiting factor for optimal wheat yield in organic Mediterranean fields, possibly due to low wheat nitrogen use efficiency in calcareous soils (Baldivieso-Freitas et al. 2018; Diacono et al. 2019; Tamburini et al. 2016). Additionally, reduced tillage resulted in decreased crop yield, likely due to a temporary delay in nitrogen mineralization, leading to a nitrogen deficit in early spring that impacts yield (Mäder and Berner 2012).

The yield of modern Florence-Aurora monoculture and cultivar mixtures depended on tillage and fertilization. The highest yields were obtained under conventional management. In contrast, traditional cultivar monocultures remained unaffected by soil management practices. These differences can be explained by the significant reliance of modern cultivars on external inputs and their poor performance driven by weed infestation and nitrogen shortage, which are common in organic crops in the Mediterranean region (Baldivieso-Freitas et al. 2018; Lazzaro et al. 2018; Reiss and Drinkwater 2018; Worthington et al. 2013).

Nevertheless, the LER analysis indicates that the cultivar mixture has neutral or limited benefits in terms of yield. LER values varied depending on tillage practices and fertilization, ranging from 0.90 in 2021 under conventional tillage practices without fertilization to 1.19 in 2021 under reduced tillage practices with fertilization. These findings are consistent with previous studies that did not show yield improvement on wheat cultivar mixtures over monocultures (Lazzaro et al. 2018; Mansion-Vaquié et al. 2019). Under reduced tillage and without fertilization, the

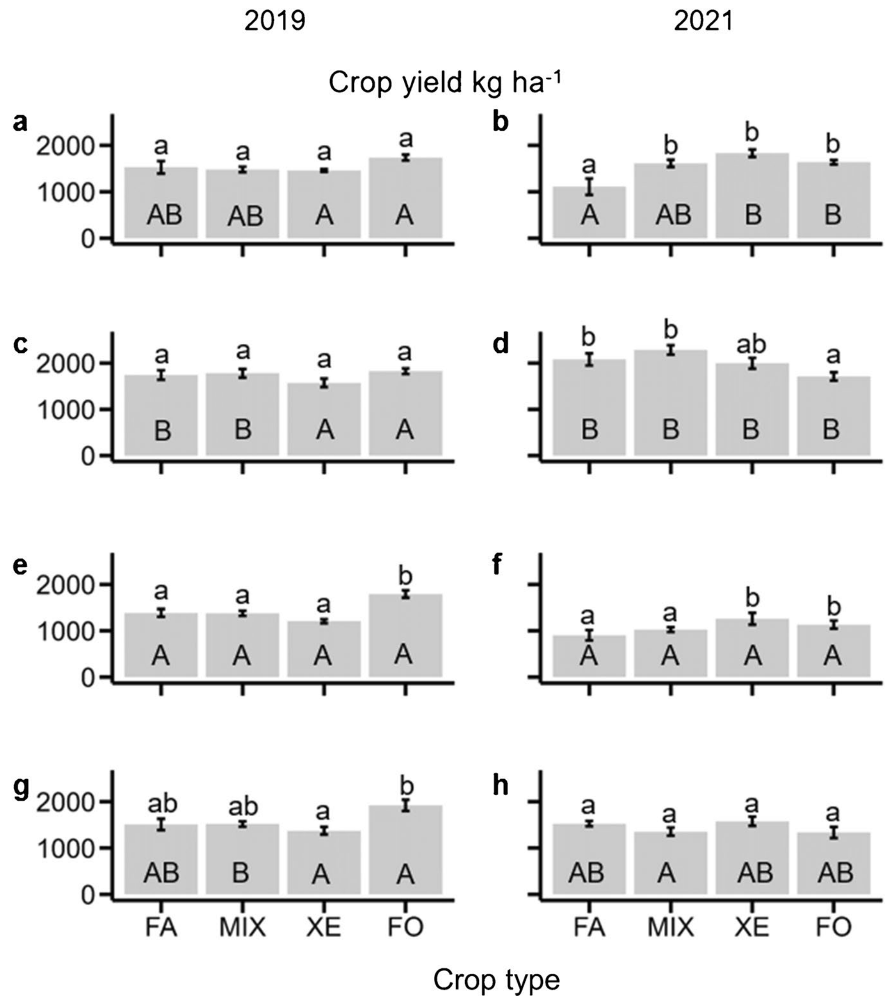

Fig. 6 Wheat yield (mean ± SE) of the different crop types (Florence-Aurora (FA), Xeixa (XE), and Forment (FO) monocultures and their mixture (MIX)) in 2019 (**a, c, e, g**) and 2021 (**e, d, f, h**). **a, b** Crop yield under reduced tillage practices and with fertilization. **c, d** Crop yield under conventional tillage practices and with fertilization. **e, f** Crop yield under reduced tillage practices and without fertilization. **g, h** Crop yield under conventional tillage practices and without fertilization. Lowercase letters denote significant differences within crop types (rows) according to Tukey-adjusted pairwise EMMS comparisons ($P < 0.05$) within each treatment, separately for each year. Capital letters indicate significant differences within columns ($P < 0.05$) for each crop type across the four tillage and fertilization treatments. Each year was analyzed independently.

LER was higher than 1.0 in both years (1.03 and 1.01). This indicates that traditional varieties may offer benefits such as weed suppression or tolerance to soil nitrogen deficiency, resulting in increased yield stability (Reiss and Drinkwater 2018).

4 Conclusions

The aim of this study was to assess the effect of a triple wheat cultivar mixture on weed and aphid control, as well as yield stability under different tillage intensity and fertilization conditions. Our study demonstrated that Florence-Aurora, Xeixa, and Forment wheat cultivars presented different height, phenology, and aphid susceptibility. We found that mixing wheat cultivars with distinguished traits had several advantages over the modern cultivar monoculture (Florence-Aurora) due to the functions offered by the traditional cultivars (Xeixa and Forment). In this respect, the cultivar mixture provided aphid control through associational resistance and weed suppression while maintaining weed diversity. Furthermore, for the first time, we proved that soil management practices influence the performance of wheat monocultures and mixtures. In particular, Florence-Aurora monoculture and the mixture yield were affected by tillage and fertilization, being lower under chisel tillage and non-fertilized plots. Therefore, this study emphasizes the importance of conducting field experiments to evaluate how agronomic factors in real farming settings might impact the functionality of cereal mixtures.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13593-024-00996-y.

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Authors' contributions FXSS, LCL, and JMBM conceptualized and designed the study. DB and ATF performed material preparation and data collection, while JMBM and ATF analyzed the data. ATFs wrote the first draft of the manuscript, and all authors commented on previous versions. All the authors have read and approved the final manuscript.

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Data availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Code availability The code for data cleaning and analysis associated with the current study is available from the corresponding author on reasonable request.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.

References

Altieri MA, Rogé P (2009) The ecological role and enhancement of diversity in agriculture. In Agriculture, Biodiversity and Markets Livelihoods and Agroecology. In: Comparative Perspective. Earthcan; London, Washington DC, pp. 15–31. ISBN: 9780415507356 https://doi.org/10.1016/S0167-8809(99)00028-6

Aqueel MA, Leather SR (2011) Effect of nitrogen fertilizer on the growth and survival of *Rhopalosiphum padi* (L.) and *Sitobion avenae* (F.) (Homoptera: Aphididae) on different wheat cultivars. Crop Prot 30:216–221. https://doi.org/10.1016/j.cropro.2010.09.013

Armengot L, Berner A, Blanco-Moreno JM, Mäder P, Sans FX (2015) Long-term feasibility of reduced tillage in organic farming. Agron Sustain Dev 35:339–346. https://doi.org/10.1007/s13593-014-0249-y

Baldivieso-Freitas P, Blanco-Moreno JM, Armengot L, Chamorro L, Romanyà J, Sans FX (2018) Crop yield, weed infestation and soil fertility responses to contrasted ploughing intensity and manure additions in a Mediterranean organic crop rotation. Soil till Res 180:10–20. https://doi.org/10.1016/j.still.2018.02.006

Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. Annu Rev Ecol Evol S 12:1–20. https://doi.org/10.1146/annurev.ecolsys.110308.120242

Barot S, Allard V, Cantarel A, Enjalbert J, Gauffreteau A, Goldringer I, Lata JC, 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 37:1–20. https://doi.org/10.1007/s13593-017-0418-x

Basso B, Fiorentino C, Cammarano D, Cafiero G, Dardanelli J (2012) Analysis of rainfall distribution on spatial and temporal patterns of wheat yield in Mediterranean environment. Eur J Agron 41:52–65. https://doi.org/10.1016/j.eja.2012.03.007

Bonnet C, Gaudio N, Alletto L, Raffaillac D, Bergez JE, Debaeke P, Justes E (2021) Design and multicriteria assessment of low-input cropping systems based on plant diversification in southwestern France. Agron Sustain Dev 41:1–19. https://doi.org/10.1007/s13593-021-00719-7

Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. Ecology 73:1045–1055. https://doi.org/10.2307/1940179

Borg J, Kiaer LP, Lecarpentier C, Goldringer I, Gauffreteau A, Saint-Jean S, Barot S, Enjalbert J (2018) Unfolding the potential of wheat cultivar mixtures: a meta-analysis perspective and identification of knowledge gaps. Field Crop Res 221:298–313. https://doi.org/10.1016/j.fcr.2017.09.006

Brooks ME, Kristensen K, Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. https://doi.org/10.32614/RJ-2017-066

Chabert A, Sarthou JP (2017) Practices of conservation agriculture prevail over cropping systems and landscape heterogeneity in understanding the ecosystem service of aphid biocontrol. Agric Ecosyst Environ 249:70–79. https://doi.org/10.1016/j.agee.2017.08.005

Chabert A, Sarthou JP (2020) Conservation agriculture as a promising trade-off between conventional and organic agriculture in bundling ecosystem services. Agric Ecosyst Environ 292:106815. https://doi.org/10.1016/j.agee.2019.106815

Coleman RK, Gill GS, Rebetzke GJ (2001) Identification of quantitative trait loci for traits conferring weed competitiveness in wheat (*Triticum aestivum* L.). Aust J Agr Res 52:1235–1246. https://doi.org/10.1071/AR01055

Costanzo A, Bàrberi P (2014) Functional agrobiodiversity and agroecosystem services in sustainable wheat production. A review. Agron Sustain Dev 34:327–348. https://doi.org/10.1007/s13593-013-0178-1

Dainese M, Martin EA, Aizen MA, Albrecht M, Bartomeus I, Bommarco R, Carvalheiro LG, Chaplin-Kramer R, Gagic V, Steffan-Dewenter I (2019) A global synthesis reveals diversity-mediated benefits for crop production. Sci Adv 10:1–14. https://doi.org/10.1126/sciadv.aax0121

Dedryver CA, Le Ralec A, Fabre F (2010) The conflicting relationships between aphids and men: a review of aphid damage and control strategies. CR Biol 333:539–553. https://doi.org/10.1016/j.crvi.2010.03.009

Di Bene C, Dolores GLM, Francaviglia R, Farina R, Blasi E, Martínez-Granados D, Calatraba J (2022) Barriers and opportunities for sustainable farming practices and crop diversification strategies in Mediterranean cereal-based systems. Front Environ Sci 10:861225. https://doi.org/10.3389/fenvs.2022.861225

Diacono M, Baldivieso-Freitas P, Sans Serra FX (2019) Nitrogen utilization in a cereal-legume rotation managed with sustainable agricultural practices. Agronomy 9:113. https://doi.org/10.3390/agronomy9030113

Ficiciyan A, Loos J, Sievers-Glotzbach S, Tscharntke T (2018) More than yield: ecosystem services of traditional versus modern crop varieties revisited. Sustain Sci 10:2834. https://doi.org/10.3390/su10082834

Gaba S, Lescourret F, Boudsocq S, Enjalbert J, Hinsinger P, Journet EP, Navas ML, Wery J, Louarn G, Malézieux E, Pelzer E, Prudent M, Ozier-Lafontaine H (2015) Multiple cropping systems as drivers for providing multiple ecosystem services: from concepts to design. Agron Sustain Dev 35:607–623. https://doi.org/10.1007/s13593-014-0272-z

Gandía ML, Del Monte JP, Tenorio JL, Santín-Montanyá MI (2021) The influence of rainfall and tillage on wheat yield parameters and weed population in monoculture versus rotation systems. Sci Rep 11:22138. https://doi.org/10.1038/s41598-021-00934-y

Gibson AK, Nguyen AE (2021) Does genetic diversity protect host populations from parasites? A meta-analysis across natural and agricultural systems. Evol Lett 5:16–32. https://doi.org/10.1002/evl3.206

Glinwood R, Ahmed E, Qvarfordt E, Ninkovic V, Pettersson J (2009) Airborne interactions between undamaged plants of different cultivars affect insect herbivores and natural enemies. Arthropod-Plant Inte 3:215–224. https://doi.org/10.1007/s11829-009-9072-9

Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa Accessed 20 Apr 2024.

Koricheva J, Hayes D (2018) The relative importance of plant intraspecific diversity in structuring arthropod communities: a meta-analysis. Funct Ecol 32:1704–1717. https://doi.org/10.1111/1365-2435.13062

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct Ecol 16:545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lazzaro M, Costanzo A, Bàrberi P (2018) Single vs multiple agroecosystem services provided by common wheat cultivar mixtures: weed suppression, grain yield and quality. Field Crop Res 221:277–297. https://doi.org/10.1016/j.fcr.2017.10.006

Lenth R (2019) emmeans: estimated marginal means, aka least-squares means. R package version 1.3.4. https://CRAN.R-project.org/package=emmeans Accessed 20 Apr 2024.

Mäder P, Berner A (2012) Development of reduced tillage systems in organic farming in Europe. Renew Agr Food Syst 27:7–11. https://doi.org/10.1017/S1742170511000470

Mansion-Vaquié A, Ferrante M, Cook SM, Pell JK, Lövei GL (2017) Manipulating field margins to increase predation intensity in fields of winter wheat (*Triticum aestivum*). J Appl Entomol 141:600–611. https://doi.org/10.1111/jen.12385

Mansion-Vaquié A, Wezel A, Ferrer A (2019) Wheat genotypic diversity and intercropping to control cereal aphids. Agric Ecosyst Environ 285:106604. https://doi.org/10.1016/j.agee.2019.106604

Ninkovic V, Abassi SA, Ahmed E, Glinwood R, Pettersson J (2011) Effect of within-species plant genotype mixing on habitat preference of a polyphagous insect predator. Oecologia 166:391–400. https://doi.org/10.1007/s00442-010-1839-2

Ninkovic V, Markovic D, Dahlin I (2016) Decoding neighbour volatiles in preparation for future competition and implications for tritrophic interactions. Perspect Plant Ecol 23:11–17. https://doi.org/10.1016/j.ppees.2016.09.005

Nowak H, Komor E (2010) How aphids decide what is good for them: experiments to test aphid feeding behaviour on *Tanacetum vulgare* (L.) using different nitrogen regimes. Oecologia 163:973–984. https://doi.org/10.1007/s00442-010-1652-y

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ Accessed 10 Sep 2022.

Reiss ER, Drinkwater LE (2018) Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. Ecol Appl 28:62–77. https://doi.org/10.1002/eap.1629

Rodriguez-Saona CR, Stelinski LL (2009) Behavior-modifying strategies in IPM: theory and practice. In: Integrated Pest Management: Innovation-Development Process; Springer, Dordrecht,pp. 263–315. ISBN: 978-1-4020-8991-6 https://doi.org/10.1007/978-1-4020-8992-3_11

Sans FX, Berner A, Armengot L, Mäder P (2011) Tillage effects on weed communities in an organic winter wheat–sunflower–spelt cropping sequence. Weed Res 51:413–421. https://doi.org/10.1111/j.1365-3180.2011.00859.x

Serra-Gironella J, Álvaro F (2017) *Varietats de blat panificables tradicionals i modernes*. 5è Simposi de Producció Agroalimentària Ecològica de Conreus extensius ecològics. IRTA, Manresa, Spain

Serra J, Doltra J, Sayeras R, Fañé J (2019) Sembra de barreges de varietats de blat. Publishing Extensius.cat. https://extensius.cat/2019/11/18/sembra-de-barreges-de-varietats-de-blat-tou/ Accessed 18 Nov 2019

Shoffner AV, Tooker JF (2013) The potential of genotypically diverse cultivar mixtures to moderate aphid populations in wheat (*Triticum aestivum* L.). Arthropod-Plant Inte 7:33–43. https://doi.org/10.1007/s11829-012-9226-z

Tamburini G, De Simone S, Sigura M, Boscutti F, Marini L (2016) Soil management shapes ecosystem service provision and trade-offs in agricultural landscapes. P Roy Soc B-Biol Sci 283:20161369. https://doi.org/10.1098/rspb.2016.1369

Tamburini G, Bommarco R, Wanger TC, Kremen C, Van Der Heijden MG, Liebman M, Hallin S (2020) Agricultural diversification promotes multiple ecosystem services without compromising yield. Sci Adv 6(45). https://doi.org/10.1126/sciadv.aba1715

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. Annu Rev Ecol Evol S45:471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tooker JF, Frank SD (2012) Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. J Appl Ecol 49:974–985. https://doi.org/10.1111/j.1365-2664.2012.02173.x

Tous-Fandos A, Gallinger J, Enting A, Chamorro-Lorenzo L, Sans Serra FX, Ninkovic V (2023) Alterations in the odor profile of plants in cultivar mixtures affect aphid host-location behavior. Front Plant Sci 14:1186425. https://doi.org/10.3389/fpls.2023.1186425

Wezel A, Casagrande M, Celette F, Vian JF, Ferrer A, Peigné J (2014) Agroecological practices for sustainable agriculture. A review. Agron Sustain Dev 34:1–20. https://doi.org/10.1007/s13593-013-0180-7

Willey RW, Rao MR (1980) A competitive ratio for quantifying competition between intercrops. Exp Agr 16:117–125. https://doi.org/10.1017/S0014479700010802

Worthington ML, Reberg-Horton SC, Jordan D, Murphy JP (2013) A comparison of methods for evaluating the suppressive ability of winter wheat cultivars against Italian ryegrass (*Lolium perenne*). Weed Sci 61:491–499. https://doi.org/10.1614/ws-d-12-00167.1

Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Res 14:415–421. https://doi.org/10.1111/j.1365-3180.1974.tb01084.x