Field Crops Research 340 (2026) 110291

Contents lists available at ScienceDirect

Field Crops Research

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

Mixed cropping of narrow-leaved lupin and oat enhances plant health and yield buffering while maintaining protein yield

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ARTICLE INFO

Keywords:
Narrow-leaved lupin
Mixed cropping
Oat
Protein yield
Food safety

ABSTRACT

Context and objectives: Diversifying arable systems with pulse-cereal mixtures can stabilise yield and reduce external inputs, yet performance data for narrow-leaved lupin (NLL, *Lupinus angustifolius* L.)–oat combinations remain scarce, especially for grain quality and protein yield. We investigated whether NLL–oat mixed cropping influences plant health and development, weed suppression, grain and protein yield, and yield quality relative to pure stands.
Methods: Within a two-year randomised complete-block field experiment at two Swiss sites, the performance of three spring-NLL varieties (Lunabor, Probor, Jowisz) and three spring-oat varieties (Bison, Lion, Troll) grown in pure and pairwise mixed stands was compared. Agronomic, health and quality traits were recorded. Linear mixed-effects models with contrast tests estimated treatment and varietal effects.
Results and conclusions: Mixed cropping significantly reduced cereal leaf beetle incidence in oats by 41 % with Lion and by 46 % with Troll. Weed volumes in mixed NLL treatments decreased by up to 87 %. Oat yield in mixtures exceeded the expected performance based on their sowing ratio, while their quality increased with regards to elevated protein content and hectolitre weight. NLL yield remained stable or was slightly reduced, while maintaining their crop quality, including their high protein contents. Lunabor mixed with Troll showed a significantly elevated land use efficiency, while all other combinations remained stable across pure and mixed stands. This buffering also applied to their protein yield. Further, mixed cropping had no effect on attributes such as plant developmental stages, height in late growth stages, and oat tiller numbers. The absence of a mixed cropping response underscores the potential for forecasting mixture performance based on monoculture data.
Significance: NLL–oat mixtures improved pest control, weed suppression and yield buffering without compromising total protein yield or land use efficiency. The investigated system offers a low-input approach to sustainable intensification. Because most structural traits were mixture-neutral, monoculture data can reliably be used to predict mixture performance.

1. Introduction

Agricultural systems act as drivers of climate change, through greenhouse gas emissions and land-use change, and simultaneously as sensitive receptors threatening their resilience and productivity (IPCC, 2019). One strategy to mitigate this bidirectional impact is to diversify agricultural production (Lin, 2011). By incorporating a wider range of crops alongside the primary staples, diversification enhances the resilience of agricultural systems to climate extremes (Renard and Tilman, 2019). Different crops exhibit varying physiological and ecological responses to abiotic and biotic stress factors, reducing the system's overall vulnerability and leading to greater yield stability compared with monoculture systems (Gaudin et al., 2015).

Amongst the macronutrients fats, carbohydrates and proteins, the latter are the ones that require the highest amount of energy to be synthesised per weight unit (Tegeder and Masclaux-Daubresse, 2018). This high energy expenditure is attributed to the high nitrogen content of proteins, and the energy-intensive metabolic pathways in the plant required to produce amino-acids (Hildebrandt et al., 2015). Additionally, producing nitrogen in an accessible form, either through the Haber-Bosch synthesis or the nitrogen-fixation, requires large amounts of energy (Erisman et al., 2008; Vitousek et al., 2013).

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https://doi.org/10.1016/j.fcr.2025.110291
Received 3 September 2025; Received in revised form 5 December 2025; Accepted 8 December 2025

Despite these costs to protein production, the global protein demand is still rising and expected to grow at a rate of 8 % per annum, which implies further sustainable protein sources need to be opened (Aschemann-Witzel et al., 2021; Kim et al., 2019). In light of agricultural diversification and a growing protein demand, narrow-leaved lupins (NLL, *Lupinus angustifolius*) can play a relevant role in producing large amounts of sustainable protein (Lucas et al., 2015). NLL contain up to 40 % of high-quality protein in their harvested grains, and their protein exhibits a high biological value for human consumption, which is comparable to that of soybean (Muranyi et al., 2016; Roman et al., 2023; Sedláková et al., 2016). NLL obtain a large proportion of their protein-bound nitrogen from the atmosphere. On average, they fix 230 kg·ha^{-1} atmospheric nitrogen and were documented to obtain above 90 % of their nitrogen demand from atmospheric nitrogen (Evans et al., 1987; Pálmason et al., 1992). Thus, NLL produce high amounts of quality-protein coupled to a low climate-impact.

In addition to diversifying agricultural production through the incorporation of different crop species, diversification can also be achieved by varying the production system itself. A successful approach thereto is to implement annual mixed crops, where multiple species are co-cultivated in the same field. This type of intercropping was shown to result in more stable yield, compared with their monoculture equivalents (Huang et al., 2024; Raseduzzaman and Jensen, 2017). Mixed cropping, the spatiotemporally coincident cultivation of more than one crop in the same field has proven oneself to be an intercropping system that is particularly suitable to mechanised agriculture, since sowing, field management and harvesting can be performed in the same fashion as with monocrops (Mousavi and Eskandari, 2011).

Particular attention has been drawn to the annual mixed cropping of pulses with cereals, a combination of crop families which leads to mutual benefit for both crops cultivated (Kumawat et al., 2022; cited in Landschoot et al., 2024). These mixed crops exhibit a positive complementarity effect and elevated land use efficiencies, which arises when the mutual resource acquisition is greater than what would be expected from their respective monocrops (Li et al., 2020; Yu et al., 2015). The resources used more efficiently by the pulse–cereal mixed crops include soil nutrients and photosynthetically active radiation. This increased efficiency is explained by the crops' different shoot and root architectures (Kumawat et al., 2022; Loreau and Hector, 2001; Oelbermann et al., 2015). Recent trait-based work further suggests that mixture performance benefits when canopy architectures are well matched (e.g. limited height asymmetry), a consideration directly relevant to pulse–cereal, inclding the NLL–oat systems (MacLaren et al., 2023).

The improvement in productivity of pulse–cereal mixed crops is also accompanied by healthier crops with regards to pest, disease and weed pressure (Trenbath, 1993). The underlying mechanism leading to reduced pest pressures is assumed to be owed to increased abundance of predators and parasites, as well as the host dilution effect through mixed cropping with another non-host species (Andow, 1991; Kumawat et al., 2022). As a result, mixed crops exhibited lower pest infestations in 52 %, and higher infestations in 15 % of the reported studies, compared with monocrops (Andow, 1991). In contrast, the trends with diseases are less clear (Kumawat et al., 2022). While the magnitude and direction of this trend varies depending on the specific mixed cropping system, diseases involved, and environmental conditions, pulse–cereal mixed cropping generally still decreased the disease infection by reducing their incidence and spread (Finch and Collier, 2000; Hauggaard-Nielsen et al., 2008; Malézieux et al., 2009; Tooker and Frank, 2012). Lastly, weed pressure was consistently lower in pulse-cereal mixed crops than in their respective pulse monocrops, and in 52 % of the studied cases, it lay below their respective cereal monocrops Huang et al. (2024). Hence, these resource and host dilution effects explain, why in 74 % of recorded cases, pulse–cereal mixed crops exhibit equal or better health and yields than their monocrop equivalent, and why pulse–cereal mixed crops are the most common mixed cropping system applied (Rao et al., 1987; Verret et al., 2017).

Pulse–cereal mixed crops with oats as cereal partner are common, and particularly stand out due to the oats strong capacity to suppress weeds and the oats' advantage in crop rotation to allows for a subsequent cereal cultivation (e.g. Gronle et al., 2015; Staniak et al., 2014; Wang et al., 2012). Within this broad class, NLL–oat mixtures are agronomically distinctive: oats' early vigour and weed-suppressive behaviour complement NLL's relatively slow early growth, both partners share cool-season phenology, and the combination offers practical advantages for mechanised harvest in temperate systems (Gresta et al., 2017; Kato-Noguchi et al., 1994). Despite this potential, varietal matching and quality outcomes in NLL–oat remain underexplored compared with major cereal–pulse pairs, which heightens the relevance of dedicated NLL–oat evaluations. A multitude of meta-analyses and reviews evaluate the on-field characteristics and post-harvest performances of pulse–cereal mixed crops, however, less information is available on quality metrics of the crop yield in mixed cropping systems (Liu et al., 2023). With regards to the protein yield, one meta-analysis by Li et al. (2023) concluded that the protein yield of mixed crops remained stable, compared with the more productive monocrop, given no nitrogen fertiliser was supplied. Similarly, two studies by Begna et al., 2021 and Liu et al., 2023 assessed the forage quality of pulse–cereal mixed crops, concluding either equivalent or improved feed quality in mixed crops compared with their monocrop equivalents, respectively, which is partially also owed to the high protein yield of the pulses (Begna et al., 2021; Liu et al., 2023). Lastly, Bedoussac and Justes (2010) as well as Lauk and Lauk (2006) reported elevated grain protein contents in durum wheat mixed cropped with pulses, whereas Hauggaard-Nielsen et al. (2008) could not detect any effect on the barley protein content when mixed cropped with NLL.

A large body of evidence thus supports the implementation of pulse–cereal mixed crops, and many aspects of mixed cropping have been thoroughly assessed for main crops, which includes wheat, pea and maize (Landschoot et al., 2024). However, studies on minor crops, such as NLL–oat mixed crops are more limited (Kumawat et al., 2022; Li et al., 2023). Furthermore, Dourmap et al. (2025) pointed out the need to perform more mixed cropping research on lupins to unfold their full potential in the agricultural production system. Integrating studies that evaluate and connect field performance, productivity and yield quality of mixed cropping are underrepresented (e.g. Hauggaard-Nielsen et al., 2008), and to the best knowledge of the authors, no study has assessed these parameters across multiple NLL–oat variety combinations yet (Landschoot et al., 2024).

With the focus on the world's rising protein demand, pulse-centric mixed cropping systems require stronger attention. Evidence from mixed cropping designs in which the pulse is nearly maintained at its full sole-crop density and a cereal companion is introduced at a low rate shows that such systems can deliver key agronomic functions while prioritising legume output: in organic field pea mixtures with barley, oats or mustard sown at graduated companion rates, mixed crops consistently suppressed weed biomass, with oats being the most suppressive. These outcomes indicate that low-share cereals can act as effective nurse crops without displacing the pulse as the principal product (Bailey-Elkin et al., 2022). For pulse–cereal systems aimed at grain-protein supply, this pulse-centric logic offers a tractable route to align land use efficiency, crop health and protein yield under reduced external nitrogen inputs.

The current study jointly evaluates on-field performance, productivity metrics and yield quality across multiple NLL–oat variety mixed crops and compares them with their respective monocrops. Compared with the monocrops, we expect the mixed crops to

- have lower weed, pest and disease pressure, i.e. the plants are healthier
- show equal growth patterns (plant height or growth stage) as their monocrops
- exhibit equal or improved land use efficiency and productivity

- produce equal or higher amounts of protein per land area, and
- display equal or improved quality parameters (such as thousand kernel weight).

2. Methods

2.1. Varieties

Three branching spring narrow-leaved lupin (NLL) and three spring oat varieties were chosen based on the breeders' fact sheets and the variety list of the German variety institute (Bundessortenamt, 2021). Branching, spring NLL and early-maturing spring oat varieties were selected to increase the probability of coincidental ripening. The selected NLL varieties were

- Lunabor, bred by Saatzucht Steinach in Germany
- Probor, bred by Saatzucht Steinach in Germany
- Jowisz (synonym: Jupiter), bred by HR Smolic in Poland

And the selected, early maturing spring oat varieties were

- Bison, bred by Hauptsaaten für die Rheinprovinz GmbH in Germany, medium tall
- Lion, bred by Nordsaat Saatzucht GmbH in Germany, medium tall
- Troll, bred by Saatzucht Bauer GmbH & Co. KG in Germany, short

2.2. Treatments and experimental design

The NLL and oat varieties were cultivated as spring crops in pure and mixed stands. In the mixed stands, each NLL variety was co-cultivated with each oat variety in a replacement design. The NLL were sown at 90 % of their pure stand's density, whereas the oats, due to their high competitiveness, were sown at 10 % of their pure stand's density (Böhm et al., 2008; Kato-Noguchi et al., 1994) (Table 1). The sowing amounts were adapted to the germination rate evaluated two weeks before sowing. The germination rate was evaluated according to the international seed testing association (ISTA) protocol. Pure oat stands were fertilised with 27.5 – 30 kgN·ha^{-1} N in a single application during early stem elongation. The applied rate was adjusted according to the measured plant-available soil N and was consistent with local recommendations, which specify a total of 90 kgN·ha^{-1} of available N. Mixed stands were not fertilised (Table 2).

The fields of this two-year study were arranged as a randomised complete block design (RCBD), consisting of four blocks. To lower the border effect to a minimum, each treatment was sown in three adjacent plots and only the middle plot was scored and harvested. The size of each harvested plot was seven square metres (Fig. 1).

Table 1
Treatments of the study: Narrow-leaved lupin and oat varieties, the stand (pure versus mixed), sowing ratios, respective sowing densities and corresponding amount of seeds per hectare (corrected to a 90 % germination rate). For the two numbers present in the mixed treatments, the first one refers to narrow-leaved lupins, the second one to oats.

Varieties	Stand	Sowing ratios (%)	Sowing density (plants·m^{-2})	Amount (kg·ha^{-1})
Bison	pure	100	300	168
Lion	pure	100	300	121
Troll	pure	100	300	110
Lunabor	pure	100	120	220
Probor	pure	100	120	170
Jowisz	pure	100	120	214
Lunabor + Bison	mixed	90, 10	108 / 30	198 / 17
Lunabor + Lion	mixed	90, 10	108 / 30	198 / 12
Lunabor + Troll	mixed	90, 10	108 / 30	198 / 11
Probor + Bison	mixed	90, 10	108 / 30	153 / 17
Probor + Lion	mixed	90, 10	108 / 30	153 / 12
Probor + Troll	mixed	90, 10	108 / 30	153 / 11
Jowisz + Bison	mixed	90, 10	108 / 30	193 / 17
Jowisz + Lion	mixed	90, 10	108 / 30	193 / 12
Jowisz + Troll	mixed	90, 10	108 / 30	193 / 11

2.3. Site, husbandry and weather data

The sites of both years were located in the same two areas in the canton of Zurich (Switzerland), Seegräben and Reckenholz, and were chosen based on their differing soil properties. The soils in Seegräben were sandy without free calcium, and pH values ranging between 6 and 6.5. The soils in Reckenholz were loamy clay, containing some free calcium (Table 2), and pH values ranged from 6.8 to 7. The sites differing in pH value and free calcium were chosen on purpose to account for the NLLs sensitivity thereto (Ding et al., 2019). Table 2 provides an overview of the sites and dates of relevant husbandry measures. The fields were ploughed three weeks and harrowed one week before sowing, respectively. Less than twelve hours before sowing, the NLL seeds were inoculated with sterile peat inoculum containing the rhizobium bacterium *Bradyrhizobium lupinus*. The inoculum was produced by Legume Technology Ltd. (Nottinghamshire, UK) and marketed under the trade name LegumeFix®. The same batch of inoculum was used in both years and stored dry and under exclusion of humidity at 10°C. After the inoculation, every 7 m^2 plot was sown individually in rows with 18 cm spacing. The plots were sown with a plot sowing tractor and RTK-GPS-orientation. The inoculation was confirmed by the presence of taproot nodules on five randomly sampled plants per plot. Mechanical weeding was performed after emergence and during early tillering on all treatments (spring-tine and shallow inter-row cultivation). The pure oats were fertilised during late tillering, before the elongation stage. The crops developed well without the need for any pest or disease control interventions.

Both cultivation seasons were characterised by temperatures above average throughout the season and high sunshine durations (Table 3). Figure S1 in the Supplemental materials provides a detailed overview of the weather during the two cultivation seasons.

Table 2
Field characteristics and husbandry measures. Free calcium was assessed by repetitive hydrochloric acid tests for carbonate. LOD = Limit of detection.

Site and year	Reckenholz 2022	Reckenholz 2023	Seegräben 2022	Seegräben 2023
Year	2022	2023	2022	2023
Latitude (°N)	47.4406	47.42937	47.34787	47.36007
Longitude (°E)	8.49807	8.51689	8.75801	8.76253
Pre-crop	Silage maize	Silage maize	Silage maize	Silage maize
Pre-pre-crop	Flower strip	Artificial pasture	Winter wheat	Winter barley
Sowing	March 4	February 16	March 10	February 22
Mechanical weeding	March 21	February 22	March 17	March 1
Mechanical weeding	April 5	April 4	March 31	April 5
Oat fertilisation (kg N)	27.5	30	27.5	30
Harvest	July 12	July 10	July 19	July 19
Soil-type	Loamy clay	Loamy clay	Sandy loam	Sandy loam
Soil-pH (H_2O)	6.9	7.0	6.2	6.4
Free calcium (HCl 10 %)	Low (0.5–2 %)	Medium (2–5 %)	<LOD	<LOD

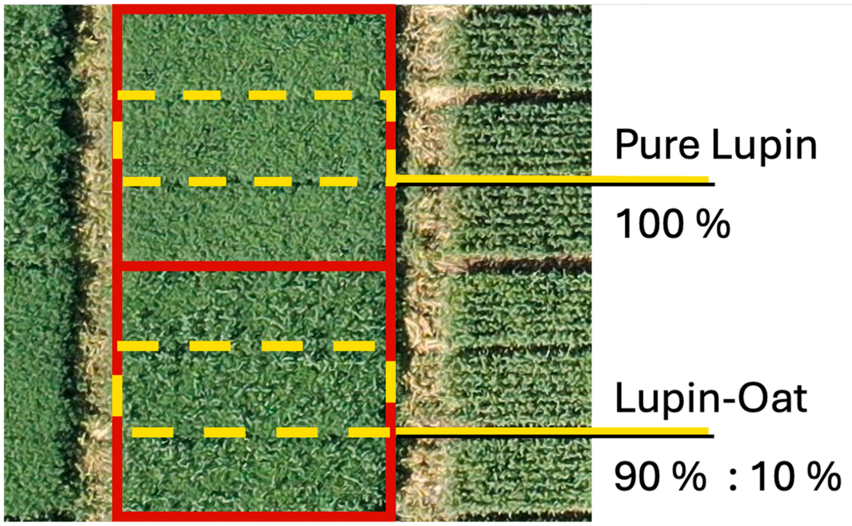

Fig. 1. Arrangement of plots to reduce border effects. The red line enfolds the three plots of the same treatment while the yellow dashed line enfolds the harvested plot. Between adjacent treatments, a 1.2-metre corridor was mowed.

Table 3
Weather data in the cultivation seasons 2022 and 2023, retrieved from the closest weather stations of MeteoSwiss. The italicised columns provide the reference values of the period 1990–2020 during the cultivation season. The distance of the weather station to the site was 0.25 to maximum 4 km. Data were retrieved daily and the average temperature and humidity as well as the sum of precipitation and sunshine hours across the cultivation period were calculated (data retrieved from MeteoSwiss).

Parameters and site	Seegräben			Reckenholz		
Year	2022	2023	1990–2020	2022	2023	1990–2020
Mean temperature (°C)	14.1	13.8	12.3	17.7	17.4	16.0
Precipitation sum (mm)	504	500	530	244	362	410
Mean humidity (%)	69	71	72	68	71	70
Sunshine sum (hours)	980	910	802	1015	950	841

2.4. On-field phenotyping

Plant growth stages were scored on a daily basis during the flowering period of the NLL, during ears emergence of the oats and before the harvest of the crops. Soil coverage was scored daily, until the date the crops fully covered the soil (fractional canopy cover above 98 %). During the ears emergence of oats and flowering of the NLL, as well as one week before harvest, average plant height, lodging area percentages of NLL and oats, and weed volumes were recorded. Weed volume was scored by multiplying the weeds' fractional canopy cover (FCC × relative height) with the weeds' plant height relative to the plant height of the crop, according to the method proposed by Andújar et al., (2016). This scoring method was chosen to obtain a more accurate estimate of the weed pressure compared with scoring the FCC only, and also due to its non-destructive nature. In the present study, the index was used as a proxy for above-ground weed biomass. Additionally, the average number of oat tillers were scored on three plants per plot after tillering. Pests and diseases that appeared were scored in the time points of their respective biological relevance (Table 4) (Pflanzenschutzdienste et al., 2003). The NLL indeterminacy at harvest was scored by the percentage of plants that resumed flowering after their first pods were ready to harvest.

Table 4
Scoring method used for pests and diseases and the growth stage, in which the pests and diseases were scored, which was the time point when they appeared and had the highest biological relevance. Interference threshold describes the severity, at which an interference is recommended according to Swiss farming practices (if applicable) (Pflanzenschutzdienste et al., 2003). NLL – Narrow-leaved lupin

Pest or disease and pathogen	Crop	Scoring method	Growth stage	Interference threshold
Anthracnose (*Colletotrichum lupini*)	NLL	Number of dead pods	All pods visible	–
Mildew (*Erysiphe lupini*)	NLL	Incidence on 20 plants * severity on 3 top leaves	Blossoming	–
Aphids (*Aphis* ssp.)	oat	Incidence on 50 ears	Anthesis	60 % of ears infected
Cereal leaf beetle (*Oulema* ssp.)	oat	Number of larvae on 10 flag leaves	Anthesis	2 larvae per flag leaf
Crown rust (*Puccinia coronata*)	oat	Incidence on 20 plants * severity on 3 top leaves	Anthesis	20 % of leaves infected
Leaf spot (*Drechslera avenae*)	oat	Incidence on 100 leaves (4th from top)	Booting	20 % of leaves infected
Mildew (*Blumeria graminis*)	oat	Incidence on 120 leaves	Anthesis	25 % of leaves infected
Septoria leaf blotch (*Septoria avenae*)	oat	Incidence on 100 leaves (4th from top)	Booting	20 % of leaves infected

2.5. Harvest and post-harvest analyses

The grains were harvested with a plot combine harvester (Wintersteiger Seedmech, Ried im Innkreis, Austria). In a second step, the grains were additionally cleaned in a vertical air sifter (in-house build). The samples were dried to 10 % moisture content. In mixed treatments, the oats were separated from the NLL with a grain cleaner (Westrup, Slagelse, Denmark), where a 6 mm oval-cut sieve was deployed. The cleaned samples were weighted to measure the yield, and then repetitively divided using a riffle divider (sample splitter RT6.5, Retsch ltd., Haan, Germany), to obtain representative 150 g samples. These representative samples were analysed for their hectolitre weight (Grain Analysis Computer, Model GAC2100 by Dickey_John® corporation, Illinois, USA), oat thousand kernel weight (seed counter Marvin®, by MARViTECH GmbH, Wittenburg, Germany), and total protein content of oats and NLL by near-infrared spectroscopy (Infratec Nova, FOSS analytical, Hillerød, Denmark).

2.6. Statistical analysis

2.6.1. Data preparation and calculations

Based on the primary data, productivity metrics were calculated to assess the partial land equivalent ratio of each crop in mixture ($pLER_{crop}$), the land equivalent ratio of the mixture (LER), the total protein yield ($Protein\_yield_{crop}$), the partial ($pTOI_{protein}$) and the total protein overyielding ($TOI_{protein}$) (Li et al., 2023; Zustovi et al., 2024):

$$pLER_{crop} = \frac{Yield_{crop,\ mixed}}{Yield_{crop,\ pure}}$$

$$LER = pLER_{lupin} + pLER_{oat}$$

$$Protein\_yield_{crop} = Yield_{crop} \times Protein\_content_{crop}$$

$$pTOI_{protein,\ crop} = \frac{Protein\_yield_{crop,\ mixed}}{Protein\_yield_{crop,\ pure}}$$

$$TOI_{protein} = \frac{Protein\_yield_{lupin,\ mixed} + Protein\_yield_{oat,\ mixed}}{\max\left(Protein\_yield_{lupin,\ pure}, Protein\_yield_{oat,\ pure}\right)}$$

Pure and mixed refer to the cultivation in monocropping and in mixed cropping, respectively, and crop stands for either NLL or oat. The metrics compare the mixed cropping system's land use efficiency, productivity, and protein overyielding relative to their monocropping equivalents.

To further prepare the data for the analysis, differences were calculated between the pure and mixed stands for the

- date when the canopy fully covered the soil
- oat ears emergence
- NLL flowering
- plant developmental stage at harvest according to Zadoks growth stage (Zadoks et al., 1974)

If the variance in the response variable was not constant, this response variable was either square-root or log10-transformed (as specified in Appendix A in the Supplemental Materials). To analyse the compensatory yield buffering, the partial plot-level yield was evaluated by means of Pearson-correlation.

2.6.2. Modelling

The (transformed) response variables were analysed using linear mixed-effects models. Four model-classes M1-M4 were designed to suit the target-variables (Table 5). The treatment, year, site, and their interaction effects were modelled as fixed effects and the block within a field as a random effect. The models were fitted using the lme4 package within the R programming language (Bates et al., 2015; R Core Team, 2025). Inferences were calculated using the lmerTest package, which provided the Satterthwaite degree of freedom adjustment for the type-III ANOVA and the contest-function, which was used to test linear contrasts (Kuznetsova et al., 2017). The contrast sum parametrisation was used to allow the interpretability of the regression coefficients to the population mean, but partially fitted intercepts were used for each group in case of the M2 and M4 models (R syntax: "y ~ 0 + group"). Post-hoc pairwise comparisons assessed varietal differences.

Table 5
Statistical models deployed to analyse the data. The characteristics explain the details of the model. Each response variable (attribute, as specified in Table S1 in the Supplemental materials) in the present study was analysed with one or more of the models listed in the table (as specified in Appendix A in the Supplemental materials).

Model	Characteristics
M1	This model answered if the response variable differed in mixtures and pure NLL (or analogously oats) across all varieties. It performed an ANOVA using the NLL/oat-variety and the binary variable stand = mixed. This model considered each species separately.
M2	M2 answered if the response variable differed in mixtures and pure NLL or oats. Here, this was achieved by computing the linear contrasts of each pure NLL/oat variety with the mean of its respective mixtures. This model considered each species separately.
M3	On the subset of mixed plots, M3 performed a two-way (mixed) ANOVA with the factors oat variety and NLL variety (adjusting for site, year, and block). This model considered both species together.
M4	M4 answered the question, if the estimated value of the treatments with mixed stands (e.g. LER) was significantly different from an expected value (e.g. LER = 1) after a Bonferroni correction (with the respective 12 coefficients).

2.6.3. Robustification

To mitigate the influence of outliers, the outlier weights were automatically adapted using the weights from the analogous model derived by the rlmer function of the robustlmm package (Koller, 2016). Target outliers were selected by applying the bounded influence function of Huber loss. This application of the robustification is indicated in the Supplemented Materials, Appendix A (robustify = TRUE).

3. Results

Amongst all attributes analysed, the following response variables exhibited significant effects of mixed cropping compared with pure stands: soil coverage, cereal leaf beetle of oats, ears emergence in oats, height of oats in mid-May, weed volumes in NLL and oats, plant growth stage at harvest of NLL and oat (Table 6), oats and NLL protein yield, partial protein overyielding and the (partial) LERs (Fig. 4), as well as thousand kernel weight, hectolitre weight and protein content of oats (Table 7). In contrast, mixed cropping showed no effect on the following attributes: lodging of NLL, plant heights of NLL, NLL plant developmental stage at flowering, plant height of oat in June and July, tiller number of oats, crown rust of oats (*Puccinia coronata*), anthracnose of NLL (*Colletotrichum lupini*), chlorosis of NLL, NLL indeterminacy, thousand kernel weight of NLL grains, protein content of NLL grains, and total protein overyielding. The following four subchapters shed light on the response variables listed above, divided into plant development, plant health, productivity and crop quality. The full analytical output is provided as Appendix A in the Supplemental Materials.

3.1. Field effects of mixed cropping

The reported significant effects in the following two subchapters on plant development and plant health are summarised in Table 6.

3.1.1. Plant development

The mixed stands covered the soil on average 19.8 days earlier than pure oats, whereas there was no significant difference between the soil coverage in pure and mixed stands of all NLL varieties. The individual NLL varieties differed moderately but significantly ($p < 0.05$), in terms of the date, when the soil was covered: On average, across both years and sites, Lunabor established a full canopy cover 3 days sooner than Jowisz, and 7 days sooner than Probor.

No difference in NLL flowering was observed between pure and mixed stands. However, the oat ears emerged significantly later in mixture than in pure stands. The strongest effect was observed in Troll

Table 6
Effect size estimates of the linear mixed-effect models of the on-field response variables (attributes). The variety columns of the narrow-leaved lupins (Lunabor, Probor, Jowisz) and oats (Bison, Lion, Troll) refer to the change of the attribute in each variety in mixed stands compared with their respective pure stands. 'Year 2022' outlines the difference from year 2022 to the year 2023, and 'Site Re' represents the difference of the site in Reckenholz to the site in Seegräben. No entry in the cell means there were no corresponding data, a zero means no significant effect was detected. All non-zero values listed in the table stand for significant effects (adjusted p-value < 0.05).

Response (unit)	Lunabor	Probor	Jowisz	Bison	Lion	Troll	Year 2022	Site Re
Soil coverage (days)	0	0	0	-19.8	-19.8	-19.8	-22	0
Ears emergence in oat (days)				1	2	2	0	0
Height mid-May NLL and oat (cm)	0	0	0	-9.9	-8.7	-6.6	7.8	0
Cereal leaf beetle oat (count)				0	-4.8	-5.4	-7.3	0
Weed volume in NLL in June (%)	-78	-80	-87				73	0
Weed volume in oat in June (%)				462	0	473	-65	-68
Oat-NLL growth stage difference at harvest (-)	0	0	0	-2.4	-2.4	-2.4	3.1	0

Table 7
Effect size estimates of the linear mixed-effect models of the crop quality data (attributes). The variety columns of the oats (Bison, Lion, Troll) refer to the change of the attribute in each variety in mixed stands compared with pure stands. 'Year 2022' outlines the difference from year 2022 to the year 2023, and 'Site Re' represents the difference of the site in Reckenholz compared with the site in Seegräben. A zero entry in a cell means no significant effect was detected. All non-zero values listed in the table stand for significant effects (adjusted p-value < 0.05).

Response (unit)	Bison	Lion	Troll	Year 2022	Site Re
Hectolitre weight of oat (kg hl^{-1})	1.5	1.8	1.9	-1.8	0
Protein content of oat (%)	2.8	2.1	3.2	0.7	-2.2
Thousand kernel weight of oat (g)	4.1	2.9	2.1	0	0

and Lion with a two-day delay ($p < 0.05$), followed by Lion with a single day later onset of ears emergence in mixed, relative to pure stands, respectively. For the plants' mutual maturity in mixed stands, the linear mixed-effect models showed an average delay of 2.4 growth stages of the oat crop compared with the growth stage of the NLL crop. However, this effect was more prominent in the year 2023, whereas the effect of the year 2022 resulted in near-coincidental maturity, i.e. in 2022, both crops became ripe during the same days, whereas in 2023 there was a slight delay of the oat crop. The NLL's indeterminacy was not affected by mixed cropping and the indeterminacy was low, ranging from 1 % to 3 %.

Amongst the recorded time series of plant heights spanning between May and July, only the oat height in May differed between pure and mixed stands, where Bison was on average 9.9 cm, Lion 8.7 cm and Troll 6.6 cm shorter in mixed than in pure stands ($p < 0.001$). In contrast, in June and July, no mixed cropping effect on the plant heights of oats and NLL was observed. The average height difference of oats to NLL amounted to 10, 31 and 43 cm in May, June, and July respectively, whereby in June and July, Troll was significantly shorter than Bison and Lion ($p < 0.01$). In the oat crops, there was no lodging present at all and in the NLL crop, no significant effect of mixed cropping was detected. The number of oat tillers was also not affected by mixed cropping. However, the site Reckenholz showed a 10 % higher number of oat tillers across both pure and mixed stands (0.24 more tillers per plant, $p < 0.001$).

3.1.2. Plant health and weed pressure

Amongst the scored pests and diseases, only crown rust (*Puccinia coronata*) and cereal leaf beetle (*Oulema* ssp.) population exceeded the interference threshold (Pflanzenschutzdienste et al., 2003), and only cereal leaf beetles exhibited a significant mixed cropping response.

The cereal leaf beetles showed higher incidences on pure stands of Lion and Troll ($p < 0.05$), compared with their respective mixed stands, whereas the cereal leaf beetle incidence did not differ significantly between pure and mixed stands of Bison. The changes reported in Table 6 correspond to a reduction of the cereal leaf beetle incidence by 41 % for Lion and by 46 % for Troll when mixed with NLL ($p < 0.05$). The linear mixed-effect models showed a strong year effect exceeding the mixed cropping effect ($p < 0.001$): In 2022, the overall incidence was significantly lower, and no recorded median exceeded the interference threshold, whereas in 2023, this case occurred for the pure stands of Troll. In 2022, the reduction of the cereal leaf beetle's incidence was more consistent but at a lower level, and in 2023, mixed cropping led to a relevant reduction of the incidence on the oat variety Troll (Fig. 2) to levels below the interference threshold according to Swiss farming practices (Pflanzenschutzdienste et al., 2003).

The dominant weed species (presence in over 33 % of all scored plots) were wild mustard (*Sinapis arvensis*) in Reckenholz 2022, field poppy (*Papaver rhoeas*) in Reckenholz 2023, and cleavers (*Galium aparine*) in Seegräben in both years. The weed volumes were significantly lower in mixed NLL stands than in pure stands, whereby the relative reduction in weed volume in mixed NLL treatments amounted to

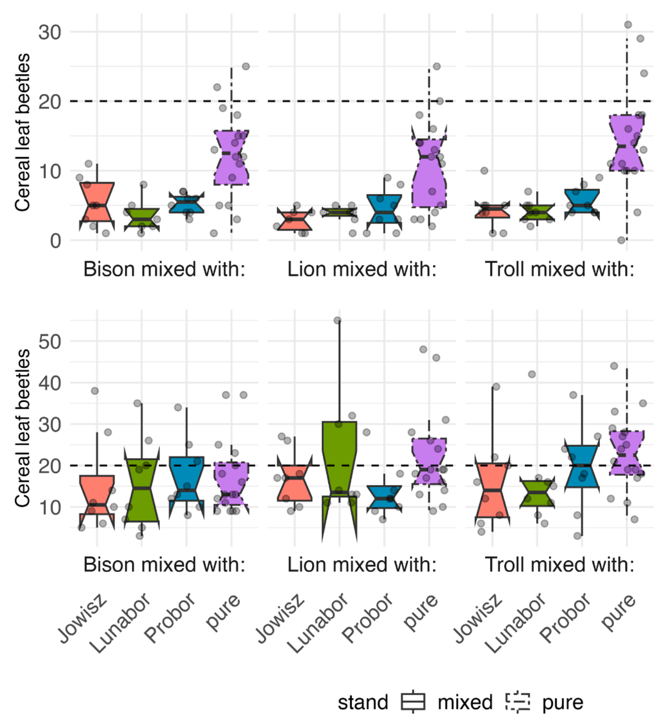

Fig. 2. Cereal leaf beetle incidence (number of larvae per 10 flag leaves) in the years 2022 (top subfigure) and 2023 (bottom subfigure) in the pure stands of the oat varieties (Bison, Lion, Troll) and in mixed cropping with the narrow-leaved lupin varieties (Lunabor, Probor, Jowisz). The dashed lines indicate the interference threshold according to Swiss farming practices (Pflanzenschutzdienste et al., 2003). Each point represents one measurement. Boxplots outlined with dashed lines denote the pure reference stands.

up to 87 % ($p < 0.005$, Table 6). The relative increase of the recorded weed volumes in mixed oats was proportional to the relative decreases in mixed NLL compared with their respective pure stands. The weed volumes in pure stands of oats were two orders of magnitude lower than the weed volumes in pure stands of NLL (Fig. 3).

3.2. Productivity and quality effects of mixed cropping

3.2.1. Productivity and compensatory yield buffering

The median NLL yields of Lunabor, Probor and Jowisz in pure stands were 3.1, 3.3 and 3.0 t·ha^{-1}, respectively. The median oat yields of Bison, Lion and Troll in pure stands amounted to 4.9, 5.4 and 5.2 t·ha^{-1}, respectively (Fig. 4A). A significant year ($p < 0.005$) and site effect ($p < 0.005$) was observed in both the NLL and oat yields: In 2022, the overall NLL yield was 0.96 t·ha^{-1} higher, and the overall oat yield 0.36 t·ha^{-1} lower than in 2023. Across both years, the site Reckenholz, compared with Seegräben, showed an overall reduced NLL yield by 1.1 t·ha^{-1} ($p < 0.01$), whereas the overall oat yield was elevated by 0.75 t·ha^{-1} ($p < 0.01$).

The land use efficiency of the studied mixtures showed the following picture: Across all nine mixtures, only Lunabor mixed with Troll exhibited a significantly elevated LER amounting to 1.16, i.e. this mixture used land 16 % more efficiently than its corresponding pure stands. The LER of all other mixtures did not differ significantly from 1, which meant their land use in mixed stands was as efficient as in pure stands. Across all mixtures, the pLERs of the oats were significantly above their expected LER (corresponding to their sowing ratio) of 0.1 ($p < 0.001$), with significantly different values between the three oat varieties in the decreasing order of Lion, Bison and Troll ($p < 0.001$). The pLER of the NLL was significantly below their expected pLER of 0.9 in case of the mixtures Jowisz x Bison, Jowisz x Lion and Probor x Lion ($p < 0.05$), all other NLL pLERs did not differ significantly from their expected value (Fig. 4B). A pronounced year effect was apparent, where in 2022, the pLER of NLL was 0.16 higher and the pLER of oats was 0.12 lower than in 2023 ($p < 0.001$). The significant site effect manifested itself in a reduction of the pLER of NLL by 0.26 and an increase of the pLER of oats by 0.13 in Reckenholz, compared with Seegräben ($p < 0.001$). Altogether, these differences in the pLERs resulted in a LER change of −0.13 in Reckenholz compared with Seegräben ($p < 0.001$), without a significant year effect.

The protein yield of pure stands was significantly higher in NLL than in oats ($p < 0.001$). The absolute protein yield of the two NLL varieties Probor and Jowisz was 272 and 282 kg·ha^{-1} lower in mixed stands

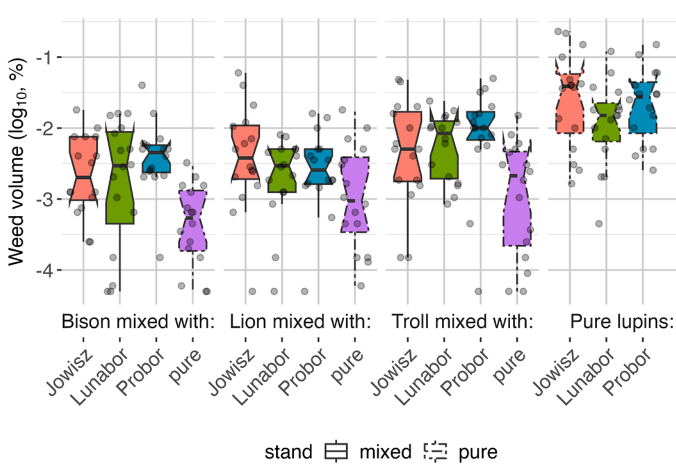

Fig. 3. Recorded weed volumes (log_{10}, %) across both years 2022 and 2023 in the pure treatments of the three oat varieties (Bison, Lion, Troll) and narrow-leaved lupin varieties (Lunabor, Probor, and Jowisz) and their mixtures. Each point represents one measurement. Boxplots outlined with dashed lines denote the pure reference stands.

compared with their pure stands ($p < 0.001$), respectively, whereas Lunabor did not show any significant reduction. The total protein yield per hectare did not vary significantly between the three pure stands of the NLL and all mixtures, adding up to 900–1150 kg·ha^{-1} (Fig. 4C). However, a strong site and year effect was also observed in case of the total protein yield of the NLL: In 2023, the protein yield in Reckenholz was 262 kg·ha^{-1} lower than in Seegräben ($p < 0.0001$), which also resulted in an overall increased protein yield in the year 2022 across both sites of 159 kg·ha^{-1} ($p < 0.0001$).

The linear mixed-effect models did not reveal any significant difference of the $TOI_{protein}$ from 1. This implies an absence of transgressive protein overyielding, i.e. the protein yield per hectare was identical in mixed stands with the protein yield of pure NLL stands, which was the crop producing higher protein yield in pure stands. However, with regards to the expected $pTOI_{protein}$, the oats yielded more than their expected value of 0.1, corresponding to their sowing proportion of 10 % ($p < 0.01$). This effect was observed across all oat varieties and the measured median $pTOI_{protein}$ oat amounted to 0.22. The $pTOI_{protein}$ NLL showed variable responses in comparison to their expected $pTOI_{protein}$, NLL of 0.9: Lunabor in mixture with Bison, and all NLL mixed with Troll were not significantly different from the expected value, whereas the remaining five $pTOI_{protein}$, NLL were significantly lower than the expected value ($p < 0.05$). Additionally, a significantly lower $pTOI_{protein}$, NLL of Jowisz, compared with Lunabor was observed ($p < 0.005$) (Fig. 4D).

The yield bufferings analysis revealed a pronounced inverse relationship between the two mixed crop partners: partial NLL and oat yield from mixed plots moved in opposite directions across both sites and years (Pearson $r = -0.73$, $p < 0.001$; Fig. 5). Hence, whenever the NLL yield component declined, the oat yield component increased, and vice versa, underscoring the underlying compensatory behaviour in the mixed cropping. This stabilising behaviour of the mixed cropping system, which was observed on an individual plot basis, and was reported on a field and year basis, exemplifies the higher yield-stability of the mixed cropping system in comparison to their pure stands, where no second crop can compensate for the yield loss.

3.2.2. Crop quality

The NLL grain quality remained unaffected by mixed cropping, as their protein content and thousand kernel weight (TKW) did not differ between the pure and the mixed stands. On the other hand, the oat grains exhibited strong mixed cropping responses, with an increase in their TKWs of 2.1 up to 4.1 g ($p < 0.001$), compared with pure stands, representing a relative increase of up to 10 %. Further, the oats hectolitre weight increased by 1.5 up to 1.9 kghl^{-1}, compared with pure stands ($p < 0.05$). In addition, compared with the pure stands, the oats protein content increased by 2.1 up to 3.2 % of the total weight, which corresponded to a relative increase in their protein content of 27 %, 21 % and 31 % for Bison, Lion and Troll, respectively ($p < 0.001$). Across both years and sites, an overall reduction of 2.2 % in the absolute protein content of the oats became apparent in Reckenholz in the year 2023 ($p < 0.001$). The reported significant mixed cropping effects on yield quality are summarised in Table 7.

4. Discussion

4.1. Plant development and soil coverage

In the mixed stands, NLL and oats displayed a marked convergence of phenological timing: Both crops reached maturity at nearly identical times, which facilitated the appropriate harvest timing. Such synchrony simplifies harvest logistics and has been identified as a key attribute explaining the high performance of legume–cereal mixed cropping systems (Demie et al., 2022). Height measurements revealed only a transient effect of mixed cropping: Oats in mixed stands were slightly shorter than their monoculture counterparts in mid-May but no

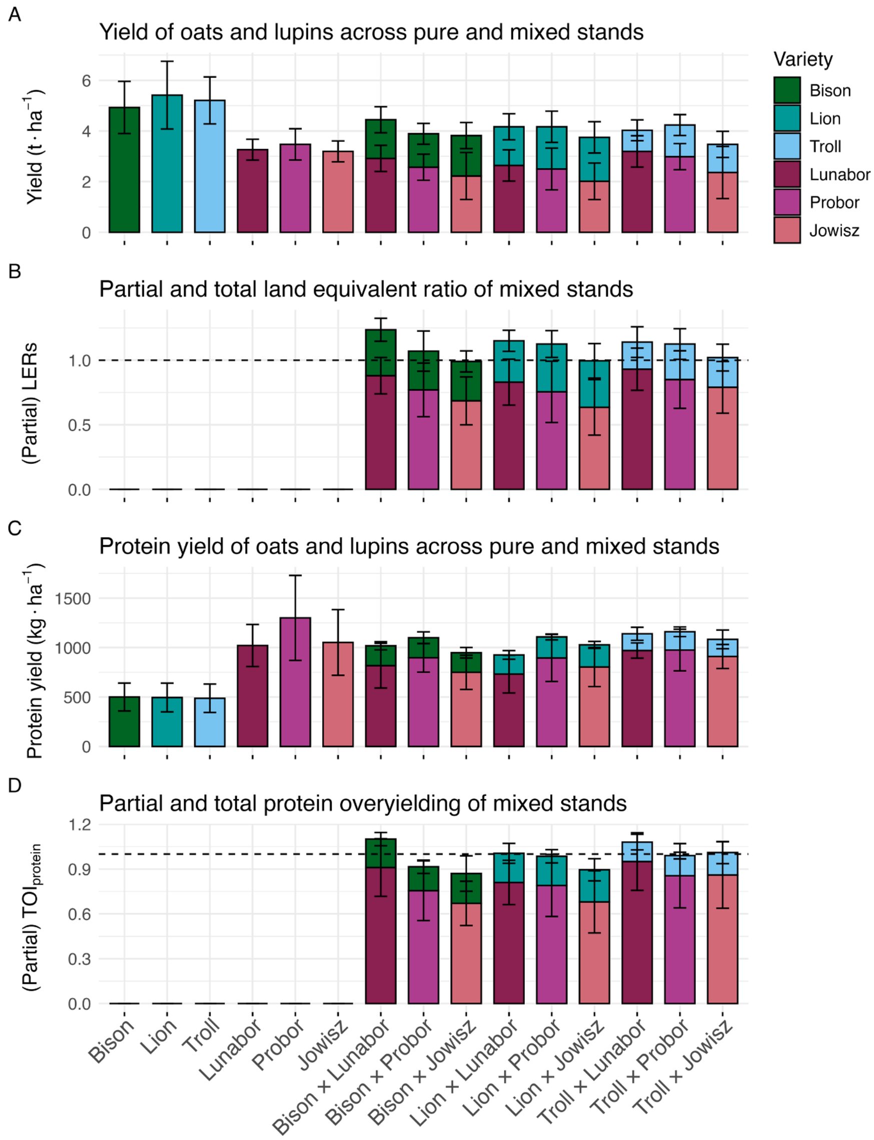

Fig. 4. A - D. Productivity overview of pure and mixed oat and narrow-leaved lupin stands (n per treatment = 16). A: yield, B: partial and total land equivalent ratio (LER), C: protein yield, D: partial and total protein overyielding ($TOI_{protein}$). For all graphs, the median value is represented by the bar height, and the variability (median absolute deviation) by the error bars. In mixed stands, the lower bar represents the partial lupin values, the upper bar the partial oat values and the whiskers refer to the variance of the individual components of either narrow-leaved lupins or oats. By definition, the transgressive protein overyielding ($TOI_{protein}$) and the LERs are 1 in pure stands, represented by the dashed line.

differences persisted in June and July, and NLL height remained unaffected throughout. Such height symmetry has been shown to be an architecture associated with superior mixture outcomes (Demie et al., 2022). Because soil exposure to sun strongly influences soil evaporation, the more rapid soil coverage of the mixed treatments supported efficient water use and may have contributed to the positive protein yield responses reported, given the total precipitation was below the norm during this study (Yu et al., 2019). Taken together, synchronised phenology, minor height differences, and superior canopy development constitute a coherent syndrome of compatibility that can largely be predicted from monoculture traits. Further, the absence of variety-specific interactions across these attributes highlights the general compatibility of NLL with oats in mixed cropping.

4.2. Plant health and weed pressure

The observed reduction in cereal leaf beetle incidence in mixed stands aligns with the principles of the dilution effect, wherein the presence of a non-host or less susceptible species reduces pest pressure on the primary host crop (Civitello et al., 2015). This phenomenon was evident in the present study: in one year, the significant reductions in cereal leaf beetle populations was even decisive that the threshold of interference was exceeded in pure stands of oats but not exceeded in mixed stands of the same oat variety. Previous research has documented that diversified cropping systems disrupt pest colonisation and feeding patterns, thereby mitigating pest impacts (Finch and Collier, 2000). In the present study, mixed stands of oats and NLL effectively diluted the cereal leaf beetle population. Similar findings have been reported by Tooker and Frank (2012), whose findings support the fact that increased plant diversity can impede pest movement and reduce localised pest aggregation. Thus, mixed cropping of NLL and oats is a viable approach to control cereal leaf beetle populations.

Mixed cropping also led to a substantial reduction of the weed pressure comparing with pure NLL stands, according to the estimated weed volumes. Thus, especially in organic cultivation, where the application of herbicides is not allowed, mixed cropping provides an

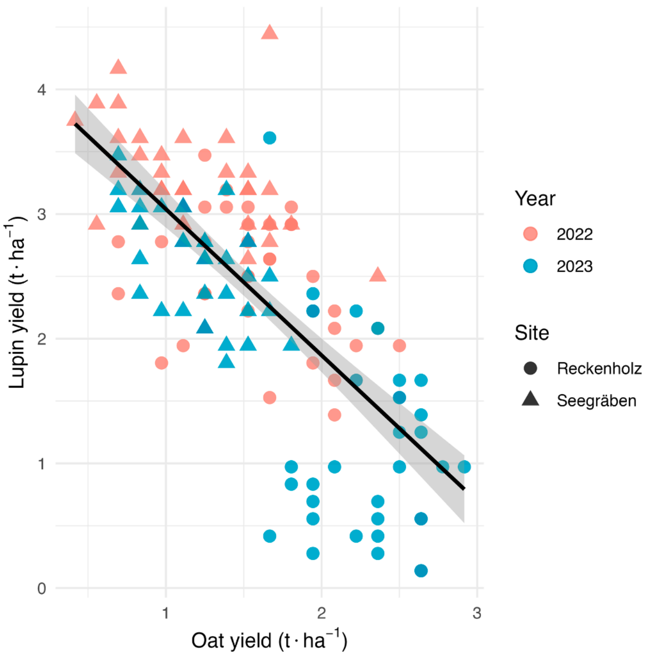

Fig. 5. Compensatory yield buffering (n = 144): correlation between narrow-leaved lupin and oat yield on a plot level. The Pearson r is –0.73 (p < 0.001). The line indicates the trend with its 95 % confidence interval (shaded area). Each dot represents the yield of the two crops recorded from an individual plot in mixed stands.

option to reduce the weed pressure in pulses (Pradhan et al., 2022; Trenbath, 1993; Verret et al., 2017). The mixed cropping system of NLL and oats in the present study led to a higher number of plants per square metre than the pure NLL stands (138 versus 120), however, this effect alone does most probably not explain the full reduction of the weed volumes by up to 83 %. The observation of strongly reduced weed volumes in pure stands of oats, suggests that oats are the main cause. In fact, oats have a strong suppressing effect on other plants, including field mustard (Baghestani et al., 1999), which was one of the dominant weed species in the current study. This effect was attributed to the root exudates of the oat plants who's strong allelopathic effects reduce the growth of other plants, which is in line with the lower weed pressure in pure oat stands than in mixed oat stand, where fewer oat plants exude allelopathic substances. Conversely, across both years and sites, mixed treatments with NLL had covered the soil earlier (closed canopy) than the pure oat stands, yet the earlier soil coverage was not accompanied by lower, but instead higher, weed pressure. Thus, irrespective of soil coverage development, the sowing of only 10 % of oats in a replacement design led to a strong effect of the oat crop suppressing weeds despite a high weed pressure.

In the 2023 cultivation season at Reckenholz, the NLL crop exhibited chlorosis symptoms, which were associated with elevated levels of free calcium in the soil and the highest pH value (7.0) of all fields. This condition likely contributed to the observed reduction in NLL yield, as both, elevated free calcium and soil pH values have been shown to induce chlorosis in NLL and reduce their growth (Ding et al., 2019). This reduced viability of the NLL crop was also reflected in lower partial protein yield and LERs of the NLL in Reckenholz in 2023. Interestingly, despite the absence of visual symptoms, the NLL also exhibited lower performances at the site Reckenholz in 2022, which can again be linked to the elevated levels of free calcium and soil pH values (6.9). These findings underscore the need for careful site selection to ensure high NLL productivity.

4.3. Productivity and yield stability

The oat companion crop on the other hand showed the opposite development of yield to the NLL and exhibited elevated yield and higher pLERs at the site Reckenholz in both years. Additionally, the strong negative correlation between the NLL and oat yield substantiates the compensatory yield buffering of this mixed cropping system over pure stands. This finding is underlined by a study of Raseduzzaman and Jensen (2017), which provided compelling evidence for the hypothesis that mixed cropping systems can enhance yield stability compared with pure stands. Although the rather high pH values and the free calcium were adverse growing conditions for the NLL, the mixed cropping system buffered against this environmental variability, by utilising complementary plant interactions and resource use efficiency. In case of nitrogen fertilisation, this phenomenon was demonstrated in a review by Pelzer et al. (2014). We thus suggest that the NLL–oat mixed crops' resilience of the current study is due to the diversification of crops with complementary stress responses, leading to more stable aggregate yield.

Beyond the improved yield stability, Lunabor × Troll achieved an elevated LER. This gain in land use coincided with the strongest suppression of cereal leaf beetles in the oat crop and the smallest canopy-height asymmetry between the oat and NLL crop in the mixture. This suggests that reduced pest pressure together with a more balanced canopy mitigated asymmetric light competition and supported more efficient land use. Presumably, this elevated LER is thus owed to an above-average decrease in the pest pressure on oats resulting in a healthier crop, and the best growth dynamics between the observed oat and NLL varieties. Such improved productivity amongst identical plant-canopy architectures was previously reported Maclaren et al., (2023).

4.4. Crop quality

The capacity of pulses to fix atmospheric nitrogen (N), enables mixed cropped cereals to acquire a greater proportion of soil N, thereby enhancing their yield relative to pure stands (Hauggaard-Nielsen and Jensen, 2005). In the present study, while NLL yield and protein yield were either maintained or slightly reduced in mixtures, the oat yield and protein yield consistently exceeded the expected values. This outcome can be attributed to the pulse's fixation of atmospheric N, reducing its reliance on soil N, and in turn effectively leaving more soil N available for the cereal partner (Jensen et al., 2020). Although direct N transfer is limited, higher N availability for the cereals in mixture thanks to the N-sparing effect has been shown to benefit cereal growth (Hauggaard-Nielsen and Jensen, 2005). Notably, NLL are known to fix even higher amounts of N in mixtures than in pure stands, further enhancing N availability for oats (Pálmason et al., 1992). The effect of the higher N availability is particularly evident by the observed elevated pLER and protein overyielding for oats in mixtures and further substantiated by consistently higher protein contents in all oat varieties in mixed stands across all mixtures, years, and sites. This effect for the cereal crop was previously also shown in a durum wheat-winter pea mixed crop (Bedoussac and Justes, 2010). In the present study, since mixtures were not fertilised, the higher oat protein content and partial protein overyielding in mixtures are thus primarily attributable to the N-sparing effect. Specifically, the N-sparing effect in mixed stands exceeded the N-fertiliser effect in pure stands.

5. Conclusion

The absence of a mixed cropping response of several other attributes, in particular agronomic traits including tiller number and plant height, underscores the potential for forecasting mixture performance based on monoculture data. Furthermore, the absence of specific variety effects for oats and NLL across these attributes supports the potential extrapolation onto other NLL and oat varieties. Still, to refine this approach, future studies should expand the range of tested varieties and sowing ratios to further substantiate the possibility to predict and optimise the mixed cropping performance based on pure stand metrics. This is particularly relevant given the importance of selecting mixtures with synchronised phenology to optimise resource use efficiency. Indeed, previous studies have emphasised the importance of matched plant height and maturation timing for optimal mixed cropping performance (Demie et al., 2022). Additionally, the observed site and year effects, likely driven by climatic differences and soil type variability, highlight the necessity to investigate soil-plant interactions onto mixed cropping systems more closely. Thus, future efforts should focus on expanding predictive tools for mixed cropping suitability that facilitate the effective identification of the best-performing NLL–oat mixtures.

This study advances the understanding of under-explored quality parameters in mixed cropping and connects quality to performance metrics by integrating the assessments of plant health, crop development, and productivity. Notably, several plant traits remained unaffected by mixed cropping, underscoring the potential for extrapolating findings across varieties and environments. Importantly, the findings reveal that the mixed cropping system exhibited greater resilience in terms of compensatory yield buffering and plant health compared with monoculture, highlighting its capacity to mitigate stress while maintaining productivity. The observed robust performance of oats in mixed stands, despite no added chemical fertiliser, further underscores the potential of mixed cropping as a viable strategy for sustainable intensification, particularly in organic systems, where chemical inputs are limited.

CRediT authorship contribution statement

Andreas Kägi: Writing – review & editing, Methodology, Investigation, Conceptualization. **Lukas Graz:** Writing – review & editing, Visualization, Software, Methodology, Formal analysis. **Susanne Vogelgsang:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization. **Johan Six:** Writing – review & editing, Methodology, Conceptualization. **Yannik Schlup:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Funding

This project was carried out within the Horizon 2020 funded project CROPDIVA (ID: 101000847). We gratefully acknowledge the financial support that made this study possible.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used GPT-4 (OpenAI, California, USA) to improve the structure and efficiency of the code to render figures and GPT-o3pro (OpenAI, California, USA) in support of writing the abstract. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the created content.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We gratefully acknowledge the field technicians for their invaluable expertise in the cultivation of NLL and oats as well as the Irene Bänziger, Eveline Jenny, interns and MSc students for their great assistance in the field and laboratory work.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2025.110291.

Data availability

The repository, including the analytical code and data, is available at https://github.com/incorey/lupin-oat-mixed-cropping.

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