Field Crops Research 297 (2023) 108923

Contents lists available at ScienceDirect

Field Crops Research

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

New insights towards breeding for mixed cropping of spring pea and barley to increase yield and yield stability

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ARTICLE INFO

Keywords:
Intercropping
Pisum sativum L.
Hordeum vulgare L.
General mixing ability
Producer associate concept
Crop diversification

ABSTRACT

Mixed cropping (MC) is a key strategy to harness agriculture for climate-change. Breeding adapted genotypes can unleash the full potential of MC, both in terms of yield potential and yield stability. To achieve this goal, concepts from both breeding and ecology have to be fused in order to develop a suitable methodology for breeding for MC. In order to advance the field of breeding for MC, we evaluated yield and trait data of pure stands (PS) and mixed stands (MS) of pea (*P. sativum* L.) and barley (*H. vulgare* L.) as a legume-cereal model system. Twenty-eight pea and seven barley lines, representing European breeding material, were grown in an incomplete factorial design at two organically managed sites across two years. The general mixing ability (GMA) of pea for total mixture yield was predominant as specific mixing ability (SMA) was absent, facilitating future breeding and seed marketing efforts. The most promising pea cultivar 'Volt' resulted in an average total mixture yield increase of 11% (+0.43 t/ha) in MC compared to the average, while the cultivar 'Florida' led to a yield decrease of − 31% (−1.23 t/ha), highlighting the importance of the choice of the genotype in MS. The analysis of separated MS yields allowed to investigate the underlying mechanistic principles in genotypes' contribution to MS yields and we revealed the major role of producer (Pr) effects in this context. The correlation between Pr effects and GMA revealed that GMA can be maximized by selecting for high Pr effects. Early vigor, onset of flowering, shoot biomass and stipule length were identified as key traits for indirect selection for high GMA in pea accounting for up to 17% of the identified variation in total mixture yield. PS yields were moderately correlated with mixture yields ($r = 0.52$, $P = 0.013$) and can serve as an additional selection criterion. Discrepancies between correlations with PS and MS yields can be exploited to identify unique MS traits that confer niche complementarity in MS. By this method we identified stipule size as such a key trait for increasing GMA of pea. Pea genotype mixtures have a stabilizing effect also in MC systems and exhibited considerably less genotype × year and genotype × location interaction than single genotypes. Our findings close existing knowledge gaps towards breeding for MC and pave the way to develop improved genotypes for diversified cropping systems as a strategy for sustainable intensification and climate change adaptation.

1. Introduction

Mixed cropping (MC), also known as mixed intercropping, is the simultaneous cultivation of two or more crops in the same field. -Playing a central part in traditional agricultural practices around the world (Jodha, 1980; Zhang et al., 2014; Hong et al., 2017), the area covered of MC in industrialized agriculture is mostly restricted to grass-legume hay and silage production and cover-crop mixtures, while monocultures are predominant for arable crops. Grain legume-cereal MC currently covers only small areas in these systems, e.g., 3% of the arable land in China

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Abbreviations: MC, mixed cropping synonymous to intercropping; MS, mixed stand; PS, pure stand; GMA, general mixing ability; SMA, specific mixing ability; Pr, producer effect; As, associate effect; BIF, biological interaction function; LER, land equivalent ratio; pLER, partial land equivalent ratio; LAI, leaf area index.

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https://doi.org/10.1016/j.fcr.2023.108923
Received 1 July 2022; Received in revised form 22 March 2023; Accepted 1 April 2023

(Hong et al., 2017) and 0.5% of arable land in Switzerland (BLW, 2019) and is mostly used to produce animal feed (Kiær et al., 2022). However, MC has known benefits in terms of per-area yield and yield stability and can serve as a key strategy to harness agriculture for climate-change (Bedoussac et al., 2015; Duchene et al., 2017; Raseduzzaman and Jensen, 2017; Lizarazo et al., 2020; Dowling et al., 2021). To exploit the full potential of MC, future development of adapted genotypes is necessary (Litrico and Violle, 2015; Annicchiarico et al., 2019). The fact that niche complementarity effects in MC exist (Bedoussac and Justes, 2010; Barillot et al., 2014), indicates that plant breeding can be used to explore available niche space more efficiently. Here we developed a model system for breeding for MC, with a focus on pea (*Pisum sativum* L.), a major protein crop in Central Europe combined with barley (*H. vulgare* L.). Pea – barley mixtures are retaining increasing interest in Central European agriculture for their potential to increase the level of domestic protein production, by improving per area yield, yield stability, lodging tolerance and weed suppression compared to pure stand (PS) of pea (Bedoussac et al., 2015, using data from both within-row mixed and alternate row mixed cropping; Dierauer et al., 2017, using within-row mixed cropping; Weih et al., 2021, within-row mixture 50:50 replacement design). Pea exhibits a wide range of morphological trait diversity, most notably regarding plant length, and the presence ('leafy') or absence ('semi-leafless') of leaflets. In the latter case, leaflets are converted to tendrils that convey higher resistance to lodging. Adapted from combining ability of F1 hybrids, general mixing ability ('GMA', the overall additive effect of a genotype on total mixture yield) and specific mixing ability ('SMA' the interaction effect of two genotypes) are suggested as key concepts in breeding for MC (Federer, 1993; Forst et al., 2019). The determination of the ratio of variance caused by GMA and SMA in mixture yields is essential to determine a breeding strategy for MC (Annicchiarico et al., 2019; Hoppe, 2016). In this context, incomplete factorials have been suggested to design efficient experiments to estimate GMA and SMA effects and their variances (Haug et al., 2021). A predominance of GMA over SMA would allow genotypes of both species to be combined without deviating effects to be expected in specific combinations (Haug et al., 2021). This simplifies breeding efforts, subsequent seed marketing, and handling by farmers. Studies investigating GMA and SMA are scarce: no SMA was observed in corn (*Zea mays* L.) - climbing bean (*Phaseolus vulgaris* L.) mixed crops (Hoppe, 2016; Starke, 2018), and a significant, yet irrelevant contribution of SMA (0.7% of total phenotypic variance) was observed in a faba bean (*Phaseolus vulgaris* L.) – wheat (*Triticum aestivum* L.) experiment (Siebrecht-Schöll, 2019). Significant GMA effects were detected in these studies for faba bean, wheat, and corn, accounting for 1%, 6% and 25% of phenotypic variance, respectively. The question arises to what extent pure stand (PS) yield performance is correlated with mixed-stand (MS) yield performance to provide synergies for indirect selection and to use these cultivation methods appropriately in different steps of breeding schemes for MC. Annicchiarico et al. (2019) in a case study of white clover (*Trifolium repens* L.), tall fescue (*Festuca arundinacea* Schreb.), common bean, cowpea (*Vigna unguiculata* (L.) Walp.) reported genetic correlations of 0.25 – 0.83 between PS and MS. Hoppe (2016) reports a genetic correlation for corn PS yields with MS yields (with common bean) of 0.75 – 1.0. Increased yield stability of MC is well documented (for review Raseduzzaman and Jensen, 2017). The stability of *mixture components*, i.e. of fraction yields, and consequently the stability of ratios has received less attention, and research mostly focusses on grassland species (e.g. Prieto et al., 2015). This topic, however, is of importance, as the ratio of marketable legume or cereal grains is of economic significance for the farmer (Dierauer et al., 2017; Viguier et al., 2018). The producer ('Pr') effect is defined as the effect a genotype has on its own fraction yield in a mixture, whereas the associate ('As') effect is defined as the effect of this genotype on the fraction yield of its companion species (Gallais, 1976). Pr effects have also been called 'direct' effects in literature (Gallais, 1976; Annicchiarico et al., 2019), while As effects have correspondence to indirect interspecific genetic effects (IIGEs; Bailey et al., 2014). Pr and As effects can be of help to understand the impact of a given genotype on mixture ratio as well as to determine the biological interactions function (BIF) of traits (Haug et al., 2021). To our knowledge, Pr and As effects, as well as their stability have not been investigated in the context of MC. While extensive research for using heterogeneous material within mixed crops of perennial forage species (for review Annicchiarico et al., 2019) and for intraspecific diversity exists (multi-genotype mixtures, populations, composite cross populations, organic heterogeneous material etc.; Clay and Allard, 1969; Knott and Mundt, 1990; Döring et al., 2015), little is known about the yield-stabilizing effects of the combination of intra- and interspecific genetic diversity in arable MC systems. In one of the few studies available, Darras et al. (2015) investigated the effect of genotype mixtures ('GMs') of peas mixed with barley, however, yield stability parameters were not determined. As in any plant community, competition is playing a major role in the performance of a mixed crop. Annicchiarico et al. (2019) suggested that the total yield of a mixture is dependent on the competitive ability of the less competitive mixture partner. Certain traits therefore can be of key-importance to improve mixture performance by improving the competitive ability of the 'weaker' partner. In pea, early vigor might be such a key trait as it influences the competitive ability towards a non-legume companion in the important early growth-stage (Mahon and Child, 1979; Corre-Hellou et al., 2006; Bedoussac and Justes, 2010; Barillot et al., 2014). Furthermore, a high leaf area index (LAI) of the top leaf layer of pea in later stages (around flowering and grain filling) is desirable as only 5% of photosynthetically usable light (400–700 nm wavelength) is transmitted to the plant parts below the top plant layer (Caldwell, 1987). Higher LAI can be achieved by selecting for higher plant-stature, fully-leafed types, or increased stipule leaf area in semi-leafless plants (see Jacob et al., 2016). While focusing on pea in a pea-barley model MC system, this study aims to (i) determine the absolute and relative sizes of GMA and SMA variance as a base to design appropriate breeding strategies for MC (ii) investigate the mechanistic relationships in mixed stand that lead to low/high GMA, using separated yield data and the Producer-Associate concept (iii) determine the size of correlation between pure stand performance and mixture performance of genotypes in order to estimate their relative importance within future breeding schemes, (iv) examine the yield stability that genotypes convey to mixed stands, and investigate the factors that influence it (v) research the role of traits to gain understanding of the specific niche complementarities between pea and barley with the goal to exploit this knowledge for indirect selection for GMA.

2. Materials and methods

2.1. Sites, soils, and trial management

The experiments were carried out over two subsequent years (2018, 2019), at two organically managed locations in Switzerland, Fislisbach ('Fis') and Uster ('Ust'). Sowing took place between March 23 and 26 and harvest between July 11 and July 20. According to the different germination capacities of individual seed lots, PS were sown with sowing densities of 100 germinable grains/m^2 for peas and 400 germinable grains/m^2 for barley. MS were sown as an additive design in a ratio of 80% of pure stand density for pea (resulting in 80 germinable grains/m^2) and of 40% of pure stand density for barley (resulting in 160 germinable grains/m^2), totaling 120% sowing density (following local recommendations of Dierauer et al., 2017). Also following these recommendations, sowing of MS was done by prior blending of pea and barley seeds, resulting in plants standing mixed within the rows. This corresponds to farmers' practice using a standard cereal sowing-machine which cannot separate the seed for the individual coulters. An experimental single-cone plot sowing machine was used (Wintersteiger Plotseed TC) and in MS homogeneous blending of pea and barley seeds within seed-bags was checked before sowing of each experimental plot. Plots were sized 1.5 m wide * 4.7 m long (7.1 m^2) in either seven rows (Fislisbach) or six rows (Uster). Available soil nitrogen (NO_3^- and NH_4^+) at sowing time ranged from 35 kg/ha (Fis 2019) to 117.8 kg/ha (Ust 2019). No supplementary fertilization or mechanic weed control was applied. See Fig. 1 for climate data and Table 1 for soil data on the experimental environments.

2.2. Plant material

Twenty-eight spring pea genotypes plus four spring pea genotype mixtures (‘GM’s) as well as seven spring barley genotypes plus one barley GM were used in the experiment. (For means of linguistic simplicity, the different categories of genotypes that were used in the experiment, like cultivars, genotype mixtures and breeding lines, will all be referred to as ‘genotypes’ in this manuscript and only referred to their sub-category when needed). Genotypes were abbreviated numerically starting with “P” for peas and with “B” for barleys. Pea genotypes were selected for phenotypic diversity (based on information from breeders and national seed authorities) with regard to plant length, leafiness and early vigor and represent mainly registered cultivars from Germany, France, Czech Republic, Poland, and Latvia and one breeding line. See Table 2 for the pea-genotypes used in the experiment. Similarly, the barley genotypes were selected for variation in stem length, flag leaf size, early plant height, planophile or erectophile growth and tillering capacity (Table 3). Genotypes were derived from Germany, Poland, Denmark, and Austria, representing European two-row spring barley. See Fig. S7 for a visual impression on morphological diversity of a subset of pea and barley genotypes used in the experiment. All used pea genotypes were for grain usage except for P28 (‘Florida’) which is advertised as a dual-use cultivar for grain and silage use. Varieties B2 (‘Eunova’) and B7 (‘Rubaszek’) are bred for livestock feed usage, all others for malting usage. Four pea genotype-mixtures (‘GM’) were created. The aim was to design GMs with either high or low trait expressions for two potential key traits plant height and leafiness, while for all other traits, these GMs remained heterogeneous. Based on breeders’ information obtained prior to setting up the experiment, the four GMs comprised the 13 short genotypes (‘GM-short’), the 8 long genotypes (‘GM-long’), the 23 semi-leafless genotypes (‘GM-semi-leafless’) and the 5 leafy genotypes (‘GM-leafy’). Due to incorrect prior information on some of the contained genotypes, GM-long not only contained long genotypes, but also medium and short ones. For barley, one GM (‘GM-

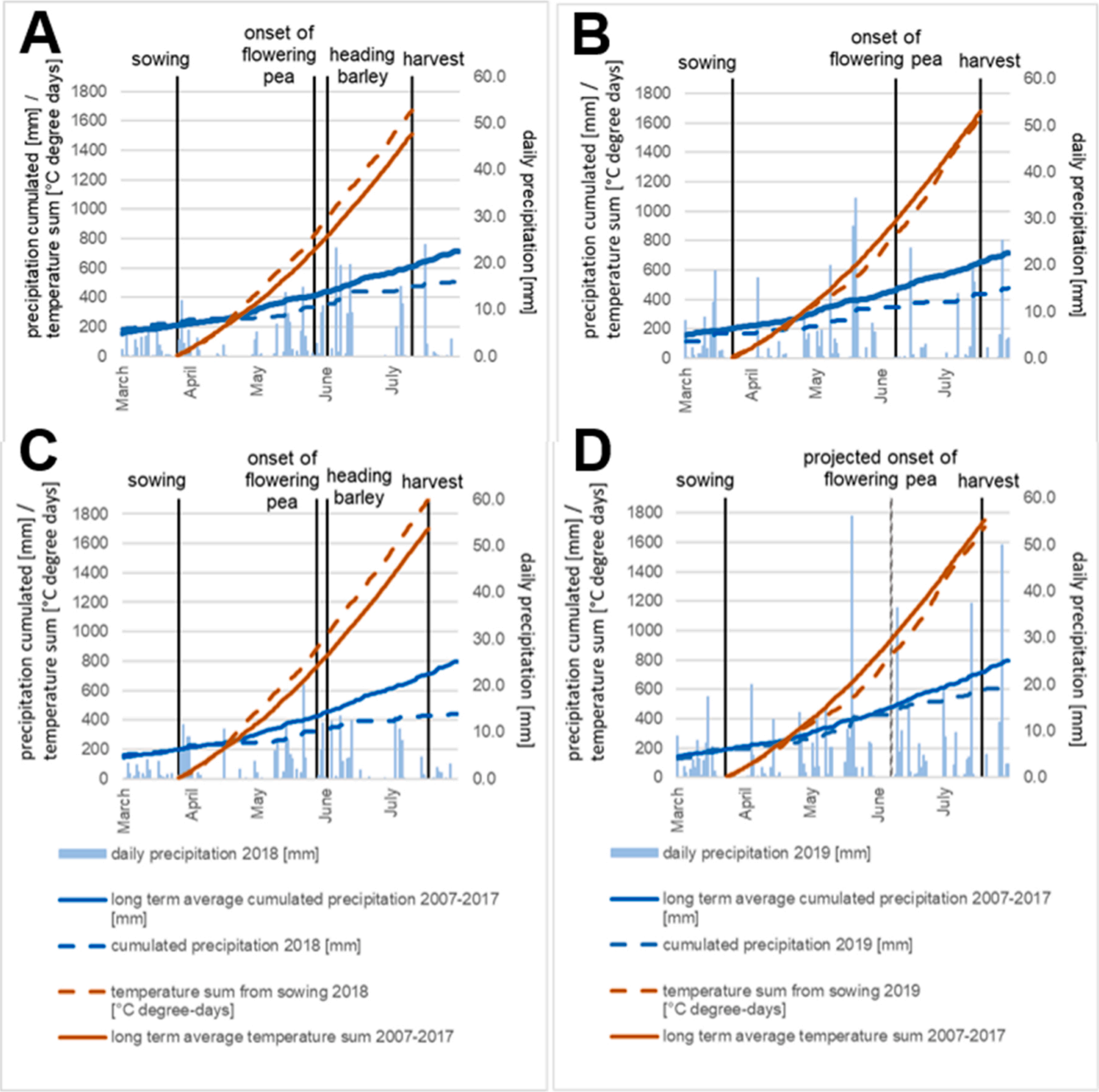

Fig. 1. Temperature, precipitation, and key events in the trials 2018–2019. The top row (A, B) shows the location Fislisbach, the bottom row (C, D) location Uster. The columns show the two experimental years, 2018 on the left (A, C) and 2019 on the right (B, D). Names of months demark the beginning of a month on the x-axis. Temperature sums were measured from the date of sowing. Cumulated precipitation was measured from January 1st onwards.

Table 1

Soil parameters of the four different experiments. Nmin comprises the total amount of water soluble NO_2^-, NO_3^- and NH_4^+. All measures refer to the 0–90 cm soil layer.

Location	Year	N_{min} [kg/ha]	Mn [mg/kg]	Soil components [%]				Soil type
				humus	clay	silt	sand	
Fislisbach	2018	41.9	294.0	2.4	14	31	52.2	sandy loam, brown earth
	2019	35.0	241.0	2.7	15	45	38.2	loam, brown earth
Uster	2018	93.2	133.0	4.3	25	29	41.7	loam, gley
	2019	117.8	87.0	4.2	36	27	33.3	clay loam, gley

Table 2

The twenty-three pea (P. *sativum* L.) genotypes used in the experiment plus the four genotype mixtures (GMs) and the five discarded genotypes, P15, P16, P17, P23 and P30. An 'x' indicates breeders' information and an 'o' empirical own measurement. When empirical trait values coincidence with breeders' information, the latter is given by an 'x/o'. GMs for stem length (GM-long and GM-short) were purely based on prior data, i.e., contain all genotypes with an 'x'.

Genotype	Pea code	Stem length			Semi-leaves		Early vigor			Breeding program (country)
		short	medium	long	present	absent	low	medium	high	
SG-L 7647	**P01**			x/o		x/o		x/o		Selgen (CZ)
Impuls	**P02**			x/o		x/o			x/o	Selgen (CZ)
Astronaute	**P03**	x/o				x/o		o		Saaten Union (NPZ Lembke) (D)
Navarro	**P05**	x	o			x/o		x	o	Saaten Union (NPZ Lembke) (D)
Gambit	**P06**			x/o		x/o			x/o	Selgen (CZ)
Angelus	**P07**	o		x		x/o	x/o			Lemarie Deffontaines (F)
Salamanca	**P08**			o		x/o		x	o	Saaten Union (NPZ Lembke) (D)
Rocket	**P10**		o			x/o	o			Lemarie Deffontaines (F)
Karpate	**P11**	x/o				x/o		o		KWS Momont (F)
Kayanne	**P12**	x	o			x/o	o			KWS Momont (F)
Mytic	**P13**	x/o				x/o	o			Agri Obtentions (F)
Protecta	**P14**			o	x/o				o	Selgen (CZ)
Mehis	**P15**				x/o			o		Estonian Crop Research Institute (EE)
Tarchalska	**P16**	x	o			x/o			o	Danko (PL)
Bluetooth	**P17**	x/o				x/o	x/o			RAGT (F)
Alvesta	**P18**	x/o				x/o		x	o	KWS (D)
Bockros	**P19**	x	o			x/o			x/o	Selgen (CZ)
Volt	**P20**		x/o			x/o	o	x		RAGT (F)
Biathlon	**P21**	x/o				x/o	o			Florimont Desprez (F)
Tip	**P22**		o	x		x/o			x/o	Selgen (CZ)
Vitra	**P23**			x/o	x/o				o	AREI (LV)
Peps	**P24**			o		x/o		x	o	Selgen (CZ)
Karioka	**P25**	x	o			x/o		o		KWS Momont (F)
Milwa	**P27**	x/o				x/o	o			SMOLICE (Hodowla Roslyn Smolice) (PL)
Florida	**P28**			x/o	x/o				o	Saaten Union (NPZ Lembke) (D)
Natura	**P29**	o			x/o			o		Selgen (CZ)
Audit	**P30**		o	x		x/o		x	o	Limagrain (F)
Starter	**P31**	x/o				x/o	o			Saaten Union (NPZ Lembke) (D)
GM-short	**P09**									GM containing all short-stemmed genotypes
GM-long	**P26**									GM containing all long-stemmed genotypes
GM-semi-leafless	**P04**									GM containing all semi-leafless genotypes
GM-leafy	**P32**									GM containing all leafy genotypes

barley'), consisting of the seven barley genotypes, was created by mixing equal seed numbers of each line. Of the original 28 pea genotypes, five had to be excluded: P15 ('Mehis') and P23 ('Vitra') due to their too late maturity and P16 ('Tarchalska'), P17 ('Bluetooth') and P30 ('Audit') due to poor field emergence in the first experimental year (more than 20% below the average pea plant density). For means of consistency, these genotypes were kept in the GMs (if present there) in both years.

2.3. *Experimental design*

An incomplete factorial design was used that randomly combined every pea genotype with two barley genotypes and every barley genotype with eight pea genotypes thus resulting in 64 MS as described by Haug et al. (2021). The experimental design used, additional information on the randomization procedure and trial layout are shown in Fig. 2

Table 3
The seven two-row spring barley (*H. vulgare* L.) genotypes and the genotype mixture (‘GM’) used in the experiment. Traits scores average zero and positive/negative values indicate deviations from the mean. Trait-values were summed up and added with + 5 in order to receive a competition score from 1 to 9.

Cultivar	Barley code	Competition score	Stem length		Flag leaf size		Planophile/ erectophile		Tillering capacity		
		(1 =low, 9 =high)	long	short	large	small	planophile	erectophile	high	low	Breeding program (country)
Grandiosa (DZB0913c)	B1	**9**	3		1		1			-1	Cultivari (D)
Eunova	B2	**8**	2				1				Probsdorfer Saatzucht (AT)
GM-barley	B3	**6**									Multi-cultivar mixture
Zeppelin	B4	**1**		-2		-1		-1			Sejet (DK)
KWS Atrika	B5	**5**	0								KWS (D)
Propino	B6	**4**	0			-1					Syngenta (D)
Rubaszek	B7	**5**	0								Smolice (PL)
KWS Irina	B8	**6**		-2					3		KWS (D)

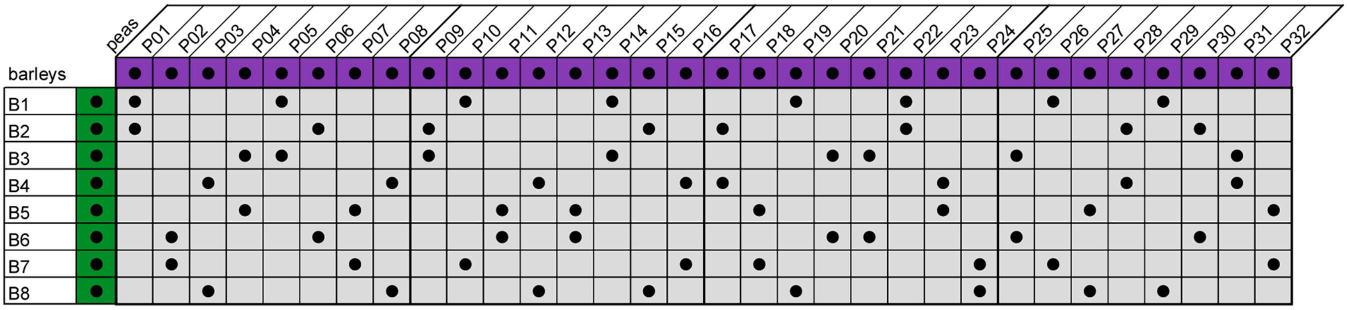

Fig. 2. Experimental design of both experimental years (2018 and 2019) arranged as an incomplete factorial. Every dot within the grey zone represents one specific mixture and empty cells represent unrealized mixtures. Dots within the green and purple zone represent barley and pea pure stands, respectively.

and Fig. S1. Details on the randomization procedure are given in the appendix under the section ‘Randomization procedure incomplete factorial’. Besides the mixed crops, pure stands of all used pea and barley genotypes, including of GMs, were grown. Each experiment comprised two blocks (replications). Field emergence was counted on a plot level to document differences in germination rate due to different seed sources three to five weeks after sowing and by counting twice 1 m per plot. Seed for the 2019 trial was taken from the 2018 trial, thus had uniform production conditions, and visual evaluation as well as counting on a sub-sample of the plots did not reveal significant differences between genotypes in field emergence in 2019. In total 960 experimental plots, comprising 616 MS plots, 64 barley PS plots and 280 pea PS plots, were sown, measured, and harvested across the two sites and two seasons of 2018 and 2019.

2.4. Measurements

Since pea was in the focus in this study, specific traits were measured in this species in addition to the yield recorded for the two species. These twelve pea traits were measured/scored in pea pure stands only: early vigor, early canopy height (at two dates), canopy height at grain filling and at maturity, onset of flowering, plant biomass, stipule length, diameter, and area (derived from length and diameter), lodging at grain filling and at maturity. See Table S1 for an overview over the data structure of the 12 traits measured. Early vigor was assessed between BBCH 25 and 36 as a score from 1 to 9 with 9 given for highly vigorous plants. The four canopy-height were measured at end of leaf development (BBCH 19), elongation (BBCH34–39), grain filling (BBCH 74–79) and maturity (BBCH 85). Onset of flowering was defined as the day after 1st of January when 50% of the plants of a plot had started flowering (BBCH 65). Plant biomass was assessed visually at onset of flowering (BBCH 65) with a scoring from 1 to 9 with 9 being plots with the highest biomass. At the same time, stipule length was measured in mm from the two most distinct tips of the 2nd topmost fully developed stipule and stipule diameter measuring the broadest part of one stipule leaf on four representative plants per plot. Stipule parameters were measured on the full set of genotypes in Fis 2018 and on a subset in the Fis 2019 experiment. Lodging was assessed in a 1–9 scale where 5 was a plot lodging in a 45° angle and 9 was a fully lodged plot. After harvest, MS and pure stand plot-harvests were wind-cleaned and MS were separated in pea and barley fraction yields with a sieving-machine. Pea and barley fraction yields were measured, and moisture standardized (14%) after NIRS measurement of water content. The total yield was then computed as the sum of these two fraction yields. When a high amount of broken pea kernels was present in the barley fraction yield, a cutoff-value of > 15% broken pea kernels was set for which the barley fraction yield data was not used, only total yield data (1.4% of all mixtures). The raw data of the four experiments, including yield and trait data, is available under https://doi.org/10.5281/zenodo.6480567.

2.5. Analysis of yield parameters: GMA, Pr/As, ratio pea, (p)LER and pure stand yield

2.5.1. Estimation of variance components for GMA, Pr- and As effects

In order to estimate variance components, the following models, (1), (2) and (3), were applied in which capital letters indicate random effects. The model for total mixture yield:

$$\begin{aligned} Y_{ijklm} =& \mu + a_k + l_l + r_{m(kl)} + G_{p_i} + G_{b_j} + S_{ij} + \left(G_p a\right)_{ik} + \left(G_p l\right)_{il} + \left(G_b a\right)_{jk} \\ &+ \left(G_b l\right)_{jl} + (Sa)_{ijk} + (Sl)_{ijl} + E_{ijklm} \end{aligned} \quad (1)$$

with Y_{ijklm} the total mixture yield of the i-th pea genotype mixed with the j-th barley genotype in k-th year, the ʟ-th location and the m-th block, μ the intercept of mixture yields, a_k the effect of the k-th year, l_l the effect of the ʟ-th location, r_m the effect of the m-th replication nested in year and location, G_{p_i} and G_{b_j} the GMA effects of the i-th pea genotype and the j-th barley genotype, respectively, S_{ij} the SMA effect, i.e. interaction, of the i-th pea genotype with the j-th barley genotype and E_{ijklm} the error term. The three-way interaction between GMA × year × location were not included (little or no influence on total variance, data not shown). The random effects and their interactions were assumed to be independent and normally distributed with respective variance components $\sigma^2_{Gp}, \sigma^2_{Gb}, \sigma^2_S$ and σ^2_E for GMA of pea and barley, SMA, and the error term, respectively, and mean zero. All variances are supposed to be homogeneous across years and locations. The models for pea and barley fraction yields for all locations and all years are shown in model (2) and model (3), respectively:

$$Y_{p\,ijklm} = \mu_p + a_k + l_l + r_{m(kl)} + P_{p_i} + A_{b_j} + S_{p_{ij}} + (P_p a)_{ik} + (P_p l)_{il} + (A_b a)_{jk} + (A_b l)_{jl} + (S_p a)_{ijk} + (S_p l)_{ijl} + E_{p\,ijklm} \tag{2}$$

$$Y_{b\,ijklm} = \mu_b + a_k + l_l + r_{m(kl)} + P_{b_j} + A_{p_i} + S_{b_{ij}} + (P_b a)_{jk} + (P_b l)_{jl} + (A_p a)_{ik} + (A_p l)_{il} + (S_b a)_{ijk} + (S_b l)_{ijl} + E_{b\,ijklm} \tag{3}$$

Model (2) with $Y_{p_{ijklm}}$ the pea fraction yield of the i-th pea genotype mixed with the j-th barley genotype in k-th year, the L-th location and the m-th block; μ_p the intercept of pea fraction yields, a_k the effect of the k-th year, l_l the effect of the L-th location, r_m the effect of the m-th replication nested in year and location on pea fraction yield; P_{p_i} and A_{b_j} the Producer effects of the i-th pea genotype and the Associate effect of the j-th barley genotype, respectively, $S_{p_{ij}}$ the interaction of the i-th pea and the j-th barley, and $E_{p_{ijklm}}$ the error term. Parameters apply in analogy for barley fraction yields in model (3). All random effects and their interactions are assumed to be independent and normally distributed with according variance components $\sigma^2_{Pp}, \sigma^2_{Pb}, \sigma^2_{Ap}, \sigma^2_{Ab}, \sigma^2_{Sp}, \sigma^2_{Sb}, \sigma^2_{Ep}$ and σ^2_{Eb} for Pr-effect of pea and barley, As-effect of pea and barley, SMAs of pea and barley fraction yields and error for pea and barley fraction yields, respectively, and mean zero. A likelihood ratio test was performed to estimate the significance of the variance components. All analysis were done with GNU R (R Core Team, 2019) using the packages 'lme4' (Bates et al., 2015) and 'lmerTest' (Kuznetsova et al., 2017).

2.5.2. Estimation of broad sense heritability

Broad sense heritabilities on mixture-mean basis of yields and of key traits were calculated assuming a balanced design (Schmidt et al., 2019), using the variance components defined in models (1), (2) and (3):

$$H^2 = \frac{\sigma^2_G + \sigma^2_S}{\sigma^2_G + \sigma^2_S + \frac{\sigma^2_{Gl}}{2} + \frac{\sigma^2_{Sl}}{2} + \frac{\sigma^2_{Ga}}{2} + \frac{\sigma^2_{Sa}}{2} + \frac{\sigma^2_E}{8}} \tag{4}$$

With σ^2_G the cumulated variance components of pea and barley genotypes (GMAs in the case of total yield, Pr- and As-effects in the case of fraction yields), σ^2_S the variance component of SMA, σ^2_{Gl}, σ^2_{Ga}, the cumulated variance components of the pea and barley treatment × location and pea and barley treatment × year interaction, respectively, σ^2_{Sl}, σ^2_{Sa} the cumulated variance components of the pea × barley × location and year interactions (SMA × location, SMA × year) and σ^2_E the cumulated variance component of the error. The denominator numbers correspond to the number of locations (2), years (2) and total plots (locations * years * replicates = 8), respectively.

2.5.3. Comparison of pure stand yields with total mixture yields and pea fraction yields of pea genotypes

Correlations between PS yields of pea and GMA and Pr effects of pea were used as a proxy for the predictive power of PS yields for these parameters. Two genotypes, P28 and GM-leafy, were excluded from the analysis due to their strong lodging. Correlations were calculated once analyzing all genotypes and once analyzing only semi-leafless genotypes (thus excluding P14, P29 and GM-long, which contained also leafy types).

2.5.4. Estimation of genotypic effects on GMA, Pr- and As-effects, on pea-ratio and on pure stand yields

Simplified versions of models (1), (2) and (3), without SMA, and setting all effects as fixed, were used to compute the effects of pea and barley genotypes on yield parameters across experiments (GMA, Pr and As effects, pea ratio of total yield, LER, and PS yields) using estimated marginal means (Lenth, 2019). The pea ratio of total yield is the pea fraction yield devided by total mixture yield. Land equivalent ratio (LER) and partial land equivalent ratios (pLERs) were calculated on a per plot basis according to Mead and Willey (1980). pLERs were calculated dividing the fraction yields of pea or barley of a mixture in each plot by the mean yield of the respective PS of the corresponding pea or barley genotypes at a given experiment, i.e., for an arbitrary pea genotype *i*, the formula was $pLER_{p_i} = y_{p_{i_{mix}}} \;/\; y_{p_{ipure}}$ (calculation for an arbitrary barley genotype *j* accordingly). The LER of a mixture plot was then calculated by the sum of both partial LERs: $LER_{ij} = pLER_{p_i} + pLER_{b_j}$. For PS yields formula (1) was used, omitting all effects of the absent species (including interactions). Within each species, all genotype-effects were tested against the null hypothesis H_0 of being indifferent to the mean, using a *t*-test with a false-discovery-rate p-value adjustment for multiple testing (Benjamini and Hochberg, 1995). For GMA, Pr- and As-effects, the sum of genotype × experiment interactions of each genotype (ecovalence, W_i) was computed as a measure of variability of genotypic effects across experiments (Wricke, 1962; Becker and Leon, 1988), using the ge_stats function of the GNU R package 'metan' (Olivoto and Lúcio, 2020) and regarding each of the four experiments as a separate environment.

2.5.5. Graphical analysis of GMA, Pr- and As-effects

Pr- and As-effects were plotted as a scatter plot and color-coded by their plant type (pea) or competitiveness (barley). Plant type of pea was described by leaf type (leafy or semi-leafless) and an *a posteriori* canopy height classification (see 'plant material', Table 2). Pr- and As- effects were plotted against GMA and Pearson correlations were calculated. A correlation and regression analysis were done with Pr and As effects in which P28 and GM-leafy were omitted due to their exceptionally high lodging.

2.5.6. Comparison between expected and observed yields of GMs

Expected values of GMA, Pr- and As- effects of all four pea GMs were calculated by taking the mean of these effects of all single genotypes that were contained in the respective mixture. GM-leafy and GM-long both contained P23 (cv. Vitra), an extremely late maturing genotype that was excluded after 2018, however, for means of consistency, was kept in these GMs also in 2019. The 2018 values of P23 were used to calculate expected values of these two mixtures in 2019. Expected vs. observed yields were compared using a *t*-test and displayed graphically.

2.5.7. Evaluation of Pr- and As-effects as predictors for yield stability

Scatter plots of the treatments' ecovalence of their Pr-effects and the ecovalence of their GMA were created and a correlation analysis was done (Olivoto and Lúcio, 2020 for As-effects).

2.6. Key trait analysis

Pairwise Pearson correlations between yield and all twelve traits were calculated (Fig. S2) followed by a procedure to select key traits for further analysis: among those traits that correlated to the total mixture yield ($r > 0.3$), the ones presenting the highest correlations were kept, discarding all "co-linear" traits, i.e. highly correlated to them ($r > 0.65$). Using this method, early vigor, onset of flowering, plant biomass and stipule length were selected for further analysis. These traits were plotted against GMA, Pr- and As effects, their correlations computed and subsequently their biological interaction function (BIF, Haug et al., 2021) was determined. The GMs were excluded from the trait analysis due to their heterogeneity and P28 (cv. Florida) was excluded due to extreme lodging, leading to an outlier value for its GMA, Pr and As effects.

3. Results

3.1. *Sizeable GMA, Pr- and As-effects and negligible SMA effects of pea and barley genotypes*

The weather conditions differed considerably between 2018 and 2019 with + 11.1% and − 3.5% temperature sums and − 31.1% and − 24.7% cumulative rainfall, respectively, compared to the long-term average (Fig. 1). Soil composition differed between sites with on average 8% higher sand and 16% lower clay content at the Fislisbach ('Fis') site compared with the Uster ('Ust') site. Available nitrogen levels were generally lower at Fislisbach (39 kg N/ha in average) compared to Uster (106 kg N/ha in average; Table 1). The overall mean of total mixture yields was 3.94 t/ha. The mean of mixture yields at the four different environments were 3.84 t/ha (Fis 2018), 3.93 t/ha (Ust 2018), 3.72 t/ha (Fis 2019), and 4.26 t/ha (Ust 2019), respectively. Plants responded to the variable conditions with variable pea and barley fraction yields in each of the four experimental environments (Fig. 3). Comparing the means of the four experimental environments, the min-to-max spread of mixed stand total yield was 0.55 t/ha while there was a much larger spread of pea and barley PS with a min-to-max spread between the means of the four environments of 1.33 t/ha for pea and 2.06 t/ha for barley (Fig. S3).

In the following, only significant variance components ($P < 0.05$) are stated. Pea fraction yield was influenced by pea genotype × year interactions and, to a smaller degree, by pea genotype and its interaction with location, as well as by barley genotype (Fig. 4). Broad sense heritability (H^2) of pea fraction yield was 0.37. Barley fraction yield was influenced by pea genotype, barley genotype and – to a lower degree – by the year and location interactions of pea and barley genotypes. Broad sense heritability H^2 for barley fraction yield was 0.75. The leafy genotypes of pea were the main reason causing the large variance component for pea genotype (As pea) on barley yield (data not shown). Total mixed stand yield was mainly influenced by pea genotype (GMA pea), pea genotype × year interactions, and barley genotype × location interactions (barley GMA variance was not significant). The broad sense heritability (H^2) of total mixture yield was 0.59. For all three yield types, variance components of SMA and its interactions with year and location were zero or close to zero. See Fig. S5 for interaction plots of all pea genotypes.

3.2. *Genotypes acted and reacted in a multifaceted manner towards mixed cropping*

Pea genotypes displayed a larger spread of yield effects than barley genotypes for all relevant yield parameters: GMA, Pr, As, ratio of pea, LER, and PS yield (Table 4). For instance, GMA effects of pea ranged from − 1.23 to + 0.43 t/ha, and from − 0.19 to + 0.24 t/ha for barley. Note that MS strongly stabilized total and fraction yields, which exhibited much lower mean ecovalences W_i than the PS ones (Table 4). When mixed with barley, 23 out of 27 pea genotypes exhibited lower W_i as in PS. Same for barley: when mixed with pea, six out of eight genotypes showed lower values for W_i as in PS. For pea, two genotypes showed a significant negative GMA effect (the leafy genotypes P28, GM-leafy) and four genotypes (the medium or long genotypes P12, P14, P20, P25) a significant positive GMA effect. Both genotypes with a negative GMA were strongly lodging (Table S2). The genotype mixture GM-semi-leafless, was the most stable genotype across all experimental environments in terms of GMA ecovalence ($W_i = 0.004$). GM-leafy was the most stable genotype regarding Pr effects ($W_i = 0.04$). Interestingly, its components, the three individual leafy genotypes P14, P28 and P29 were the least stable for Pr and GMA, with ecovalence values of these genotypes ranging between 1.23 and 1.97, and 0.83 and 2.40, for Pr and GMA respectively. The average ratio of pea in the total mixture yield was 0.46, hence lower than the sowing-ratio (0.66). Average LER across all treatments and experiments was 1.09 with individual LER values ranging for pea genotypes from 0.99 (P18) to 1.48 (P28). Only leafy genotypes and GM-long (containing a considerable portion of leafy genotypes) showed significant positive LERs.

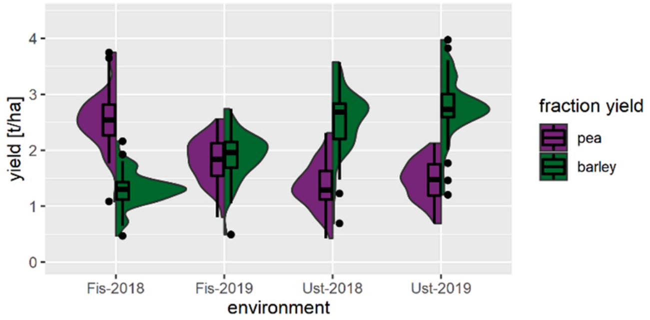

Fig. 3. Violin plots and boxplots of fraction yield data of the mixed stands for the two locations Fislisbach (Fis) and Uster (Ust) in two years. For pure stand yields see Fig. S3.

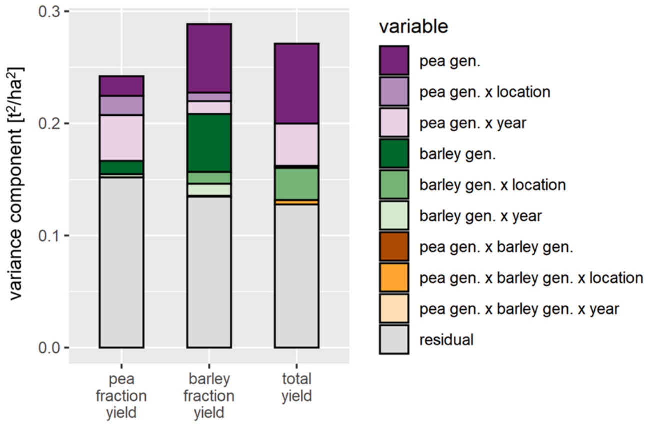

Fig. 4. Size of variance components for the mixed stands' fraction yields and total mixture yield in t^2/ha^2. In the case of pea fraction yield, pea genotypic variance ('pea gen.') corresponds to Pr (producer) variance of pea and barley genotypic variance ('barley gen.') to As (associate) variance of barley. Consequently, for barley fraction yield, pea genotypic variance corresponds to As variance of pea and barley genotypic variance to Pr variance of barley. For total yield, pea genotype and barley genotype correspond to the GMA of pea and barley. For all yield types, pea genotype × barley genotype interactions correspond to the specific SMA variances.

For barley, differences between genotypes for the various yield measures were generally much lower than for pea. MS with B7 resulted in significantly lower LER (−0.08), while B6 had lowest PS yield. B2 had highest GMA and Pr effect, while B1 was highest yielding in PS (Table 4). Stability of the barley genotypes for the different yield parameters was considerably higher compared with the pea genotypes.

A negative correlation ($r = -0.65$, $p < 0.001$) with a slope of − 0.93 was observed between Pr and As effects of pea (Fig. 5A). Six genotypes were observed to break with the Pr/As trade-off pattern, having a significant positive or negative GMA (Fig. 5A, Table 4). Among those with a positive GMA, a broad spectrum of different trait- and effect-patterns was associated with their positive effect on mixture yield. For example, for P20 the above average GMA was associated with a positive As-effect (Table 4, Fig. 5A), while the positive GMA of P14 was due to a high, positive Pr effect that wasn't offset by an equally strong negative As effect. Three out of the four pea genotypes with significant positive GMA on total mixture yield were medium-sized and showed a dominant Pr effect. Short- and long-sized genotypes did not exhibit a clear pattern regarding GMA (positive or negative), however, long sized genotypes, either leafy or semi-leafless, were spread mostly in sectors with positive

Table 4

Yield parameters of the tested pea-barley mixed crop combinations and their corresponding PS yields for the 27 pea and 8 barley genotypes. All variables are expressed as effects, i.e., centered around the mean of each variable within each species over all blocks, locations, and years. Significances are given for a t-test against the mean. The size of genotype × experiment interaction of each genotype is given in the form of ecovalence (W_i) with higher values indicating stronger G×E interaction.

	Plant size and leafiness[a]		Total yield		Pea fraction yield		Barley fraction yield		Ratio pea of total yield		LER	Pure stand yield	
Pea genotype			GMA pea [t/ha]	W_i	Pr-effect pea [t/ha]	W_i	As-effect pea [t/ha]	W_i	%	W_i		Pure stand yield pea [t/ha]	W_i
P01-SG-L 7647	**L**	**s. leafl.**	-0.24.	*0.69*	-0.14	*0.47*	-0.11	*0.28*	0.00	*0.012*	-0.09*	0.12	*0.60*
P02-Impuls	**L**	**s. leafl.**	0.17	*0.10*	0.41**	*0.50*	-0.22	*0.46*	0.09**	*0.030*	-0.03	0.43*	*0.98*
P03-Astronaute	**S**	**s. leafl.**	0.03	*0.33*	-0.02	*0.42*	0.05	*0.04*	-0.02	*0.010*	-0.08.	0.41*	*0.45*
P05-Navarro	**S**	**s. leafl.**	0.01	*0.28*	-0.08	*0.06*	0.08	*0.34*	-0.01	*0.003*	-0.06	0.27	*0.39*
P06-Gambit	**L**	**s. leafl.**	0.12	*0.31*	0.41**	*0.50*	-0.30*	*0.33*	0.10***	*0.014*	-0.09*	0.38*	*0.46*
P07-Angelus	**S**	**s. leafl.**	-0.15	*0.13*	-0.23	*0.20*	0.08	*0.56*	-0.04	*0.017*	-0.08.	-0.03	*0.23*
P08-Salamanca	**L**	**s. leafl.**	0.23	*0.20*	0.17	*0.31*	0.11	*0.36*	0.00	*0.017*	-0.05	0.70***	*0.54*
P10-Rocket	**M**	**s. leafl.**	0.04	*0.38*	-0.20	*0.63*	0.23	*0.49*	-0.06*	*0.038*	-0.06	0.50**	*0.71*
P11-Karpate	**S**	**s. leafl.**	0.11	*0.21*	-0.06	*0.40*	0.17	*0.04*	-0.03	*0.011*	-0.01	0.14	*0.36*
P12-Kayanne	**M**	**s. leafl.**	0.32*	*0.17*	0.26	*0.17*	0.09	*0.01*	0.01	*0.003*	0.01	0.30	*0.75*
P13-Mytic	**S**	**s. leafl.**	-0.11	*0.73*	-0.21	*0.92*	0.11	*0.07*	-0.04	*0.031*	-0.06	0.15	*2.48*
P14-Protecta	**L**	**leafy**	0.40***	*0.93*	0.47***	*1.97*	-0.07	*0.48*	0.06*	*0.049*	0.15***	-0.55**	*1.12*
P18-Alvesta	**S**	**s. leafl.**	-0.07	*0.16*	-0.08	*0.11*	0.00	*0.15*	-0.01	*0.003*	-0.10*	0.47*	*1.64*
P19-Bockros	**M**	**s. leafl.**	0.10	*0.56*	-0.19	*0.51*	0.25.	*0.28*	-0.06.	*0.011*	-0.03	0.12	*2.60*
P20-Volt	**M**	**s. leafl.**	0.43***	*0.13*	0.06	*0.49*	0.37**	*0.75*	-0.03	*0.032*	0.04	0.46*	*1.26*
P21-Biathlon	**S**	**s. leafl.**	0.13	*0.11*	-0.04	*0.45*	0.18	*0.21*	-0.02	*0.024*	0.03	-0.12	*0.24*
P22-Tip	**M**	**s. leafl.**	-0.06	*0.15*	0.03	*0.40*	-0.10	*0.86*	0.02	*0.031*	-0.07	0.25	*0.11*
P24-Peps	**L**	**s. leafl.**	0.08	*0.35*	0.05	*0.96*	0.02	*0.18*	0.00	*0.040*	-0.08.	0.61**	*0.65*
P25-Karioka	**M**	**s. leafl.**	0.30*	*0.05*	0.20	*0.25*	0.10	*0.33*	0.02	*0.015*	-0.05	0.83***	*1.26*
P27-Milwa	**S**	**s. leafl.**	-0.12	*0.10*	-0.32*	*0.10*	0.19	*0.06*	-0.07**	*0.007*	0.02	-0.45**	*1.54*
P28-Florida	**L**	**leafy**	-1.23***	*2.40*	-0.23	*1.49*	-1.00***	*0.54*	0.11***	*0.020*	0.39***	-2.35***	*0.59*
P29-Natura	**S**	**leafy**	-0.15	*0.83*	-0.37**	*1.23*	0.22.	*0.16*	-0.09**	*0.039*	0.03	-0.83***	*3.12*
P31-Starter	**S**	**s. leafl.**	-0.15	*0.39*	-0.33*	*0.26*	0.19	*0.54*	-0.08**	*0.019*	-0.06	-0.08	*0.28*
P09-GM-short	**M**	**both**	0.14	*0.23*	-0.03	*0.09*	0.16	*0.05*	-0.01	*0.002*	-0.03	0.21	*0.67*
P26-GM-long	**L**	**both**	0.06	*0.14*	0.37**	*0.14*	-0.31*	*0.15*	0.09**	*0.004*	0.03	-0.26	*0.38*
P04-GM-semi-leafless	**M**	**s. leafl.**	0.19	*0.00*	0.06	*0.11*	0.13	*0.15*	0.00	*0.006*	0.02	0.06	*0.43*
P32-GM-leafy	**L**	**leafy**	-0.58***	*0.30*	0.04	*0.04*	-0.62***	*0.53*	0.11***	*0.020*	0.33***	-1.73***	*2.00*
min. (effect)			-1.23	*0.00*	-0.37	*0.04*	-1.00	*0.01*	-0.09	*0.002*	-0.10	-2.35	*0.11*
mean (effect)			0.00		0.00		0.00		0.00		0.00	0.00	
max. (effect)			0.43	*2.40*	0.47	*1.97*	0.37	*0.86*	0.11	*0.049*	0.39	0.83	*3.12*
mean			**3.94**	*0.38*	**1.79**	*0.49*	**2.14**	*0.31*	**0.46**	*0.019*	**1.09**	**3.72 (pea)**	*0.96*
Barley genotype	**Competition score[2]**		GMA barley [t/ha]	**W_i**	As effect barley [t/ha]	**W_i**	Pr effect barley [t/ha]	**W_i**	Ratio pea of total yield	**W_i**	**LER**	Pure stand yield barley [t/ha]	**W_i**
B1-DZB0913c	**9**		0.14*	*0.24*	-0.22**	*0.27*	0.37***	*0.35*	-0.07***	*0.016*	-0.01	0.34*	*1.08*
B2-Eunova	**8**		0.24*	*0.72*	-0.19	*0.09*	0.43***	*0.36*	-0.08***	*0.001*	0.02	0.23.	*0.30*
B3-GM-barley	**6**		-0.07	*0.02*	-0.07	*0.05*	-0.01	*0.08*	-0.01	*0.004*	0.02	-0.29*	*0.46*
B4-Zeppelin	**1**		-0.02	*0.00*	0.15	*0.06*	-0.18.	*0.05*	0.05*	*0.001*	-0.03	0.15	*0.32*
B5-KWS Atrika	**5**		0.11	*0.14*	0.14	*0.01*	-0.03	*0.17*	0.02	*0.004*	-0.02	0.30*	*0.21*
B6-Propino	**4**		-0.19*	*0.38*	0.09	*0.16*	-0.28***	*0.35*	0.03.	*0.007*	0.05	-0.70***	*0.26*
B7-Rubaszek	**5**		-0.19*	*0.04*	0.08	*0.13*	-0.27***	*0.13*	0.04*	*0.008*	-0.08**	0.20	*0.44*
B8-KWS Irina	**6**		-0.01	*0.09*	0.02	*0.12*	-0.04	*0.18*	0.01	*0.008*	0.04	-0.23.	*0.32*
min. (effect)			-0.19	0.00	-0.22	*0.01*	-0.28	*0.05*	-0.08	*0.001*	-0.08	-0.70	*0.21*
mean (effect)			0.00		0.00		0.00		0.00		0.00	0.00	
max. (effect)			0.24	0.72	0.15	*0.27*	0.43	*0.36*	0.05	*0.049*	0.05	0.34	*1.08*
mean			**3.94**	*0.20*	**1.79**	*0.11*	**2.14**	*0.21*	**0.46**	*0.016*	**1.09**	**3.78 (barley)**	*0.42*

[a] Plant sizes: S(hort), M(edium) and L(ong); leafiness: semi-leafless ('s. leafl.') or 'leafy', [2]Ranging from low, i.e. '1′, to high, i.e. '9′, competition, see main text

Pr effects (Z, U and V in Fig. 5). Pr and As effects were both positively correlated with GMA ($r = 0.50$, $p = 0.008$, slope 0.69 and $r = 0.72$, $p < 0.001$, slope 0.80 respectively, Fig. 5 B and C). When the two highly lodging genotypes P28 and GM-leafy were excluded, the correlation of Pr effects with GMA remained ($r = 0.71$, $p < 0.001$, slope 0.52, Fig. 5 B) but the correlation between As-effects and GMA vanished ($r = 0.07$, $p = 0.736$, slope 0.07; Fig. 5C; by definition, all intercepts of regressions in Fig. 5 (A-C) and Fig. 6 (A-C) are zero).

For barley, a negative correlation ($r = -0.89$, $p = 0.003$) with a slope of − 1.65 was observed between Pr- and As-effects (Fig. 6A). Two genotypes (B6, B7) showed a significantly negative and two genotypes (B1, B2) a significantly positive GMA. As for pea, barley GMA was positively correlated with its Pr effect ($r = 0.89$, $p = 0.003$, slope 0.51; Fig. 6 B), while the negative tendency between GMA and As effects was not significant ($r = -0.59$, $p = 0.123$, slope -0.51; Fig. 6C).

Ecovalence W_i of GMA was positively correlated with the W_i of the Pr effects of pea ($r = 0.77$, $p < 0.001$) and barley ($r = 0.84$, $p = 0.009$) and was uncorrelated with the W_i of As effects of both pea and barley (Fig. 7, Fig. S8).

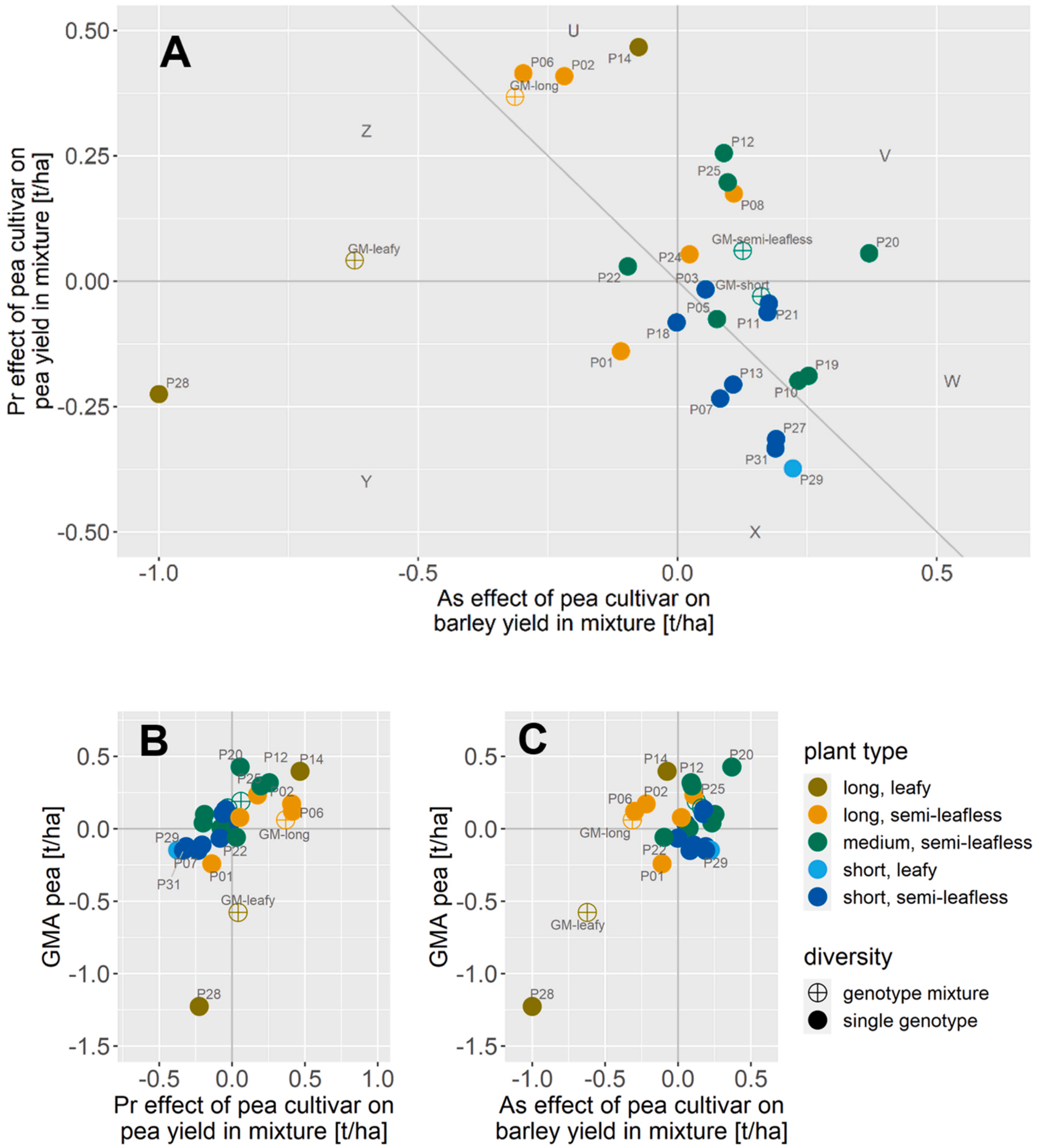

Fig. 5. (A) Scatterplot of Pr- and As-effects of 27 pea genotypes grown in mixture with barley over two years and two locations. The diagonal line with slope –1 and intercept 0 separates genotypes with positive (above) and negative (below) GMA. According to their positive or negative Pr, As or GMA effects, genotypes group into different sectors (U to Z). (B) Scatterplot of Pr and GMA of pea. (**C**) Scatterplot of As and GMA of pea.

3.3. Correlation of pea GMA and Pr-effects with pure stand yields is associated with leafiness

Correlations of PS yields with GMA and Pr effects were dependent on the presence of foliar leaves (and consequently the absence of large tendrils) in pea (Fig. 8A, following page). All leafy genotypes and GM-long (containing, amongst others, long, leafy genotypes) were strongly lodging in PS (Table S2). No significant correlation was observed neither between pea PS yield and GMA ($r = 0.31$, $p = 0.123$) nor between pea PS yield and Pr effect of pea when all genotypes were considered ($r = 0.28$, $p = 0.182$; Fig. 8 A). However significant correlations were observed between PS yields and GMA ($r = 0.52$, $p = 0.013$) and PS yields and Pr effects ($r = 0.60$, $p = 0.003$) when only semi-leafless genotypes were analyzed (Fig. 8A). In analogy to these correlations between PS yield and GMA, semi-leafless pea genotypes showed no interaction with growing condition (mixed stand or PS; Table S4). Barley GMA was significantly correlated with PS yield ($r = 0.631$, $P < 0.05$; Fig. S4), however barley genotypes showed significant interaction with growing condition (Table S4). Both pea and barley genotypes reacted to their cropping condition (mixed or PS) by exhibiting altered phenotypes with respect to plant height and width (see Fig. 8 B and Fig. S9 for representative examples).

3.4. Pea genotype mixtures (GMs) promoted yield stability in one case yield performance

All four pea GMs were within the eight pea genotypes with the most stable Pr effects (Table 4). Three GMs (GM-short, GM-long, and GM-semi-leafless) were among the six genotypes with the most stable pea ratios in mixture. An analysis of variance of the four GMs revealed that GMs exhibited considerably less genotype × year and genotype × location interactions than the 23 single genotypes for GMA as well as

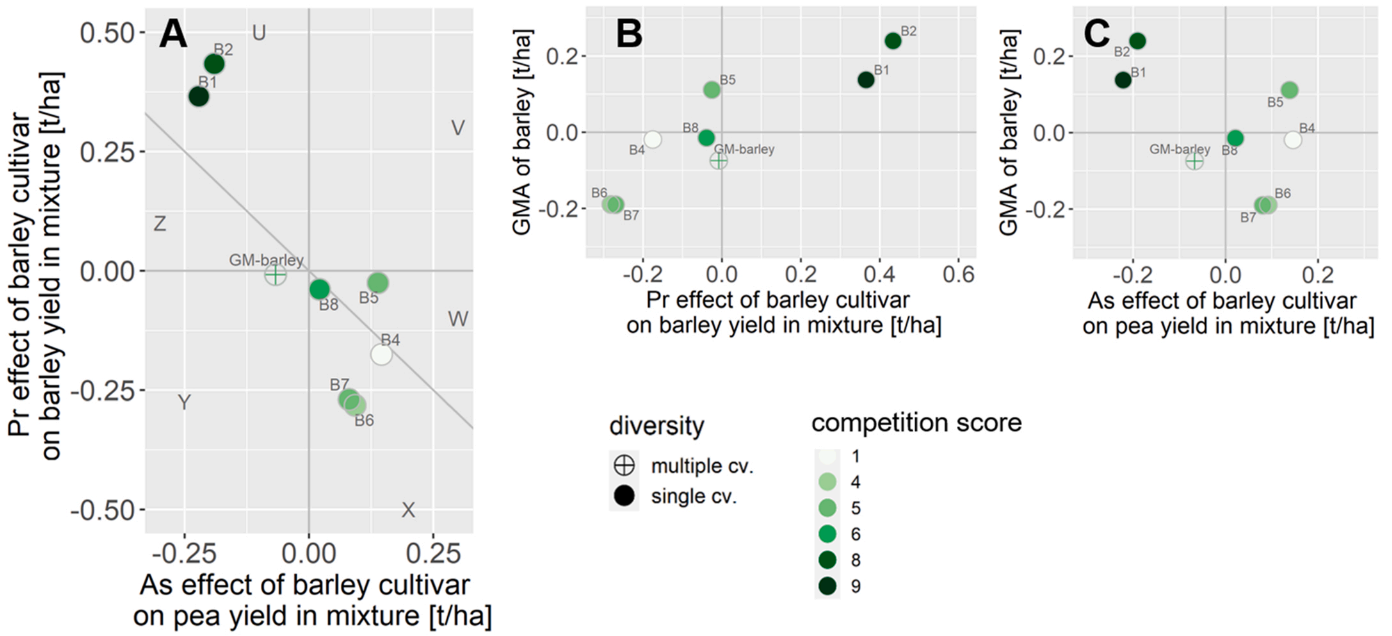

Fig. 6. (A) Scatterplot of Pr- and As-effects of eight barley genotypes grown in mixture with pea over two locations and two years. The diagonal line with slope –1 and intercept 0 separates genotypes with positive (above) and negative (below) GMA. (B) Scatterplot of Pr-effects and GMA of barley and (C) Scatterplot of As-effects and GMA of barley.

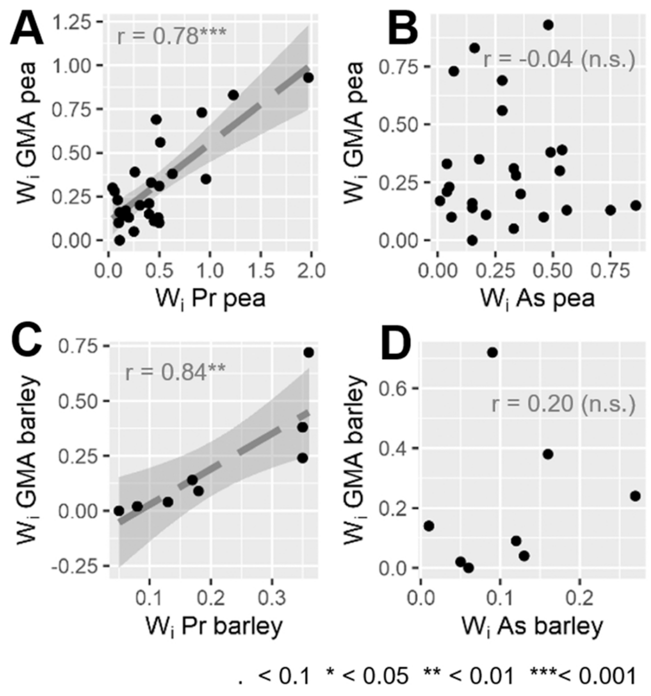

Fig. 7. Regression plots of Ecovalence (Wi) of Pr- and As-effects of pea and barley with the W_i of their corresponding GMA. In cases where correlation was significant, dashed lines indicate the corresponding linear regression with 95% confidence intervals.

for Pr and As effects (Table S3). GM-long provided a significantly higher pea ratio (+9%) at a high stability, as well as a significantly higher GMA compared to the calculated mean of its components (i.e. the compared to the expected value, Fig. 9). Significant differences in GMA between realized and expected values were only observed for GM-long with + 0.39 t/ha (p = 0.040) realized yield. Significant differences in Pr and As effects between realized and expected values were only observed for GM-leafy with a − 0.20 t/ha (p = 0.040) realized As effect.

3.5. *Analysis of key traits and determination of their biological interaction functions (BIFs)*

Broad sense heritabilities of the four key traits, early vigor, onset of flowering, biomass, and stipule length were 0.49, 0.86, 0.71 and 0.89, respectively. Stipule length showed a significant correlation with GMA (r = 0.45, p = 0.034) and early vigor tended towards a significant correlation with GMA (r = 0.41, p = 0.058), while onset of flowering and biomass were not significantly correlated with total mixture yield (Fig. 10).

Concerning biological interaction functions (BIFs) of pea traits (Haug et al., 2021), early vigor was associated with an antagonistic (opposite slopes in Pr and As regressions) as well as with a commensalistic BIF. Biomass, however, corresponded to a clear antagonistic trait action among the two crops. Onset of flowering showed a tendency towards an amensalistic trait action. Stipule length showed a tendency towards a mutualistic or commensalistic trait action. Early vigor was associated with higher PS yield (r = 0.43, p = 0.048), and biomass tended to stimulate higher PS yields (r = 0.42, p = 0.051). Neither onset of flowering, nor stipule length were associated with higher PS yields. Table S2 shows the mean value of traits for of all 27 pea genotypes and Fig. S2 shows a correlation-matrix of the twelve putative key traits.

4. Discussion

4.1. *Consequences for breeding for mixed cropping*

This study investigated the genetic effects of a morphologically diverse panel of 27 spring pea and 8 spring barley genotypes representative of European breeding material on total and fraction yields of their mixed crops in the scope of providing insights on breeding for MC in general and for pea and barley in particular. The fact that according to our findings SMA in this mixed crop was low or absent, simplifies future efforts to select, market, and grow superior genotypes for this system. In breeding, after a test for GMA, specific combinations of genotypes do not have to be verified any more (test for SMA) and thus substantially

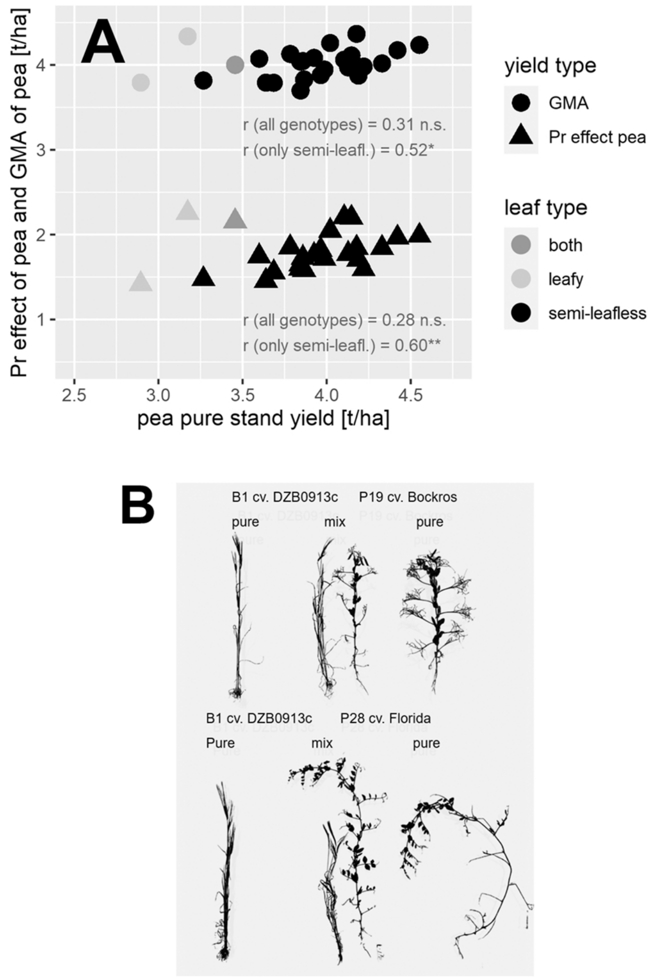

Fig. 8. (A) Regression plot of GMA and pea Pr effect as a function of pea PS yield. Two correlations were computed per effect, one using all genotypes (Pearson correlation ‘r’) and the other using semi-leafless genotypes only (black symbols). (B) Pictures of plants from PS and mixture plots of two exemplary MS (representative plants taken from plots at the Fis 2019 experiment).

reduces experimental effort; in seed marketing this creates flexibility for retailers as they can combine seeds of both species by their preference; finally, farmers can combine genotypes of both species without having to fear unexpected behavior by the choice they have made. The non-significant SMA might be due to the low morphological diversity available in released spring barley genotypes in Europe, as all of them were two-row types. Previous on-farm trials with winter pea and winter barley in Switzerland resulted in the recommendation of two-row for MC as six-row barley were too competitive (Dierauer et al., 2017). It might thus be related to the situation in modern elite corn/climbing bean material (Hoppe, 2016; Starke, 2018), where lack of SMA was also assumed to be related to the low morphological diversity in German (silage) corn breeding material. On the pea side, morphological diversity of modern elite material was higher (and could yet have been increased by the use of landraces or gene-bank accessions). Thus, depending on what material is used, SMA should be regularly monitored in future breeding efforts. That is particularly true for genotypes that are specifically developed for MC and whose traits change important parameters such as the leaf area or phenology (see also Section 4.4 on key traits). For the status quo, our results suggest that currently available pea and barley material can readily be combined and genotypes of both species with high GMA are expected to produce best results. Our findings are in line with other findings in corn-common bean MS (Hoppe, 2016; Starke, 2018) and wheat-faba bean MS (Siebrecht-Schöll, 2019) that SMA plays a negligible role in cereal – legume MS. The highest GMA in pea was attained by a leafy genotype and given the small number of genotypes registered, it might be tempting to consider this plant type for breeding of pea for MC. However, the high G×E of these genotypes, observed in our data, is an undesirable feature and breeding programs should focus on semi-leafless types (see Section 4.3.2). Under the given pedoclimatic conditions of the experiment (maritime influenced central European climate), the use of leafy types in pea genotype mixtures (GMs) for MC however should be examined further, as one mixture, containing both leafy and semi-leafless genotypes (GM-long), showed higher GMA than the mean of its components would suggest (see also Section 4.3.3 for its higher yield stability) hinting to an increased plant-community resource capture when these two leaf types are combined. Some superior pea genotypes, all from the semi-leafless type, showed potential to produce above-average mixture yields and might give important insights on how to improve mixture yields by targeted selection, especially regarding stem length. The fact that among semi-leafless pea genotypes best performances were achieved solely by genotypes of medium stature (P12, P20 and P25, all mapping to sector V in Fig. 5 A, i.e., having both positive Pr and As effects) indicates that this group of genotypes explored free niches in the plant community more efficiently than long or short genotypes. Therefore, trying to increase GMA by long plants as suggested by Annicchiarico et al. (2019) is only possible to a certain degree. Our observation also underpins the theory that productivity of plant communities is governed by an optimal balance between competitiveness of the two species (Wendling et al., 2017), avoiding too strong selection effects of any of the species involved (Schöb et al., 2015; Brooker et al., 2021). The fact that three semi-leafless pea genotypes of medium-size (P12, P20 and P25) having either neutral or advantageous trait values for the key traits identified in Section 3.5 (early vigor, onset of flowering, and stipule length), might be an explanation for their positive GMA. However, two medium-sized semi-leafless pea genotypes (P10 and P22) had a disadvantageous value in one of the mentioned key traits (Table S2). This highlights the importance of keeping – besides leafiness and stem length – the traits early vigor, onset of flowering and stipule length in mind for selection of superior pea genotypes for MC (see Section 4.5). Even though an in-depth analysis of barley for its aptitude for MC wasn’t the scope of this research, the significant positive GMA of B1 and B2, both having a high ‘competition score’ (and a high Pr effect, see Section 4.4), might hint towards possible selection strategies. Our results indicate that barley genotypes with traits that provide above average competitive ability (tillering capacity, planophile leave angle, stem length, flag leave size) might be recommendable to attain a high GMA when mixed with pea.

4.2. Pure stand yield as a proxy for GMA estimation

The significant correlation observed in this study between PS yield of pea and mixture yield allows the use of PS yield information for several purposes in MC. At least for semi-leafless leaf types, it can be usefully integrated into a MC breeding program, and farmers and seed retailers can use PS yield of the corresponding pea genotype as a proxy for total and pea fraction yield. The observed correlation between PS and mixture yield ($r = 0.52$) lies in the range of previously reported values (Annicchiarico et al., 2019; Hoppe, 2016) and neither justifies a completely independent breeding program for MC, nor will a selection by PS yields alone lead to high selection gain in MC.

4.3. Stability

4.3.1. Higher yield stability in mixed stand vs. pure stand

Our results show a clear advantage of mixing pea with barley in terms of yield stability as shown by the dramatic reduction of min-to-max ranges of yields in mixture versus pure stand, as well as by the overwhelmingly lower values of ecovalence W_i in MS compared to PS. In our case, the combination of two different years (2018: dry and hot,

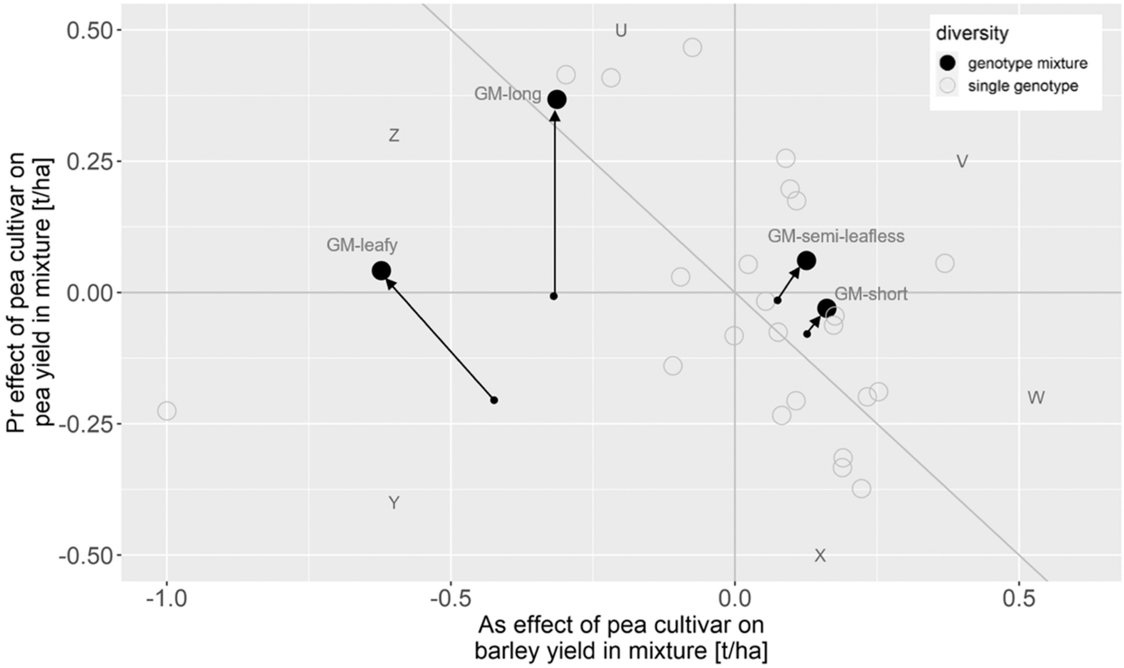

Fig. 9. Expected versus realized values of genotype mixtures (GMs). The small black dots are the expected value of the GM that are based on the arithmetic means of the Pr- and As-effects of the genotypes that are contained in the corresponding GM. The black arrows connect the expected mean of the mixture with the realized value (large black dots). The higher the change of distance to the diagonal line, the stronger the effect on GMA. Only the positive realized GMA of GM-long and the negative realized As-effect of GM-leafy were significant.

2019: dry but normal temperatures) and two different locations (Fis: low soil-N-availabity, Ust: high soil-N-availability) provided a suitable environment to demonstrate the buffering capacity of mixed crops under divergent pedo-climatic conditions under a low-fertilization regime (e.g., organic agriculture). Our results are in line with earlier observations (e.g. Rao and Willey, 1980), and were lately confirmed for pea and barley MS by a meta-study (Raseduzzaman and Jensen, 2017). However, the methodology of this latter study, which used the coefficient of variance (CV) to determine yield stability, was disputed by other authors, who themselves used a different measure for yield stability, i.e. an adjusted CV (Döring and Reckling, 2018), which accounts for the dependency of the size of the variance from the yield level of a data set, and who did not find evidence for higher yield stability in mixed stand for pea and barley (Weih et al., 2021). In their study, fertilization levels were considerably higher than under our experimental setup and pea and barley was sown in a ratio of 50:50, respectively (our study: 67:33), probably resulting in high barley plant densities and barley ratios in the harvest. Such unbalanced MS might not profit from the (presumably) stabilizing effect of a more balanced mixture. Based on our findings, a general recommendation of MC of pea and barley to stabilize yields thus can be given with a certain reservation for low-fertilization regimes such as organic agriculture, as our results clearly do indicate a stabilizing effect of MC.

4.3.2. *Fully leafed peas showed low yield stability*

The difference in temperature of the two experimental years probably caused the high genotype × year (G×Y) interaction for pea genotypes for total and fraction yields (Fig. 4). A large part of the strong G×Y interaction of pea genotypes is attributable to leafy types (Fig. S6 A). This particular plant type has a higher tolerance towards drought stress due to a generally more vigorous rooting system and higher rooting depths, as well as a capacity to change leaf exposition to sunlight, leading to an increased water use efficiency (Ali et al., 1994; Armstrong et al., 1994). This might have been a particular advantage over semi-leafless types in the dry and hot year 2018, while in the colder year 2019, these genotypes became too vegetative (i.e. biomass) and couldn't realize the same yield potential as in 2018. The use of leafy pea genotypes for MC with barley thus cannot be recommended based on our findings for maritime-influenced European climates.

4.3.3. *Genotype mixtures have potential to stabilize mixed stand yields*

While already investigated in grasslands (Prieto et al., 2015), to our knowledge, this is the first study that investigated the combined effect of interspecific (mixed cropping) *and* intraspecific diversification (genotype mixtures) on the performance and stability of an annual mixed crop. The fact that this GM-long (unintentionally containing also medium and short genotypes; see Section 2.1) performed significantly better in terms of pea fraction yield and total and fraction yield stability compared with the expected mean of its components might be caused by a positive effect of high trait diversity. This GM effectively presents divergences for one or several of the three traits leaf type, plant height and lodging resistance. The problem of assembly rules in plant mixtures is a matter of current scientific discussion (Louarn et al., 2020; Montazeaud et al., 2020). Our observation might suggest these three traits as a starting point for assembly rules in pea. All GMs of both pea and barley showed generally higher GMA and Pr stability than the average of twenty-eight cultivars when mixed with barley. This is in line with earlier reports on stabilizing effects of cultivar mixtures in pure crop (Reiss and Drinkwater, 2018) and in grassland species mixtures (Prieto et al., 2015; Carlsson et al., 2017). Thus, intraspecific diversification of mixed crops can be an important future strategy to maintain high and stable yields of a desired component in a mixture.

4.4. *Producer effects are the key for increasing GMA*

Instability of a both a pea and barley genotype's Pr effect led to instability of its GMA, while instability of its As effect did *not* lead to instability of its GMA (Fig. 7). Stability of mixed stand yields is thus mainly mediated by the stability of producer effects, in agreement with the strong relationship between Pr effects and GMA and no relationship between As effects and GMA, as observed in both species (Fig. 5 B, C and Fig. 6 B, C). It has been recommended for pea (and in general) to

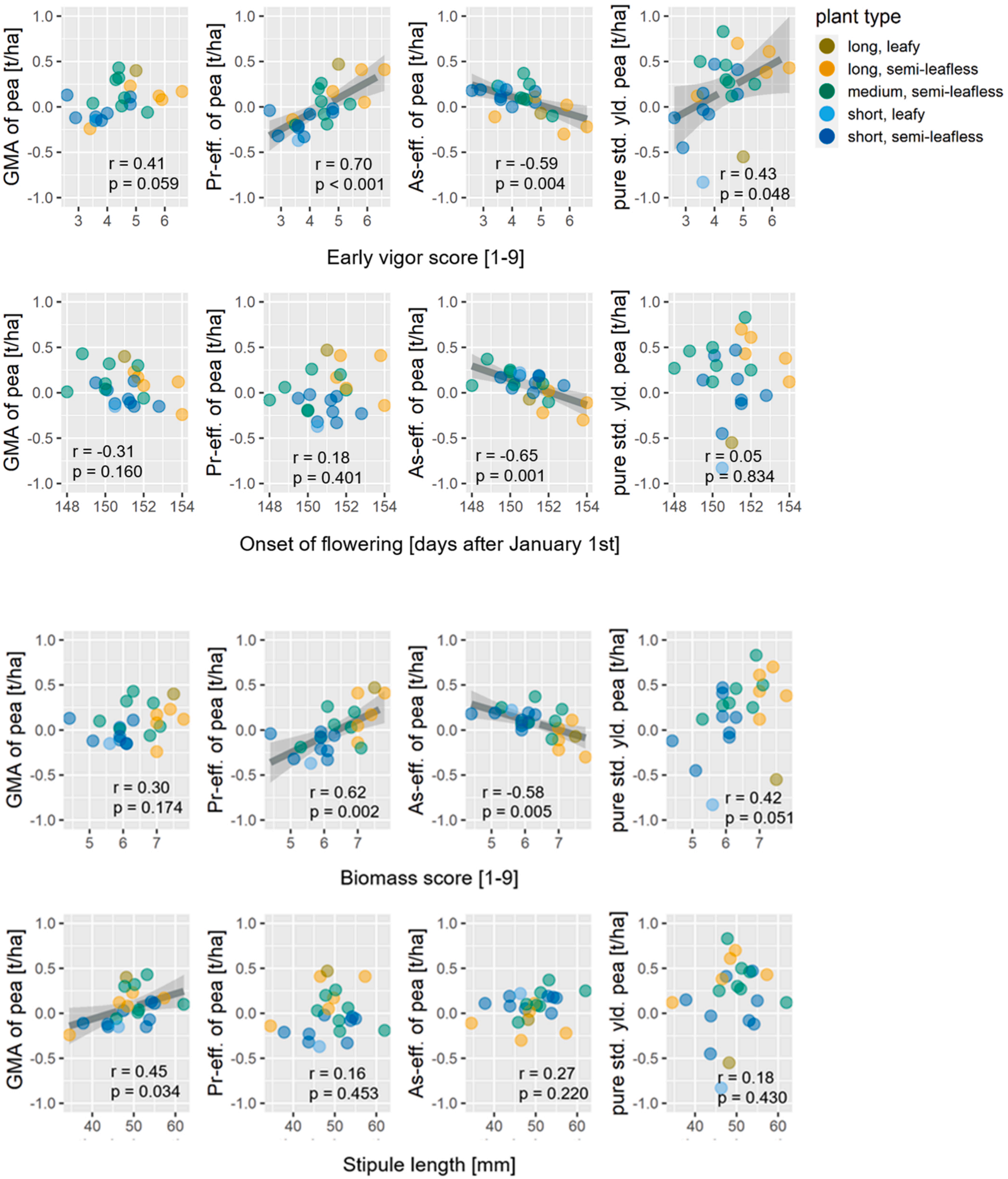

Fig. 10. GMA, Pr and As effects and pea pure stand yields as functions of four putative pea key traits: early vigor, flowering time, biomass, and stipule length. The grey line denotes the linear regression with 95% confidence intervals, 'r' the Pearson correlation coefficient with its level of significance ('p'). GMs were excluded due to heterogeneous trait measurements, and P28 was excluded due to strong lodging.

strengthen competitive ability of a species that is in competitive disadvantage to maximize mixture yields (Annicchiarico et al., 2019). In a scenario where one species is at competitive disadvantage, it would thus be expected to see a positive relationship between the Pr effect and GMA in only this *dominated* species (and an absent or negative correlation between the Pr effect and GMA in the *dominating* species). The shift from a sowing ratio of 0.67 to a harvested ratio of 0.46 of pea indicates such a competitive disadvantage of pea versus barley. However, our observations break with the expectation that in such a case mixed stand yield is maximized only by genotypes with high Pr effects of the dominated species, as Pr effects of genotypes of *both* species were positively correlated with their GMA (Fig. 5 B and Fig. 6 B). We suspect that in such a scenario, there are resource capacities that are blocked for both species by intraspecific competition in PS, but that are available in mixed stand due to smaller interspecific rather than intraspecific competition (Annicchiarico et al., 2019). This points towards a commensalistic character of this bilateral interaction, and that there is potential to select genotypes that occupy yet unused free niche space (Brooker et al., 2021). As previously discussed, there are the semi-leafless, medium-sized genotypes that 'escape' the tradeoff between Pr and As effects. Such genotypes are of particular interest as such 'escaping' genotypes might be critical to better understand the mechanistic processes that underpin resource complementarity in mixed stand. Acknowledging the relationship of Pr effects and GMA, future breeding for MC of pea with barley should mainly focus on traits that are correlated with Pr effects and uncorrelated with As effects in order to maximize GMA.

4.5. Indirect selection for GMA via key traits

The three pea-traits early vigor, onset of flowering and stipule length should be considered as indirect selection criteria for breeding pea for MC. Same as for common bean (in MS with corn, Zimmermann et al., 1984), also in pea traits could be identified that were not correlated with yield in PS but with yield when pea was combined with barley (onset of pea flowering with barley fraction yield/As effect of pea and stipule length with total yield/GMA, Fig. 10) and thus deserve a special focus in dedicated breeding programs of pea for this specific mixed crop. Pea biomass is a known proxy for plant length and its use as a selection criterion is thus to be gauged in the context of lodging. Early vigor of pea (i.e., high early shoot biomass) is usually assessed at growth stages when high shoot biomass corresponds with high root biomass (BBCH 25–35, Wille et al., 2020). This suggests that pea plants with high early vigor are able to compete better with barley for soil mineral-N at this crucial early growth stage, ultimately leading to higher nodulation in the pea crop (Corre-Hellou et al., 2006). Higher nodulation/nitrogen fixation by pea, mediated by early vigor, might thus drive niche complementarity in this mixed crop and therefore explain the surprising commensalistic BIF we observe for this trait. Our results are in line with the prognoses made from prior experiments (Corre-Hellou et al., 2006; Barillot et al., 2014) and effectively display the importance of early vigor as a key trait for improving GMA in pea. The significant negative correlation of onset of flowering of pea with As effects might be evidence for a more complementary resource use pattern for light or other resources, i.e., temporal complementarity, achieved with earlier flowering pea genotypes. Bedoussac and Justes (2010) observed a complementarity for leaf area index (LAI) in pea and wheat canopies over the growing season. Therefore, changes in flowering time of one species, here earlier onset of flowering avoids an undesired temporal overlap for these peak LAI values and thus optimizes the light use efficiency of the mixed crop as a whole. When it comes to increasing actual leaf area, three strategies can be proposed to increase pea LAI in the top layers of the canopy of mixed crops: select for (i) higher pea plant stature (ii) leafy pea genotypes and (iii) higher pea stipule length. Selection for higher plant stature is not recommended due to increased lodging risk (see Section 4.1). The selection of leafy genotypes should be considered with caution, due to the high G×E that was observed with this leaf type (see Section 4.3) and its strong competition towards barley. Selection for higher stipule length appears as a viable strategy to equip medium-sized, semi-leafless plants with good competitive ability for light. We observed a positive correlation between stipule length (and eventually size) and GMA that is in line with findings of a previous study by Jacob et al. (2016). Mixed stand measures might further increase GMA predictability by traits such as stipule length due to possible trait plasticity as indicated in Fig. S9. Pea plants with the genotype StSt have larger stipule sizes yet weaker stems than those with the stst genotype (Hebblethwaite et al., 2013). That's why until now the latter genotype has been preferred in pea breeding to confer lodging resistance. The StSt genotype however could provide an interesting option for MC, as lodging resistance is provided by the companion crop. Its high heritability and broad phenotypic variance make stipule size an attractive target for indirect selection to increase GMA in general and for marker-assisted selection in particular.

5. Conclusions

Our findings underpin a high LER and yield stability of legume-cereal mixtures and provide important insights for breeding for MC of pea and barley. We could demonstrate that pea genotypes can be selected for improved total mixture yield (i.e., high GMA effects) as well as pea fraction yield (i.e., high Pr effects) under MC. The proportion of pea fraction yield on total mixture yield varies substantially between locations and years and is mainly influenced by pea x year interaction, and pea and barley genotype, while the pea x barley interaction (SMA) can be neglected. As a consequence, any barley genotype can be used for direct selection of pea for MC, while a mix of several pea lines might be advisable to select for the best barley genotypes for MC. The proposed separation of GMA into Producer and Associate effects allows to select for improved stability of GMA. We uncovered indirect prediction measures for GMA in pea, amongst which was PS yield. Discrepancies between PS and MS yields can be exploited for doing trait analysis, revealing unique key-traits that can be used to select for mixture performance. These key-traits comprise for pea: stipule length, onset of flowering and early vigor. We recommend to use PS performance and key-traits in PS for selection for MS at early stages, but this should be complemented with selection in MS at later stages. We do not recommend leafy pea genotypes in breeding for mixed cropping for regions with high precipitation due to low yield stability across years. Our results indicate that pea genotype mixtures (GMs), especially with high diversity for plant length and leaf type, are promising in terms of yield potential and –stability under MC. However, further investigations are needed to assess the potential of genotype mixtures (GMs) in species mixtures. Experimental design, analytic approaches and breeding strategies as outlined for pea-barley can be transferred to other crops. This will foster research and breeding dedicated to MC systems aiming for higher yield stability in order to face the global challenges of climate change.

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.

Acknowledgements

The authors thank the Rindisbacher farmer family and the Berchtold farmer family for providing the on-farm trial locations and Getreidezüchtung Peter Kunz for the trial management, and post-harvest processing. We thank Agroscope for the sowing and the harvest of the field trials. We further thank the seed companies for the initial seed supply and the FiBL-interns for their support in trial management and data acquisition. We thank Emma Forst for the valuable input that this project profited from. The authors want to thank Hans-Peter Piepho, Nathalie Moutier, Samuel Wuest, Alison Karley, Niels Anten, Wolfgang Link and Cyril Firmat for valuable discussions and feedback.

This work was a part of the project ReMIX "Redesigning European cropping systems based on species MIXtures," funded by the EU's Horizon 2020 Research and Innovation Programme (Grant Agreement No. 727217) and the Swiss State Secretariat for Education, Research and Innovation (SERI, contract number 17.00091), and part of the project PROMISE, funded by the Swiss Federal Office for Agriculture (FOAG).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2023.108923.

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