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ABSTRACT

Three-breed rotational crossbreeding can improve the functional traits of dairy cows, but few farmers in most Western countries use it. This could be due to a lack of knowledge of its medium- and long-term effects on animal performance at the herd level, regardless of the initial states of the farm and herd, the crossbreeding programme(s) used and changes in farm management and structure while transitioning to it. We aimed at assessing changes in animal performance of dairy cattle herds transitioning towards three-breed rotational crossbreeding and at identifying factors that explained them. We sampled 13 French dairy cattle farms for which animal performance data were available for a 9-year period (2009–2017) and described their trends in herd management and the farming system when introducing crossbreeding. We calculated five herd performance variables: mean milk productivity per cow-year (**MilkCow**), mean Milk solids content (**FatProtCont**), and the percentages in the herd of cows with no more than 117 days open (**FertileCow**), with mean somatic cell score less than 4 over the lactation period (**HealthyLact**) and with four lactations or more (**L4+**). We defined 15 variables related to herd and farm structure and management. We applied linear regression to each variable over the study period and used the intercept and slope to describe their initial values in 2009 and their trends, respectively. We performed partial least squares (**PLS**) regression to assess relationships between the trends in herd performance variables and potential explanatory variables, including the initial values of herd performance variables and the initial values of and trends in herd and farm structure and management variables. Linear regressions showed that within herds, median MilkCow decreased (–177 kg/cow per year), FertileCow increased (+1.5%/year) and FatProtCont either remained stable or increased (+0.1 g/kg per cow). Conversely, changes were less distinct for HealthyLact and L4+. From 2009 to 2017, herd size increased in most farms (med = +1.2 LU/year). The PLS regression highlighted that herds in which MilkCow decreased the most over time were those in which HealthyLact and L4+ decreased and increased the most, respectively. Moreover, for herds in which FertileCow increased the most, FatProtCont either decreased, or increased less. Based on association scores from the PLS, changes in the genetic composition of the herd influenced changes in herd performance variables more than did changes in overall farm management (|0.28|–|0.59| vs |0.26|–|0.50|). Our findings suggest that dairy crossbreeding is relevant to rebalance herd performance between production and functional traits.

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Implications

Understanding the dynamics of herd performance variables when implementing dairy crossbreeding is critical to support farmers' decision-making. We provided insights into such dynamics based on the analysis of data gathered on commercial dairy cattle farms using rotational crossbreeding from purebred Holstein herds over a 9-year period. Using crossbreeding improves reproductive performances and increases milk solids content of the herds. However, it decreases milk yields and has a variable influence on udder health and cow longevity. These changes depend mainly on the rate at which crossbreeding was implemented and, in most cases, are accompanied by an increase in herd size.

Introduction

Reproductive performance and animal health and longevity are becoming critical for sustainable farm management in the context of climate change, resource depletion and price volatility (Fourichon et al., 2001; Inchaisri et al., 2010; De Vries, 2017). This is true for grassland-based farms, which require synchronising calving periods with grass availability, and concentrate-based farming systems that rely on large amounts of purchased inputs (Buckley et al., 2014). The Holstein breed is predominant on both types of farms in Western countries (Labatut and Tesnière, 2019). However, the increased inbreeding of the Holstein breed and its historically milk productivity-driven selection programmes have worsened cow functional traits and decreased profitability (Dezetter et al., 2015). This has been partially addressed by increasing consideration of functional traits in selection indexes since the 2000s (Cole and VanRaden, 2018). Although additional genetic progress on these traits can be made (Berry et al., 2014), it will require a long time to be effective (Ferris et al., 2018). For these reasons, and because other dairy cattle breeds have better milk quality, reproduction and health than Holstein (Delaby et al., 2009; Dezetter et al., 2015), crossing Holstein females with other breeds seems an effective and relatively faster solution for dairy farmers than selecting purebred Holstein (Brito et al., 2021). Among the types of crossbreeding, the three-breed rotational practice maximises heterosis over generations and minimises the complexity of managing the diversity of genetic types within a herd. Despite this advantage, the practice remains rare in France (Dezetter et al., 2015) and many other Western countries (Hazel et al., 2017; Clasen et al., 2019). This lack of development is both the cause and consequence of a lack of information about its benefits for actual and diversified dairy cattle farming systems and situations (Magne and Quénon, 2021).

To fill this gap, many studies have estimated additive and non-additive genetic parameters of crossbreeding (i.e. heterosis and recombination losses for production and functional traits) (VanRaden and Sanders, 2003; Dezetter et al., 2015) and compared a variety of traits of Holstein cows to those of crosses from specific three-breed rotational crossbreeding programmes (Malchiodi et al., 2014; Maurmayr et al., 2018; Shonka-Martin et al., 2019a). At the herd level, a few studies simulated animal and economic performances of crossbred herds using specific crossbreeding programmes and showed that fully crossbred herds were more economically profitable than purebred Holstein herds (Lopez-Villalobos et al., 2000; Clasen et al., 2020). Dezetter et al. (2017) demonstrated similar benefits when simulating the dynamics of animal and economic performances of Holstein purebred herds during their transition towards herds with only crosses from three-breed rotational crossbreeding programme. These results were based on modelling the herd and can be used to assess long-term effects of different dairy crossbreeding programmes and compare them to those of purebred Holstein management. However, they have limited benefits for training and advising future farmers as they assume that each farmer implements only one specific crossbreeding programme and that all farmers do so at the same pace into and up to the entire herd, without changing anything else in the farm's structure or management. However, these assumptions are only partially consistent with how dairy farmers actually manage rotational crossbreeding. Quénon et al. (2020) identified three technical pathways (i.e. sets of herd management practices) to move from purebred to three-breed rotational crossbred herds in France, two of which depended on-farm scale changes and included trials and combinations of different crossbreeding programmes. However, several questions remain:

What are the trends in herd performance variables when managing three-breed rotational crossbreeding, regardless of the initial situation of the farms, the crossbreeding programme(s) chosen or the changes farmers make simultaneously to the structure and management of the farm and herd? What are the main factors that explain changes in herd performance variables during the transition from purebreeding to crossbreeding? To what extent does rotational crossbreeding explain changes in herd performance variables? To address these questions, we assessed trends in herd performance variables of dairy cattle herds transitioning towards three-breed rotational crossbreeding over time to identify explanatory factors, including changes in the herd, farm structure and crossbreeding practices. Indeed, we assumed that using rotational crossbreeding as such had less effect on herd performance variables than changes in farm structure and management.

Material and methods

Farm sampling

We used a retrospective case-study approach to consider rotational crossbreeding and general breeding practices as dairy farmers actually manage them, as this approach can help to understand phenomena as they occur in real-life situations (Lune and Berg, 2017). From an initial sample of 26 French dairy cattle farms that had been classified by their transition pathways towards three-breed rotational crossbreeding (Quénon et al., 2020), we selected a subsample of 13 farms that had been enrolled in the French Milk Record Organisation throughout the entire study period (from 2009 to 2017). These farms were located in four main regions of dairy production in France: Brittany (n = 4), Auvergne-Rhône-Alpes (n = 4), Normandy (n = 3) and Hauts-de-France (n = 2). Their structure and management varied (Table 1). Of the 13 farms, five remained in conventional farming throughout the study, three remained in organic farming (i.e. converted before 2009) and five converted to organic farming.

Data collection and editing

Herd performance variables

To calculate herd performance variables for each year from 2009 to 2017, we used data provided by the French Milk Record Organisation for lactation and reproductive performances of females in the 13 sampled herds (6 628 lactations from 2 726 females). We considered five variables (Table 2) related to milk productivity, milk quality, fertility, udder health and longevity. We first calculated the mean milk yield of the cows in each herd (**MilkCow**, in kg per cow). We calculated the mean total Milk solids content (**FatProtCont**, in g/kg per cow) as the sum of mean fat and protein contents in the herd. We did not consider fat or protein yields as both were correlated with MilkCow (Supplementary Fig. S1). To assess herd fertility, we calculated the percentage of cows in the herd with no more than 117 days open (**FertileCow**, in %), which was the number of days open for the 25% most fertile dairy cows in French dairy herds (i.e. first quartile) from 2009 to 2017 (Reproscope, 2017). To assess udder health, we calculated the percentage of cows in the herd without clinical mastitis (**HealthyLact**, in %) i.e. mean somatic cell score of less than 4 over the lactation period (Lipkens et al., 2019). Somatic cell score was calculated using somatic cell count values as Ali and Shook (1980): Somatic Cell Score = $3 + \log_2$(Somatic Cell Count/100 000). To assess cow longevity, we calculated the percentage of cows in their fourth lactation or above (**L4+**, in %).

Table 1

Main characteristics of the sampled dairy cattle farms at the beginning and end of the 2009–2017 study period.

Characteristic	2009			2017		
	Median	Minimum	Maximum	Median	Minimum	Maximum
Farm size (ha)	80	45	390	95	43	225
Grassland area (% of MFA)	82	12	100	92	16	100
Herd size (LU)	40	23	84	54	28	139
Stocking rate (LU/ha)	0.70	0.43	3.49	0.88	0.51	2.95
Crossbred cows (% of the herd)	2	0	65	66	28	99
F_1 crosses (% of the herd)	0	0	56	24	5	48
G_2 crosses (% of the herd)	0	0	8	12	0	44

Abbreviations: F_1 = first-generation crosses; G_2 = second-generation crosses from three-breed rotational crossbreeding programmes; LU = Livestock unit; MFA = main fodder area.

Table 2

Variables used to describe farm structure, farming practices, crossbreeding practices (all explanatory) and dairy cattle herd performances (response).

Category	Variable name (unit)	Description
Farm structure	UAA (ha)	Utilised agricultural area: it includes arable land, areas always under grass cover, and permanent crops.
	HerdSize (cow)	Herd size
Farming practices	FarmManagement (category)	Farm type (Stable conventional, Stable organic or Converting to organic farming)
	TechPathGroup (category)	Group of technical pathways towards crossbreeding[1]
	MFA (ha)	Main fodder area: fodder crops, grass and permanent grassland and meadows used to feed dairy herd
	PercMFA (%)	Percentage of main fodder area in the utilised agricultural area
	GrassInMFA (%)	Percentage of grassland in the main fodder area
	StockRate (LU/ha MFA)	Stocking rate
Crossbreeding practices	PB (%)	Percentage of purebred cows
	AllCross (%)	Percentage of all crosses in the herd
	F1 (%)	Percentage of first-generation crosses
	G2_alterabs (%)	Percentage of second-generation crosses from alternative or absorption crossbreeding programmes
	G2_3b (%)	Percentage of second-generation crosses from other three-breed rotational crossbreeding programmes
	G3_3b	Percentage of third-generation crosses from three-breed rotational crossbreeding programmes
	DivCross (%)	Percentage of crosses from other crossbreeding generations
Herd performances	MilkCow (kg/cow)	Mean amount of milk produced
	FatProtCont (g/kg per cow)	Sum of the mean fat and protein contents of the cows' milk
	FertileCow (%)	Percentage of cows with no more than 117 days open
	HealthyLact (%)	Percentage of cows with a mean somatic cell score < 4
	L4+ (%)	Percentage of cows in fourth lactation or more

Abbreviations: ha = hectares; LU = Livestock unit.
[1] Quénon et al. (2020).

Variables related to herd and farm structure and management

We selected variables of herd genotypic composition, farm structure and farming practices to explain trends in herd performance variables during the transition towards rotational crossbreeding. To define each herd's genotypic composition over the 9 years considered, we used the breed and pedigree data provided by the French National System of Genetic Information for each female. As all crossbred cattle animals in France are identified by the same breed identification code (i.e. 39), we used pedigree data to reconstruct the crossbred genotype (i.e. breed combination for each female). Due to the large diversity of crossbred genotypes in the 13 herds (Supplementary Fig. S2), we defined more inclusive genetic classes (Quénon and Magne, 2021) based on breed combinations and the coefficient of heterosis, which we calculated as $Heterosis = 1 - \sum s_i d_i$, where s_i and d_i are the proportions of sire genes and dam genes, respectively, from breed i (VanRaden, 1992). Grouping genetic classes that had too few individuals among the sampled herds resulted in defining six genetic classes (Supplementary Table S1). To describe the genetic composition of each herd (i.e. the percentage of each genetic class), we aggregated these data for each herd × year (Table 2) to calculate the percentages of purebred females (**PB**, in %), first-generation crosses (**F1**, in %), second-generation crosses from two-way or absorption crossbreeding programmes, second-generation crosses from three-way rotational crossbreeding programmes (**G2_3b**, in %), third-generation crosses from three-way rotational crossbreeding programmes (**G3_3b**, in %) and crosses from other crossbreeding generations or crossbreeding programmes, with few females.

We calculated seven variables related to farm structure and farming practices (Table 2) using survey data collected from farmers in 2018 (Quénon et al., 2020). We first considered five quantitative variables: total utilised agricultural area, percentage of main fodder area in the total utilised agricultural area (**PercMFA**, in %), percentage of grassland in the main fodder area (**GrassInMFA**, in %), herd size (in livestock units (**LU**) and stocking rate (**StockRate**, LU/ha). We also considered two categorical variables: the type of farm management i.e. remained in conventional farming, converted to organic farming (**ConvertingOF**) or remained in organic farming and the technical pathway group followed to manage rotational crossbreeding: most farmers customised one or more rotational crossbreeding programmes to redesign their farm (i.e. convert it to organic farming or a grass-based forage system) and then implemented them quickly (i.e. "technical pathway group 1", n = 4) or slowly (i.e. "technical pathway group 2, n = 7). Two farmers predefined one crossbreeding programme that is well known for maintaining high milk yields and implemented it quickly to correct fertility issues of purebred cows without changing the farming system (i.e. "technical pathway group 3").

Data analysis

We adapted the statistical approach (Supplementary Fig. S3) developed by Martin et al. (2017) and applied by Bouttes et al. (2019) and Perrin et al. (2020) to describe (i) trends in herd performance variables during the period that dairy farmers introduced and increased the use of three-breed rotational crossbreeding,

(ii) changes in herd and farm structure and management throughout this period and (iii) relationships between these changes and the trends in herd performance variables. We chose this method of holistic analysis because it relates response variables (here, trends in herd performance variables) to potential explanatory variables that describe, here, herd and farm structure and management (herd composition, farm structure and farming practices).

Linear regressions to describe trends in response and explanatory variables

We used two parameters to describe the trends in response and explanatory variables: the initial value and the trend. Therefore, we first applied linear regressions to each quantitative variable (both response and explanatory) from 2009 to 2017 for each herd. We then extracted the intercepts and slopes of all regressions i.e. the prefix "I." indicates the intercept of the linear regression for a given variable and the prefix "S." indicates the slope of the linear regression for a given variable, respectively (Tables 3 and 4). Intercepts reflected the state of the variables in 2009, while slopes (positive, null, or negative) reflected trends in the quantitative variables, which increased, remained stable or decreased, respectively, from 2009 to 2017. We used the minimum, maximum and median (**med**) slopes of the linear regressions to describe the trends.

Partial least square regressions to test explanatory factors

We performed partial least square (**PLS**) regressions to investigate relationships between response variables i.e. trends in herd performance variables (S.MilkCow, S.FatProtCont, S.FertileCow, S. HealthyLact and S.L4+) and potential explanatory variables, including (i) intercepts of herd performance variables and (ii) intercepts and (iii) slopes of herd composition, farm structure and farming-practice variables (Table 2). PLS regression generates linear combinations of variables (called "components") by maximising the square covariance between the response and explanatory variables. We chose this method for two reasons: first, unlike linear

Table 3
Association scores between dairy cattle herd performance (response) and explanatory variables for the first component of the partial least squares regression. A positive or negative value indicates that the increase in the response variable is associated with an increase or decrease, respectively, in the explanatory variable.

Explanatory variable	Response variables		
	S.MilkCow	S.HealthyLact	S.L4+
Component 1			
I.AllCross	+0.59	+0.45	−0.54
I.F1	+0.58	+0.45	−0.53
S.G3_3b	+0.52	0.00	−0.47
I.G2_3b	+0.49	0.00	−0.45
TPG3[1]	+0.44	0.00	0.00
ConvertingOF	−0.50	0.00	+0.45
I.G3_3b	−0.51	0.00	+0.46
S.F1	−0.58	−0.44	+0.52
I.PB	−0.59	−0.45	+0.54

S.<Variable> = slope of the linear regression for a given variable; I.<Variable> = intercept of the linear regression for a given variable; Abbreviations: AllCross = percentage of all crossed cows in the herd; ConvertingOF = converted to organic farming from 2009 to 2017; F1 = percentage of first-generation crosses in the herd; G2_3b = percentage of second-generation crosses in the herd from a three-breed rotational crossbreeding programme; G3_3b = percentage of third-generation crosses in the herd from the three-breed rotational crossbreeding programme; HealthyLact = percentage of females in the herd with a mean somatic cell score < 4; L4+ = percentage of females in the herd in fourth lactation or more; MilkCow = milk productivity; PB = percentage of purebred cows in the herd; 1; TPG3 = technical pathway's group 3: group of farmers who introduced and managed rotational crossbreeding from 2009 to 2017 by using one well-known crossbreeding programme in advance and implementing it quickly to correct fertility issues in purebred cows without changing the farming system (Quénon et al., 2020).

Table 4
Association scores between dairy cattle herd performance (response) and explanatory variables for the second component of the partial least squares regression. A positive or negative value indicates that the increase in the response variable is associated with an increase or decrease, respectively, in the explanatory variable.

Explanatory variable	Response variables	
	S.FatProtCont	S.FertileCow
Component 2		
S.AllCross	+0.45	−0.31
I.FertileCow	+0.45	−0.30
I.GrassInMFA	+0.35	0.00
I.PercMFA	+0.35	0.00
TPG1	+0.35	0.00
S.StockRate	+0.31	0.00
S.G2_3b	+0.28	0.00
I.FatProtCont	−0.32	0.00
S.PercMFA	−0.33	0.00
I.StockRate	−0.39	+0.26
I.MilkCow	−0.40	+0.27
S.PB	−0.45	+0.31

S.<Variable> = slope of the linear regression for a given variable; I.<Variable> = intercept of the linear regression for a given variable; AllCross = percentage of all crossed cows in the herd; FatProtCont = total milk solids content; FertileCow = percentage of females in the herd with no more than 117 days open; G2_3b = percentage of second-generation crosses in the herd from a three-breed rotational crossbreeding programme; GrassInMFA = percentage of grassland in main fodder area; MilkCow = milk productivity; PB = percentage of purebred cows in the herd; PercMFA = percentage of main fodder area in total agricultural area; StockRate = stocking rate; TPG1 = technical pathway's group 1: group of farmers who introduced and managed rotational crossbreeding from 2009 to 2017 by customising one or several rotational crossbreeding programmes to support a whole-farm redesign and implemented it quickly (Quénon et al., 2020).

regression, PLS regression is not restricted to a single response variable (Tenenhaus, 1998), which enabled us to consider trends in five herd performance variables simultaneously. Second, PLS regression can analyse incomplete and correlated data well (Wold et al., 2001), as in the current study (e.g. trends in the percentages of purebred vs crossbred cows in the herd were inversely correlated) (Supplementary Fig. S4). We performed PLS regressions using the "mixOmics" package (Lê Cao et al., 2016) in RStudio software (v. 4.0.4, Rstudio Inc., Boston, MA, USA). To assess the predictive ability of the PLS regression, we used the total Q^2 value and defined the appropriate number of PLS regression components, including a PLS component when $Q^2 > 0.0975$ (Tenenhaus, 1998). We calculated association scores from the latent components of the PLS regression. Association score is the similarity value between a pair of variables and is obtained by calculating the sum of the correlations between the original variables and each of the latent components of the PLS regression (Lê Cao et al., 2016).

Results

Trends in farm and herd structure and management variables from 2009 to 2017

The slopes and intercepts of the variables that described herd composition, farm structure and farming practices varied from 2009 to 2017 (Fig. 1). Herd size initially ranged from 22 to 92 LU (med = 47 LU) and increased on 11 out of 13 farms (med = +1.2 LU/year, i.e. +10 LU/herd on average over the 9-year period). At the same time, farm size, which initially ranged from 45 to 287 ha (med = 80 ha), remained unchanged for 10 farms (med = 0 ha/year; min = −11 ha/year; max = 10 ha/year). As for the stocking rate, it was initially low (med = 0.8LU/ha of main fodder are) and it remained almost constant for six farms (med = 0.0 LU/ha of main fodder area per year) while it increased and decreased
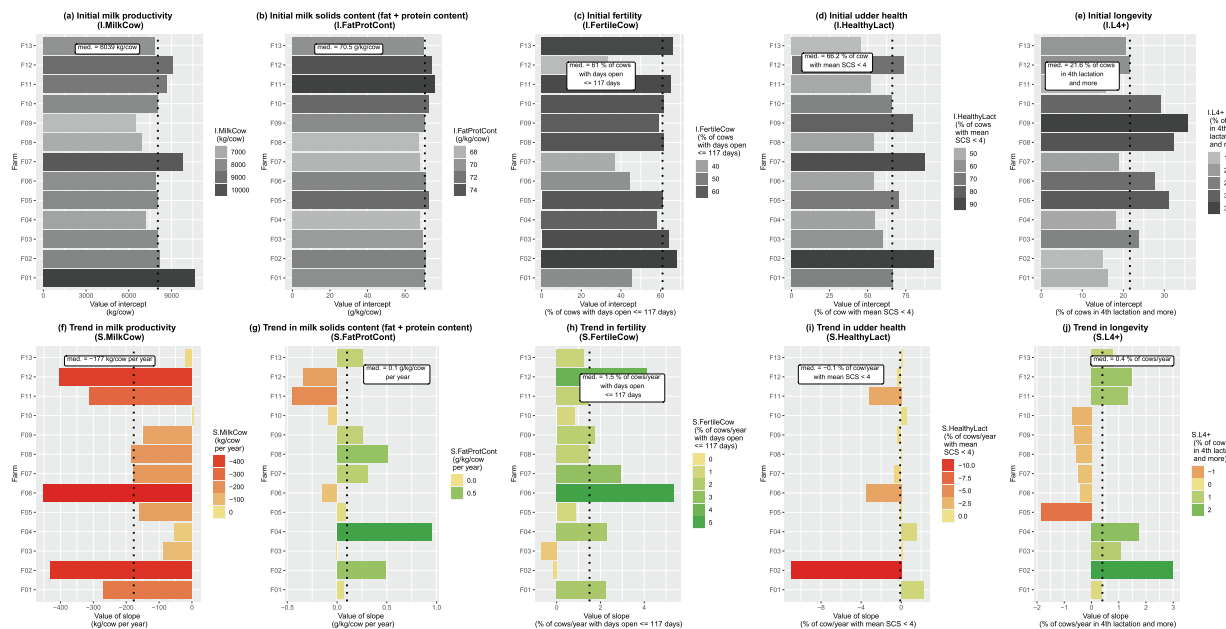
Fig. 1. Intercepts and slopes of linear regressions of variables describing farm characteristics among the 13 dairy cattle herds sampled: (a, f) utilised agricultural area, (b, g) herd size, (c, h) main fodder area, (d, i) grassland and (e, j) stocking rate. Abbreviations: UAA = utilised agricultural area; med. = median; MFA = main fodder area; LU = livestock unit (other abbreviations used are defined in Tables 3 and 4).

for five and two farms, respectively. The percentage of grassland in main fodder area was initially high (med = 86%) and usually did not change (med = 0%/year), while it increased by 2–5%/year on three farms. Finally, eight farms were organic in 2017, five of which had converted since 2009, while the other five farms had remained in conventional farming.

Regarding genetic composition, the herds were sampled at different stages of rotational crossbreeding (Fig. 2): in 2009, nine farms had no crosses, while the other four had between 15% and 79% of crossbreeds. These four farms already had F1 crosses (3 to 66% of the herd), and two of them even had G2_3b crosses (12% and 21% of the herd, respectively). However, none of the farms had reached the first backcross stage of three-breed rotational crossbreeding, and thus, no farms initially had G3_3b crosses. From 2009 to 2017, the percentage of crosses increased in all herds

(Fig. 2) by +3 to +14%/year (med = +6%/year), which is consistent with the fact that most of the farms began dairy crossbreeding in 2009. The percentage of F1 crosses increased in 11 herds, ranging from +0.8% to +7% per year (med = +3%/year). Similarly, the percentage of G2_3b crosses increased in 12 herds, ranging overall from 0% to +5%/year (med = +1%/year). Conversely, the percentage of G3_3b crosses remained constant and null in all but two herds, whose percentage of F1 crosses decreased due to already having more than 40% of crosses in 2009. Farmers introduced crossbreeding to these two herds long before 2009, resulting in a large intercept (I.F1) and low slope (S.F1); F1 cows were replaced with the crosses from subsequent crossbreeding generations. This also explained the negative correlation between the initial percentage of a specific genetic class of crosses and its trend (e.g. I.F1 vs S.F1, I.G2_3b vs S.G2_3b) (Supplementary Fig. S4).
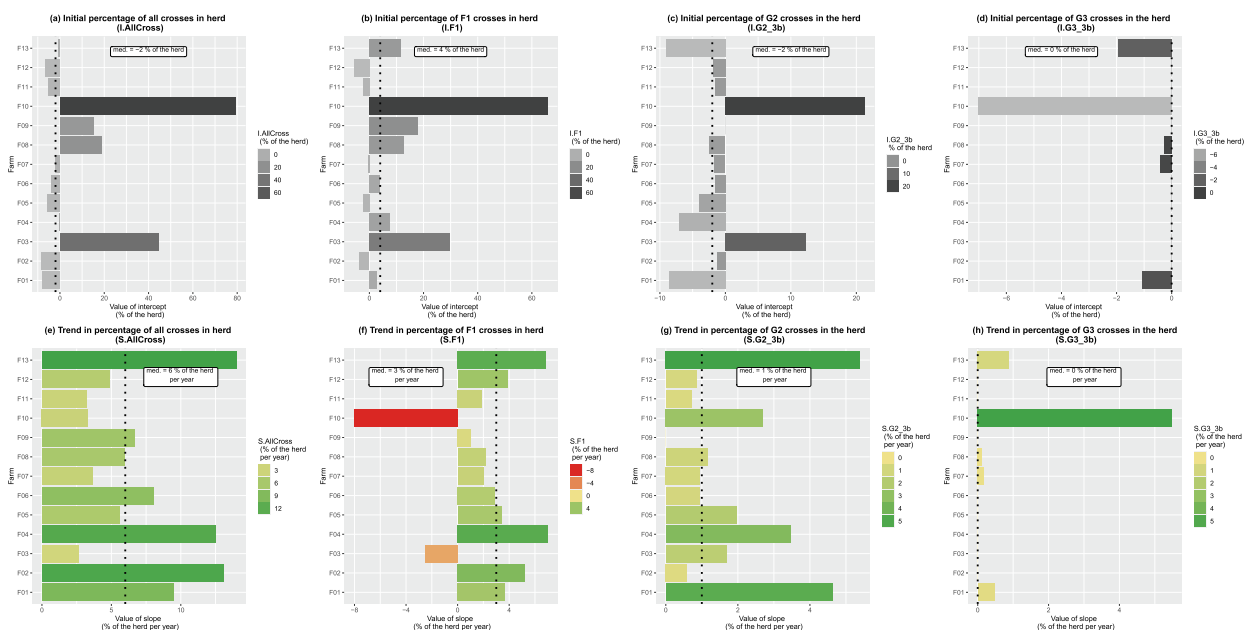

Fig. 2. Intercepts and slopes of linear regressions of variables describing herd genetic composition among the 13 dairy cattle herds sampled: percentage of (a, e) all crosses, (b, f) F1 crosses, (c, g) G2 crosses and (d, h) G3 crosses in the herd from three-breed rotational crossbreeding programmes. Abbreviation: med. = median (other abbreviations used are defined in Tables 3 and 4).

Trends in herd performance variables from 2009 to 2017

Among the 13 sampled herds, MilkCow (Fig. 3) ranged from 6 505 to 10 647 kg/cow (med = 8 039 kg/cow), and I.FatProtCont ranged from 67.5 to 75.6 g/kg per cow (med = 70.5 g/kg per cow). I.FertileCow averaged 61% in 2009 and ranged from 33 to 68%; four herds had less than 50% cows with no more than 117 days open in 2009.I.HealthyLact ranged from 46 to 94% (med = 66%), and I.L4+ ranged from 15 to 36% (med = 22%).

Two types of trends in herd performance variables were observed from 2009 to 2017 among sampled herds: trends in Milk-Cow, FatProtCont and FertileCow were relatively similar for all herds, while trends in HealthyLact and L4+ differed greatly from one herd to another (Fig. 3). Among the three similar trends in performance, MilkCow decreased in 12 herds, with S.MilkCow ranging from −19 to −452 kg/cow per year (med = −177 kg/cow per year) and increased slightly only in one herd (+4 kg/cow per year). Conversely, FertileCow increased in 11 herds, with S.FertileCow ranging from +0.8 to +5.3%/year (med = +1.8%/year), and decreased slightly in two herds (−0.2 and −0.7%/year, respectively). Similarly, FatProtCont increased or remained stable in six and three herds, respectively, and decreased in four herds, with S.FatProtCont ranging overall from −0.5 to +1.0 g/kg per cow per year (med = +0.1 g/kg per cow per year). Among the two contrasted trends in performance, HealthyLact increased slightly in three herds, remained stable in seven herds and decreased in three herds, with S.Healthy-Lact ranging overall from −11.0 to +2.2%/year (med = −0.1%/year). Finally, L4+ increased in seven herds and decreased in six herds, with S.L4+ ranging overall from −1.9% to +3.0%/year (med = +0.4%/year).

Key determinants of trends in herd performance variables from 2009 to 2017

We selected the first two components of the PLS regression to analyse relationships between trends in herd performance variables and explanatory variables ($Q^2 > 0.0975$). The projection on the first component (Fig. 4) compared S.MilkCow and S.Healthy-Lact to S.L4+. In it, herds in which S.MilkCow decreased

significantly from 2009 to 2017 were also those in which S. HealthyLact decreased and S.L4+ increased. The projection on the second PLS component (Fig. 4) compared S.FatProtCont to S.Fer-tileCow. In it, herds in which S.fertileCow increased significantly from 2009 to 2017 were also those in which the Milk solids content decreased or did not increase as much.

On the first two components, the association scores between trends in herd performance variables and initial values of and trends in herd composition variables (i.e. I.AllCross, S.AllCross, I. F1, I.G2_3b, S. G2_3b, S.G3_3b, I.G3_3b, I.PB, S.PB) were higher in absolute value than those between trends of herd performance variables and initial values of and trends in farming-practice variables (i.e. ConvertingOF, I.GrassInMFA, I.PercMFA, S.PercMFA, I. StockRate, S.StockRate): for example, the association scores ranged from |0.49| to |0.59| between S.MilkCow and S.AllCross, I.F1, S.F1, I. G2_3b, I.G3_3b and S.G3_3b, respectively, while it ranged from | 0.44| to |0.51| between S.MilkCow and TPG3 and ConvertingOF, respectively (Tables 3 and 4).

On the first component alone, association scores between trends in herd performance variables and explanatory variables showed that S.MilkCow and S.HealthyLact were negatively associated with S.F1 (−0.58 and −0.44, respectively) and I.PB (−0.59 and − 0.45, respectively) (Table 3): mean milk productivity per cow and per year and the percentage of cows with healthy lactations decreased even more in herds in which the percentage of purebred cows was low in 2009 and the percentage of F1 crosses highly increased over 2009–2017, i.e. in which the more extensively and quickly crossbreeding was introduced over this period (Table 3). S.MilkCow and S.G3_3b were positively associated (+0.52) i.e. milk productivity of cows decreased less or remained stable in herds in which the percentage of G3 crosses increased, which may be due to backcrossing with Holstein bulls. S.MilkCow and ConvertingOF were negatively associated (−0.50) i.e. converting to organic farming from 2009 to 2017 was also linked to a decrease in milk productivity of cows. Conversely, S.MilkCow were positively associated with TPG3 (+0.44): milk productivity of cows decreased less or remained stable in herds that followed TPG3 (i.e. that used a high-yielding dairy breed in crossbreeding programmes and did no change in the forage system while moving towards crossbreeding).
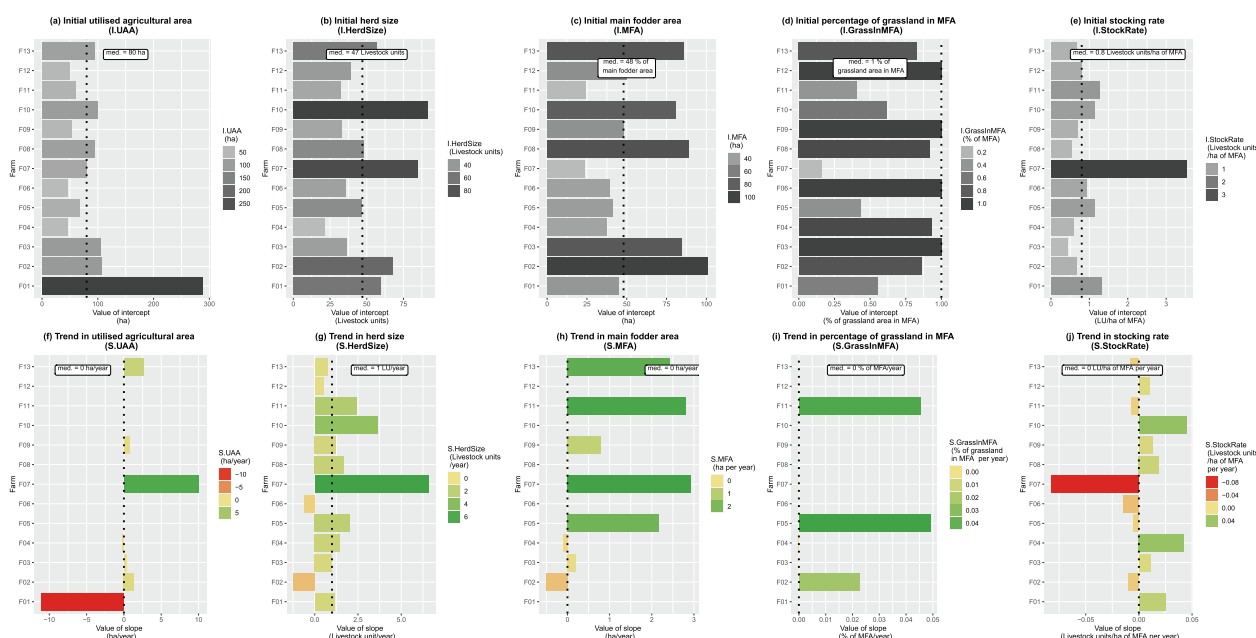

Fig. 3. Intercepts and slopes of linear regressions of variables describing performances of herds among the 13 dairy cattle herds sampled: (a, f) milk productivity, (b, g) Milk solids content, (c, h) fertility, (d, i) udder health and (e, j) longevity. Abbreviations: med. = median; SCS = somatic cell score (other abbreviations used are defined in Tables 3 and 4).
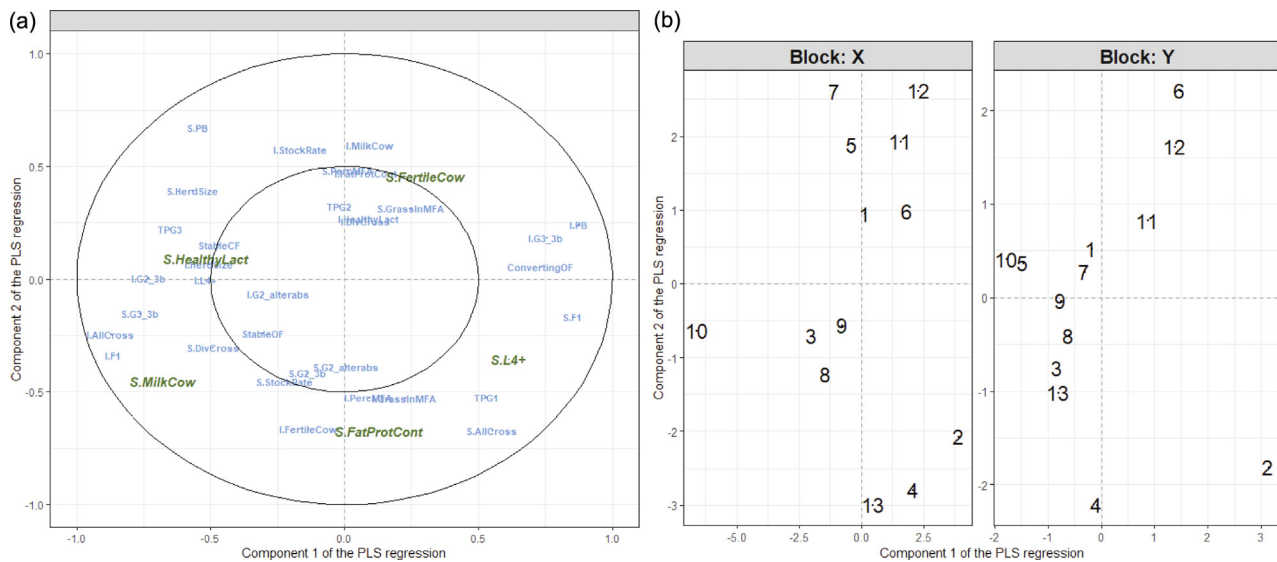
Fig. 4. Results of the partial least squares (PLS) regression: (a) projection of explanatory variables (in blue) and response variables (in green italics) and on the two selected components ($Q^2 \geq 0.0975$); (b) projection of individuals i.e. dairy cattle herds (n = 13) on the two selected components according to (left) explanatory or (right) response variables. Abbreviations used are defined in Tables 3 and 4.

On the second component alone, association scores between trends in herd performance variables and explanatory variables showed that S.FatProtCont was positively associated with S.All-Cross (+0.45) and S.G2_3b (+0.28): Milk solids content increased as the percentage of crosses increased in the herd, especially G2_3b crosses (i.e. the more quickly that crossbreeding was introduced and G2_3b crosses were produced) (Table 4). S.FatProtCont was also positively associated with TPG1 (+0.35): Milk solids content also increased more in herds that followed TPG1 (i.e. in which crossbreeding was introduced quickly to support whole-farm redesign towards low inputs). S.FatProtCont was also negatively associated with I.StockRate (–0.39) and positively associated with S.GrassInMFA (+0.35) and S.StockRate: Milk solids content increased more in grassland-based farming systems with an initially low stocking rate that increased from 2009 to 2017. S.FatProtCont was negatively associated with I.MilkCow and I.FatProtCont (–0.40 and –0.32, respectively): Milk solids content increased more in herds that had initially low milk productivity and Milk solids content. S.FertileCow was positively associated with S.PB (+0.31) and negatively associated with S.AllCross (–0.31): the percentage of fertile cows increased less in herds in which S.AllCross increased the most and S.PB decreased the most (i.e. in which crossbreeding was introduced the most quickly). S.FertileCow was also positively associated with I.MilkCow (+0.27) and I.StockRate (+0.26) (Table 4) and negatively associated with I.FertileCow (–0.30): cows' fertility increased more in herds with initially low fertility performances and high milk performances, and on farms with a high stocking rate in 2009.

Discussion

Three-breed rotational crossbreeding: an effective method to rebalance herd performance variables rather than a magic wand for win–win trade-offs

Functional traits are "characters of an animal that increase efficiency not by higher outputs of products but by reduced costs of input" (Groen et al., 1997). Improving functional traits is one of the main reasons dairy farmers implement rotational crossbreeding (Buckley et al., 2014; Magne and Quénon, 2021). Many studies

at the animal level focused on the benefits of crossbreeding for these traits, especially cow fertility (Buckley et al., 2014), health (Vance et al., 2013), feed efficiency (Shonka-Martin et al., 2019b) and longevity (Hazel et al., 2021). Conversely, few studies have analysed the effects of implementing dairy crossbreeding on animal performances at the herd level (Dezetter et al., 2017; Clasen et al., 2020). These studies, based on simulating specific three-breed rotational crossbreeding programmes within a herd, showed that the performance of functional traits improved at the expense of milk productivity and that profitability increased. In agreement with these studies, we provided empirical evidence that implementing three-breed rotational crossbreeding in an initially pure-bred Holstein herd is an effective method to rebalance herd performance variables between milk production and some functional traits over the medium term and long term, regardless of the crossbreeding programme(s) used. We demonstrated that, regardless of the initial states of the farm and the herd, the crossbreeding programme(s) used and changes in farm management and structure during the transition, it usually improved reproductive performance, increased Milk solids content and decreased milk productivity per cow, which reflects a biological trade-off between these traits (Brito et al., 2021). Conversely, trends in herd performance variables related to cow longevity and udder health differed more among the sampled herds. These results agreed with Hazel et al. (2021) for the former trait and Vance et al., (2013) and Dezetter et al. (2019) for the latter. This can be explained by the fact that these two animal characteristics depend not only on intrinsic factors (i.e. genetics or animal traits) but also on rearing conditions and farm and herd management such as milking management for udder health (Owusu-Sekyere et al., 2023). Thus, our findings highlight that trends in herd performance variables are not always consistent or clear and depend mainly on the performance variable considered, followed by the initial herd situation and trends during the transition period. Consistent with Dezetter et al. (2017), this shows that farmers should not consider crossbreeding as a magic wand that solves every problem.

Our findings stressed that all five herd performance variables cannot improve at the same time, as improving reproductive performances while implementing crossbreeding decreases milk productivity. We also showed that it was in herds in which milk productivity of cows decreased the most, that cows' longevity

and udder health increased and deteriorated the most, respectively. This result can be explained in different ways. First, three-breed rotational crossbreeding, by increasing cows' fertility, may enable farmers to keep cows in the herd longer. This is in accordance with Hazel et al. (2021), who showed that, at animal level, the first and second generations of crosses had longer herd life compared with their respective Holstein herdmates. In addition to the improvement of herd reproductive performance, the increase in herd size observed on most of the sampled farms over the study period may explain that the decrease in milk productivity of cows did not result in voluntary culling as previously shown by Owusu-Sekyere et al. (2023). Then, it was shown that the risk of disease in dairy cows tends to increase with the number of lactations (Fleischer et al., 2001), which may counteract the benefits of heterosis in health at the herd level when the mean age of the cows increases (Clasen et al., 2020). Yet, agreed with Owusu-Sekyere et al. (2023), our results suggest that udder health itself does not have a significant effect on dairy herd longevity. Finally, this result can also be interpreted with respect to changes in the overall herd and farm management along the use of dairy crossbreeding such as the conversion to organic farming and the rate at which it was implemented. This often means changes in cows' feeding practices, which may have negative impacts on their health before they adapt to them. In the same way, we showed that the more rapidly fertility increased, the lower the mean Milk solids content became. This could be because the rapid decrease in milk productivity related to the rapid increase in fertility while implementing crossbreeding requires farmers to change how they feed the cows, which is not always controlled well initially. In so doing, the trends in herd performance variables not only depend on genetic correlations between milk yield production and other traits at the animal level (Pryce and Veerkamp, 2001) but on interactions between cow biology and farming practices (Tichit et al., 2011; Magne et al., 2019). In addition, farmers' decisions to prioritise specific performance variables over others are strongly related to the initial level of the performance variables, which reflect the farmers' 'room to manoeuvre' to make decisions. Like Dezetter et al. (2017), our results highlight the strong influence of the initial level of the performance variables on the trends after the introduction of dairy crossbreeding. We showed that dairy crossbreeding had a major influence on trends in herd performance variables, but that it required consistent integration into the overall management of the herd and the farm. On this point, our findings hilighted that, together with the use of crossbreeding, herd size increased on most of the sampled farms, often independently of an increase in the size of the main fodder area. There are three possible reasons for that. Firstly, the increase in herd size was independent of the use of crossbreeding. Secondly, farmers wanted to compensate for the loss of milk productivity per cow, in order to maintain the total milk production of the herd they had with purebred cows. Thirdly, it was a non-voluntary consequence of the transition towards crossbreeding: by improving reproductive performance, farmers had less need to cull animals and therefore kept more cows and heifers, which led to an increase in herd size (Quénon, et al., 2020).

Three-breed rotational crossbreeding requires managing a dynamic mixture of functionally different cows in the herd

Our results showed that trends in herd performance variables depended on the stage of development in the crossbreeding process, and thus on the number of generations of lactating crosses in the herds. Introducing crossbreeding, which replaces purebred cows with F_1 cows, increased the percentage of cows with no more than 117 days open in all sampled herds and thus improved herd reproductive performance. This provides empirical evidence of decreased fertility in the Holstein breed related to breeding objectives before the 2000s (Brito et al., 2021) and the higher fertility of F_1 crosses, which generally decreases in post-F_1 generations (Dezetter et al., 2017; Quénon and Magne, 2021). In accordance with Dezetter et al. (2017), we also showed that once G2_3b crosses began replacing older cows, milk solids content increased. However, this may be due more to the lower milk productivity of crossbred cows, particularly beyond F1 crosses, which greatly benefits from heterosis effects, than by the ability of G2_3b crosses to produce higher milk solid yields (Saha et al., 2018; Quénon and Magne, 2021). Finally, our results also showed that milk productivity decreased less as the percentage of G3_3b crosses increased, which is a later stage of rotational crossbreeding that dairy farmers may reach eventually. This highlights that implementing three-breed rotational crossbreeding in initially purebred herds enables farmers to produce cows (i.e. at each backcross) with relatively high milk yields. While these results seem consistent with the breeding goals of the Holstein breed and the theory of rotational crossbreeding, to our knowledge, they are the first empirical demonstration of the latter based on on-farm data.

Our findings highlight that introducing and managing dairy crossbreeding requires farmers to manage a dynamic mixture of functionally different cows within the herd over time. However, the sampled farmers did not appear to develop optimal strategies to do so. Indeed, the trends in the variables related to herd composition over the study period suggested that the farmers implemented dairy crossbreeding to change from a purebred herd to a fully crossbred herd, which agrees with the assumptions of Dezetter et al. (2017) in their experimental design for simulations. By contrast, they did not maintain the percentage of F1 crosses without adding further crossbreeding generations, which is one option to maximise the heterosis effect. To manage such mixed Holstein-F1 herds, dairy farmers can cross-dairy breed females with both dairy and beef breed sires, in order to both increase the slaughter value of crossbred male calves and cows (Berry et al., 2018, Martín et al., 2021) and regulate herd replacement for maintaining its mixed composition. Sexed semen can also be used in such mixed herds to have more flexibility in the replacement of the different genotypes (Clasen et al., 2020).

Further research has to be done to identify if combining genetic classes is beneficial for the overall herd performance and which herd composition (i.e., the combination of Holstein, F1, G2, etc.) allows to take advantage of the potential complementarity of their performance profiles (Quénon and Magne, 2021). For that, it would be necessary to extend analysis to the breeds used in crossbreeding programmes, which lacking in our study. For example, in F1 crosses, 50% of genes come from another breed than Holstein, but this other breed is not specified in our method. However, depending on whether it is Swiss Brown, Montbéliarde or Jersey, the characteristics provided by the breed may differ (Albertí et al., 2008; Magne et al., 2019), and therefore, the performance of resulting cross with Holstein or at least the performance gap compared to Holstein may differ too (Dezetter et al., 2017; Clasen et al., 2020; McClearn et al., 2020). This may explain why we did not observe similar trends in some herd performance variables as those related to udder health and longevity. This may have been even more difficult if we had investigated performance characteristics, such as slaughter value for calves and cows, for which there is a particularly high variability between breeds (Albertí et al., 2008; Berry et al., 2018). However, in our sample, although there was a diversity of types of crosses, certain combinations of breeds were more represented: Holstein × Montbéliarde for F1, Holstein × Montbéliarde × Brown swiss or Scandinavian Red for G2, and their backcrosses for G3 (Supplementary Fig. S2). These combinations are among the most documented crossbreeding programmes (Dezetter et al., 2019), which may explain why the trends

in herd performance variables we identified were in line with what was observed in the literature.

Perspectives for research

Following the method adapted from Martin et al. (2017), we showed that three-breed rotational crossbreeding strongly influenced trends in the five herd performance variables we considered, among other explanatory factors related to the trends and initial farm structure and farm and herd management. This holistic method can consider complex and diversified farming practices that dairy farmers use to manage and benefit from crossbreeding. It enabled us to consider the initial state of farm structures and practices, which influences trends in herd performance variables. It is even more relevant to use it to analyse data from commercial farms, which cannot be compared over time with systems that are identical except for having purebred cows (i.e. a control group), unlike data from experimental systems (Shonka-Martin et al., 2019b) or simulation models (Dezetter et al., 2017; Clasen et al., 2020). However, one limit is that linear regression modelling cannot adequately capture trends in variables that describe demographics of a herd in which dairy crossbreeding is introduced (e.g. percentage of F1 cows, which initially increases, then decreases after producing G2 crosses). This leaves certain methodological perspectives open.

In the present study, we used a case-study approach to collect fine-scale information on herd management practices (Quénon et al., 2020). As some farmers had left the Milk Record Organisations when they adopted dairy crossbreeding (Magne and Quénon, 2021), we were able to analyse only a few farms. Consequently, our findings must be evaluated with a larger sample of farms.

In our study, we only investigated five performance traits related to milk production, fertility, udder health, and longevity, which is limited to accurately estimate the benefits of dairy crossbreeding on farms. Therefore, there is a need to consider other production performance characteristics, such as those regarding meat production associated with the use of dairy crossbreeding i.e. the carcass weight and slaughter value of crossbred cull cows and crossbred calves (Berry et al., 2018; Martín et al., 2021, Piazza et al., 2023). As the slaughter values of crossbred cows and calves depend on the potential growth of the breeds involved in the crossbreeding programmes (Albertí et al., 2008), it will be necessary to go beyond the genetic categorisation we proposed here, as already stated. In the same way, there is a need to extend the indicators related to functional performance characteristics, such as feed conversion efficiency (Shonka-Martin et al., 2019a; Dezetter et al., 2019), health status, stillbirths, mortality or young stock survival to consider the herd's overall health (Hazel et al., 2020). For instance, for health status, even if no diagnoses data were available, the proportion of cows with fat-protein quotients greater than 1.5 or less than 1.0 could have been included to reflect the metabolic status in the herds.

Finally, we discussed trends in multiple herd performance variables based on five indicators calculated from the individual performances of the cows in each herd over the study period. This helped to address trade-offs among these performance variables and to promote the existence of diverse 'optima' depending on a dairy farmer's objectives. However, using quantitative aggregate indicators (e.g. economic) (Dezetter et al., 2017; Clasen et al., 2020) would provide a more explicit (or at least summary) assessment of consequences on the overall performance of herds in which farmers introduce and manage dairy crossbreeding. Although economic indicators are useful for such multi-criteria assessments, other aggregate indicators have been used more generally to assess the benefits of a practice or technical change e.g.

quantification and qualification of work (Cournut et al., 2018), changes in farmers' satisfaction (Perrin et al., 2020). In the same way, additional studies are also needed to include environmental criteria to assess the effects of transitioning towards the use of dairy crossbreeding on the overall herd performance. Including them would better consider the fact that farmers often compensated for the decrease in the milk yield per cow by increasing the herd size.

Conclusion

Our on-farm case-study provided empirical evidence that implementing three-breed rotational crossbreeding in purebred dairy cattle herds is a key factor for rebalancing herd performances for production and functional traits, especially reproduction ones. However, trends in herd performance during the transition towards crossbred herd also depended on the rate at which crossbreeding was implemented and on the initial state and the systemic changes implemented along with crossbreeding. Additional studies are needed to assess these initial empirical results with a larger sample, to include additional criteria to assess overall herd performance and to better identify the effect of the crossbreeding programmes.

Supplementary material

Supplementary material to this article can be found online at https://doi.org/10.1016/j.animal.2023.100983.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository. The data and regression models are available upon request.

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

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Declaration of interest

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