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Review: Genetic selection of high-yielding dairy cattle toward sustainable farming systems in a rapidly changing world

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ABSTRACT

The massive improvement in food production, as a result of effective genetic selection combined with advancements in farming practices, has been one of the greatest achievements of modern agriculture. For instance, the dairy cattle industry has more than doubled milk production over the past five decades, while the total number of cows has been reduced dramatically. This was achieved mainly through the intensification of production systems, direct genetic selection for milk yield and a limited number of related traits, and the use of modern technologies (e.g., artificial insemination and genomic selection). Despite the great betterment in production efficiency, strong drawbacks have occurred along the way. First, across-breed genetic diversity reduced dramatically, with the worldwide use of few common dairy breeds, as well as a substantial reduction in within-breed genetic diversity. Intensive selection for milk yield has also resulted in unfavorable genetic responses for traits related to fertility, health, longevity, and environmental sensitivity. Moving forward, the dairy industry needs to continue refining the current selection indexes and breeding goals to put greater emphasis on traits related to animal welfare, health, longevity, environmental efficiency (e.g., methane emission and feed efficiency), and overall resilience. This needs to be done through the definition of criteria (traits) that (a) represent well the biological mechanisms underlying the respective phenotypes, (b) are heritable, and (c) can be cost-effectively measured in a large number of animals and as early in life as possible. The long-term sustainability of the dairy cattle industry will also require diversification of production systems, with greater investments in the development of genetic resources that are resilient to perturbations occurring in specific farming systems with lesser control over the environment (e.g., organic, agroecological, and pasture-based, mountain-grazing farming systems). The conservation, genetic improvement, and use of local breeds should be integrated into the modern dairy cattle industry and greater care should be taken to avoid further genetic diversity losses in dairy cattle populations. In this review, we acknowledge the genetic progress achieved in high-yielding dairy cattle, closely related to dairy farm intensification, that reaches its limits. We discuss key points that need to be addressed toward the development of a robust and long-term sustainable dairy industry that maximize animal welfare (fundamental needs of individual animals and positive welfare) and productive efficiency, while also minimizing the environmental footprint, inputs required, and sensitivity to external factors.

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Implications

Genetic selection is the main pillar sustaining continued and incremental improvements in milk production in dairy herds, which is paramount for supplying nutritious dairy products for a growing market. The increase in productivity has been accompanied by an alarming loss of genetic diversity, unfavorable genetic responses in multiple correlated traits, and reduced selection pressure in traits related to environmental efficiency, animal health and welfare, and overall resilience in comparison to performance traits. In this paper, we discuss the role of genetic selection in high-yielding dairy breeding schemes and potential routes toward the development of more sustainable dairy cattle farming systems.

Introduction

Sustainable agriculture is paramount to address the major challenges facing humankind, including human demography and food security, climate change, energy use, biodiversity, and the environmental footprint of human activity. The current world population of 7.5 billion is expected to reach 9.8 billion people by 2050 (FAO, 2020). Human diets need to become healthier, more diversified, and better distributed across geographical regions and families with divergent economic incomes, as there are over 690 million undernourished people in the world (FAO, 2020) and obesity is rising in many regions across the globe. In this context, dairy products and ruminant meat provide essential amino-acids, minerals (calcium, zinc, selenium), and vitamins (A, B3, B6, B12, D), highlighting the fundamental importance of dairy farming for human agri-food systems.

There are currently more than 270 million dairy (or dual-purpose) cows in the world, with a global average milk yield of around 2 600 kg/cow/year. However, only 33 countries have a national average milk yield greater than 6 000 kg/cow/year (FAOSTAT, 2018; Fig. 1), which represents only a small fraction (~13%) of the world dairy cattle population but more than 40% of the total world milk. Yet, the strong focus of the dairy industry on ensuring food security through higher productivity raises concerns on other sustainability dimensions (Clay et al., 2020). This requires us questioning continued selection strategies for milk yield in populations (or countries) that have reached very high production levels, but simultaneous selection for productivity and functional traits (e.g. adaptation, welfare, resilience) should be applied in low-producing populations, especially in local breeds and developing-country populations.

Since the early stages of cattle domestication (~10 000 years ago), differential selection processes have resulted in the development of about 1 200 cattle breeds (FAO, 2015) with distinct characteristics such as milk yield level, milk composition, environmental adaptation, coat color, body size, fertility, and overall resilience. Currently, ~95% of the high-yielding dairy cows raised in the main dairy producing regions around the globe are represented by only three breeds: Holstein (or Holstein-Friesian), Jersey, Brown Swiss, and their crosses. The worldwide spread of these few breeds is mainly due to their greater milk production levels and responsiveness to high-input production systems. In these breeds and even for less common ones, both overall and per animal production levels are still rising (Fig. 2). The main drivers for this increase in milk productivity are related to the industrialization of dairy production; growing demand from worldwide consumers where large industries with high export and processing capacities (advanced infrastructure to transport and store large amounts of dairy products) urge dairy farmers to be increasingly competitive. As a result, the increase in the overall milk production of many industrialized or developing countries has been accompanied by a reduction in the total number of dairy farms and cows, and consequently, larger herds are becoming more common in these countries (e.g., United States and China; FAOSTAT, 2020).

Intensification of dairy production systems

The development of intensive dairy systems has been fueled by a consistent flow of innovations and technological breakthroughs, among which conventional genetic selection played a major role over the past decades (Miglior et al., 2017). Animal breeding and genetics has been extensively conceptualized in artificial and standardized environments, where the linear equation: P (observed phenotype/performance) = G (additive genetic merit) + E (environmental effects) proved to be highly efficient, especially under controlled environmental conditions and high-input production systems. However, when not accounting for the interactions between genotype and environment (also termed Genotype-by-environment interactions (**GxE**)), selection for high-producing animals depends on the availability of high-quality (and usually well-controlled) environments for the expression of the traits of interest. Indeed, together with genetic selection, the dairy industry has also benefited from major advancements in nutritional practices, precision management, wide adoption of reproductive technologies (e.g., artificial insemination, embryo transfer, sexed semen), and precision health and care management. These advancements are not independent from each other and it is clear

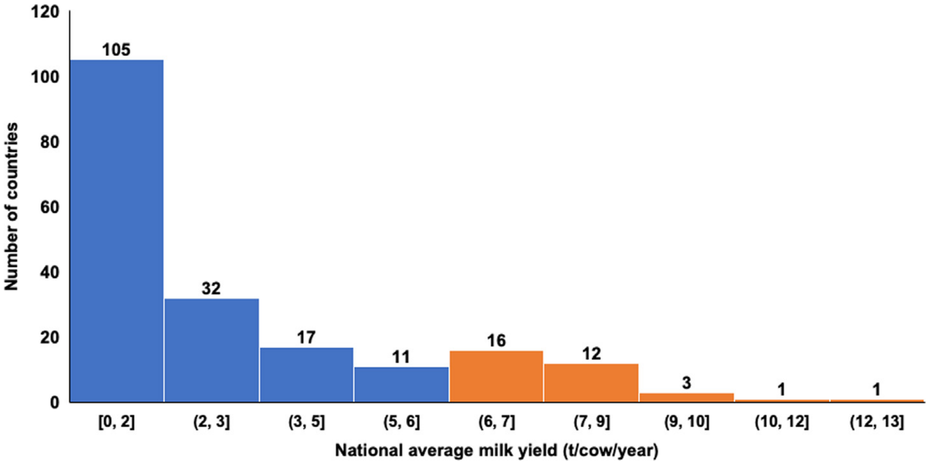


Fig. 1. Distribution of countries according to their national average dairy cattle milk yield (t/cow/year). Data source: FAOSTAT, 2020.

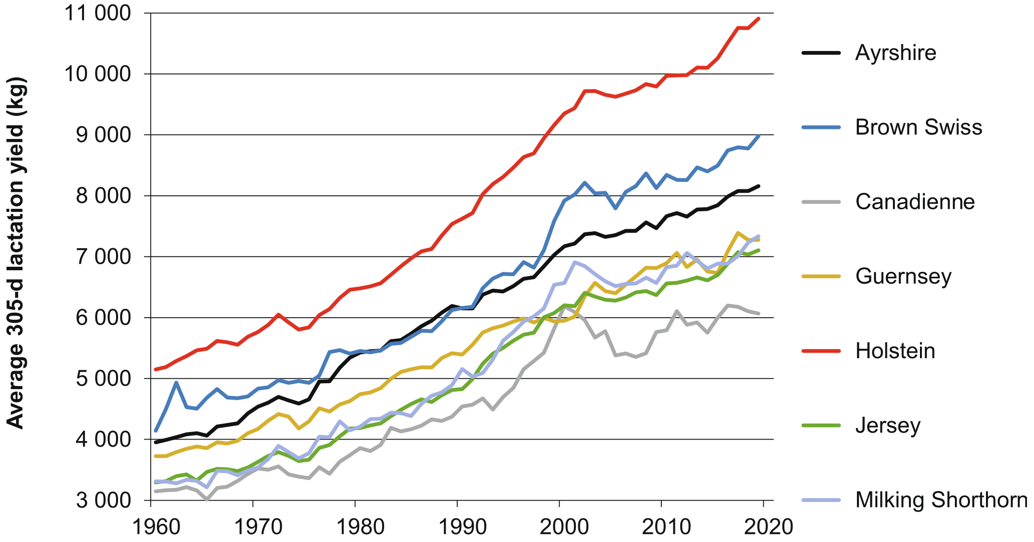


Fig. 2. Average 305-d lactation milk yield (kg) in dairy cattle breeds in Canada (thicker lines indicate the main worldwide dairy breeds). Data source: Canadian Dairy Information Centre, 2020 (www.dairyinfo.gc.ca).

that many of them have increased the effectiveness of genetic selection for increased productivity. From this perspective, the high-producing dairy cow is thus more than the simple result of high genetic merit for key biological mechanisms and adequate environmental factors; it also reflects complex positive feedback between these two components that took place during the industrialization and intensification of dairy production.

Genetic selection for increased milk yield has been a key driver of dairy intensification leading to the development of highly specialized milk production systems, with increasing herd size, and heavily relying on cereals and protein-sources (FAO, 2006). Locally, the concentration of intensive dairy farms can have a large environmental impact due to the large amounts of waste produced. Thus, there is growing evidence that uncoordinated levels of intensification in high-input dairy production systems are not sustainable (Willett et al., 2019; Clay et al., 2020). Despite the major signs of progress in productivity, the long-term success of the dairy industry depends on the adoption of more sustainable breeding goals and management practices, especially from an agroecological perspective (Phocas et al., 2016a and 2016b). Current high-producing systems need to be refined with a greater focus on animal health and welfare, environmental efficiency, climatic adaptation, and more preparedness for future challenges through the conservation of a diverse genetic pool. Some breeding programs have recently included several of these traits in the breeding goals, but there is still a need for substantial improvements. For a review of the current worldwide selection indexes, please see Cole and VanRaden (2018). As an example, US selection indexes include traits such as health, SCS, livability, productive life, feet and leg traits, and calving ability (CDCB, 2020). The transition toward lower-input (with improved usage of resources) production systems also needs to be favored. This is required to minimize the environmental footprints of the industry, meet the food demands of a steadily growing population in face of rapid scientific and technological innovations, limited resources and land availability, greater environmental and ethical awareness of animal husbandry practices, demand for higher-quality products produced with lower use of antibiotics, and natural challenges (e.g., new pathogens and diseases, climate change). The role of genetic selection in non-economic dimensions of dairy farm sustainability has mainly concerned animal welfare. However, unfavorable genetic relationships among traits of great relevance to the industry (e.g., milk yield and fertility or welfare) have deteriorated some economically important traits, which has consequently motivated the development of more efficient breeding strategies for increased long-term sustainability of the dairy cattle industry (Von-Keyserlingk et al., 2013; Cole and VanRaden, 2018). Yet, to contribute to dairy farm sustainability, genetic selection needs to consider its direct and indirect effects on the multiple sustainability dimensions. In our view, the extent to which the dynamics of genetic specialization are interrelated with dairy farm intensification is key to address the contribution of genetic selection to the development of sustainable production systems. In this context, dairy industry stakeholders will continue seeking alternatives to further increase the profitability and sustainability of dairy production. Key players such as breeding companies and national genetic evaluation systems will continue refining the selection indexes used in face of emerging threats and opportunities. However, in some cases, there might be a need for greater governmental involvement to support changes in certain directions, especially toward better animal welfare and environmental footprints, as well exemplified by policies implemented in some European countries.

Objectives: High-yielding dairy cows for sustainable farming systems

The main objective of this paper is to discuss the potential contribution of genetic selection in the high-producing dairy cow given the close relationship between genetic specialization and dairy farm intensification. We first highlight the importance of selection for milk yield (and related variables) as the driver of dairy farm intensification and its sustainability from the single perspective of genetics. We then question the ability of the farm environments to keep up with genetic trends. Given the genetic background of sustainability-related traits as well as recent advances in genetic and genomic selection, we discuss how breeding programs and the management of genetic resources could favor the developments of more sustainable dairy systems. Finally, from the description of alternative production systems, we present prospects for future research in the field of genetics of high-producing dairy cows.

Selection for milk yield as an intensification driver

Over the past centuries, milk production and composition were the main selection goals in dairy cattle breeding programs (Miglior et al., 2017) and, as a consequence, milk yield has increased dramatically (Fig. 2). From an economic perspective, the success of selection for increased milk yield or improved feed efficiency in high-producing dairy cows primarily stems at the animal level from the dilution of maintenance requirements with increasing production levels (Vandehaar, 1998; Brito et al., 2020a). The economic return from increased milk yield has been the main pillar for continuing genetic selection for higher milk yield. Moreover, greater milk yield is often considered as a key solution to address the global challenges of ensuring food security and reducing greenhouse gas emissions, as the dilution of maintenance results in both better feed efficiency and reduced methane emissions per kg of milk produced (Capper et al., 2009). Improvements in efficiency at the animal level alone will not necessarily result in mitigation of global effects (e.g., methane emission) if there is an absolute increased requirement of inputs at the farm scale. Although progress in milk yield depends on the farm environment, there is no evidence that it has been or will be genetically limited (Hill, 2016).

Inbreeding levels

Population genetic diversity is paramount for the long-term success of the dairy industry, as genetic progress depends directly on genetic variability. Furthermore, reduced genetic diversity (e.g., allelic losses and greater inbreeding levels) has strong negative effects on productive and reproductive efficiency, health, survival, and overall resilience (Makanjuola et al., 2020a). Low-genetic-diversity populations are also less suitable to respond to biological threats in future unforeseen circumstances such as new pathogens or environmental pressures. The main factors that have increased the rates of genetic diversity loss are: intensive selective breeding for a limited number of traits, genetic drift, intensification of production systems (lower animal dependency on external environmental factors), progeny testing of a limited number of bulls (prior to the genomics era), adoption of a small number of breeds worldwide (and limited, if any, investments in genetic selection in local breeds), and globalization of breeding programs (e.g., use of semen from common bulls across the whole world). The rates of inbreeding have increased substantially over time (Fig. 3) and the implementation of genomic selection in the large majority of dairy cattle breeding programs over the past two decades has also contributed to a much faster rate of inbreeding accumulation per year (Makanjuola et al., 2020b).

As previously indicated, much lower selection intensity has been placed in local breeds, especially because the industry has economically supported (paid for) a reduced set of production outcomes (e.g., milk yield and fat/protein composition). Consequently, selection for a limited number of traits combined with reduced population size (number of breeding animals; and consequently, effective population size) have further increased inbreeding levels. Selection for a larger number of traits (combined with strategies to minimize inbreeding such as optimal contribution selection; Meuwissen, 1997) is expected to contribute for minimizing the rates of inbreeding as a greater set of animals could have similar genetic merit based on a more complex selection index in comparison to selection for a reduced number of traits. Therefore, when implementing breeding programs in local breeds, it is important to maintain a large enough breeding population and develop selection indexes that emphasize a broader range of traits. In addition, key industry stakeholders (and potentially governmental agencies) should reinforce the use of techniques to minimize inbreeding such as the use of optimal contribution selection (Meuwissen, 1997).

Depletion of genetic variation

From a genetic point of view, evidence for selection limits to daily milk production is thought to be limited, especially when genomic selection enables a better assessment of Mendelian sampling and a shorter generation interval in dairy breeding schemes. However, depletion of genetic variation in milk yield seems unlike (Hill and Bünger, 2004; Hill, 2016), but it can happen (as observed in other animal species). This is likely due to the highly polygenic nature of milk yield and other traits of interest. Furthermore, as selection indexes reduce the emphasis on milk yield to simultaneously select for many other important traits, greater genetic variability is expected to be maintained in the long term (i.e., more diverse genetic make-up of individual animals).

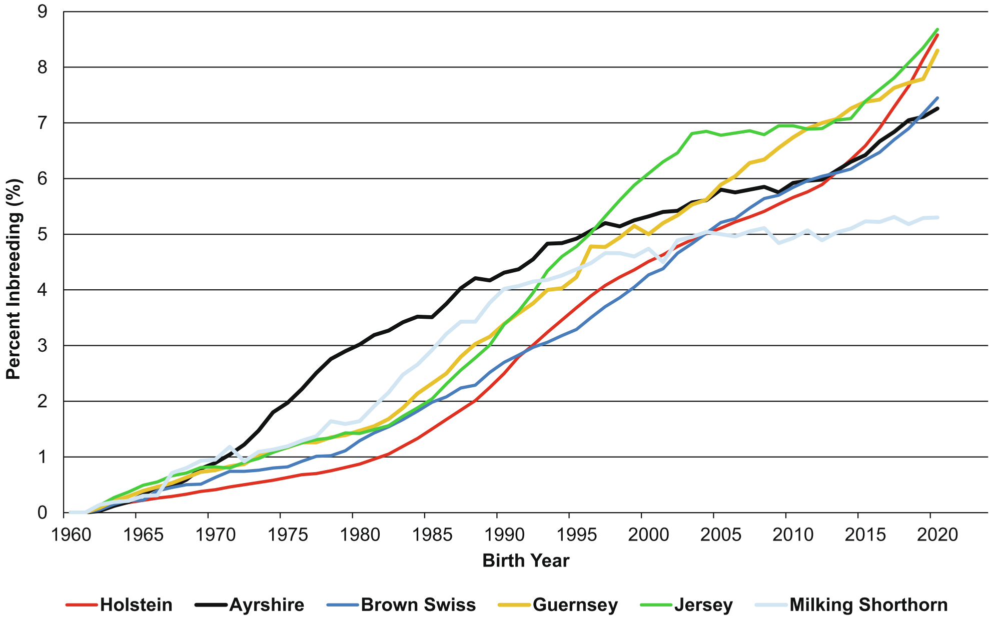


Fig. 3. Trends in inbreeding coefficients of cows from the six major US dairy breeds (thicker lines indicate the main worldwide dairy breeds). Source: Council on Dairy Cattle Breeding (https://queries.uscdcb.com), August, 2020.

Unfavorable relationships between key traits

Intense selection on production traits has led to unfavorable correlated responses on other important traits (Rauw et al., 1998; Rauw, 2012). These trade-offs between biological functions are commonly interpreted under the "resource allocation theory": when two (or more) biological processes share the same resources, they are competing in the situation of limited resources (Rendel, 1963). Various cases suggest that antagonistic relationships between production traits and fitness-related traits linked to reproduction (e.g., conception rate) or health (e.g., somatic cell count – **SCC**) can be dealt with using appropriate multi-trait selection methods (Berry et al., 2016; Cole and VanRaden, 2018). The resource allocation theory modeling can also be applied to select for antagonistic traits, as discussed in Douhard (2013). Thus, at first sight, further increasing milk yield of high-producing dairy cows appears both desirable and possible. But situations in which limited resources are more likely to occur in the future because animal production systems are changing to more sustainable ones, might include: less control over the environment (e.g., temperature, relative humidity, wind speed), lower dependence on inputs (producing more cereals, proteins, high-quality forages, and fertilizer on the farm), and the use of more preventive management strategies of health and welfare than ever before (Dumont et al., 2013; Phocas et al., 2016a and 2016b). These (extensive) systems are more exposed to external perturbations such as a shortage of feedstuffs that cannot be produced on the farm (e.g., by-products such as meals), droughts, or disease outbreaks. In this context, high-producing animals tend to be more sensitive to perturbations (Friggens et al., 2017). Genetics of resource allocation and the dynamics thereof will likely become more important in the future to select animals capable of maintaining different phenotypes of interest (e.g., milk production and resistance to pathogens or parasites) under challenging conditions.

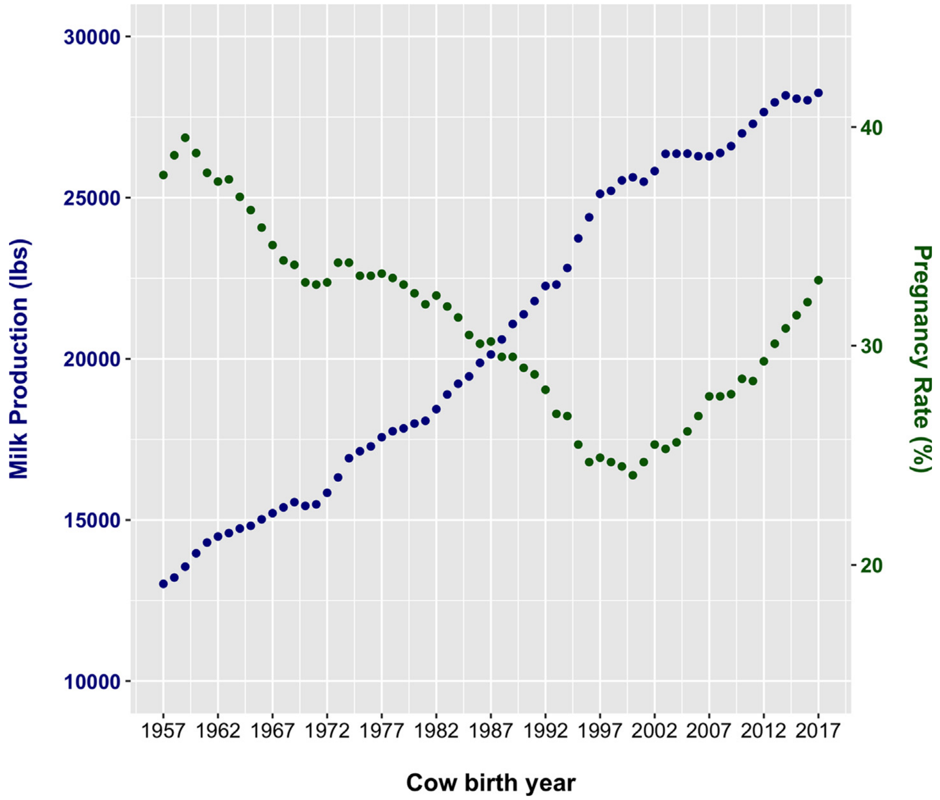
Genetic improvement requires sophisticated approaches, as the large majority of relevant traits are quantitative traits and genetically intercorrelated in both favorable and unfavorable directions. Therefore, sustainable breeding goals require the measurement and proper weighting of all relevant traits in selection indexes to enable simultaneous genetic progress in the desired direction for all traits of interest. For instance, reproductive inefficiency results in increased involuntary culling rates, increased calving intervals, increased veterinary costs, decreased milk production, and delayed genetic progress, which leads to significant economic losses for dairy farmers (Inchaisri et al., 2010). Production and fertility are negatively correlated (Bedere et al., 2018) and therefore, selection programs that have emphasized milk production and at the same time ignored fertility, have experienced a decline in reproductive performance (Royal et al., 2002; Berry et al., 2016). Fig. 4a displays the phenotypic trends in milk production and pregnancy rate in Holstein cows in the USA over the last six decades. While milk production increased markedly due to intense selection from 1960 to 2000, pregnancy rate declined steadily. Genetic evaluations for reproductive traits were introduced in early 2000 in order to counter the decline in cow fertility (VanRaden et al., 2004). Indeed, the incorporation of female fertility traits into breeding programs, together with the development of reproductive management tools, and improvements in nutrition, health, and cows' comfort have significantly improved cow fertility in the last two decades. Now, despite these advances, the reproductive performance of dairy cows remains suboptimal (Norman et al., 2018). Fig. 4b shows the changes in daughter pregnancy rate over time in USA Holstein cattle, in which the greater improvements seem to be in the environmental components, but also a slight increase in the genetic merit of the animals. Even using genomic information, it will take several generations to restore the initial genetic merit for the trait (Fig. 4b). The importance of certain reproductive traits also depends on the production system adopted. For example, calving interval is less important in high-input and intensive production systems, but of greater relevance in pasture-based systems (e.g., Ireland, New Zealand), where greater availability of feeding resources (grasslands) need to coincide with the milk production peaks of the herds.

Health events result in substantial economic losses, including losses due to on-farm death, increased veterinary and treatment costs, premature culling, and reduced milk production (Liang et al., 2017). Production and functional traits are negatively correlated, and the intense selection for milk production in the last decades has compromised health and fitness and increased environmental sensitivity (Egger-Danner et al., 2015; Friggens et al., 2013, 2017). For instance, intense selection for production has led to modern high-yielding dairy cows often experiencing a state of negative energy balance in early lactation, which in turn leads to an imbalance in metabolic processes giving rise to metabolic diseases (Friggens et al., 2013). It is not surprising that genetic correlations between milk production and metabolic diseases, such as ketosis and displaced abomasum, are mostly unfavorable (Pryce et al., 2016). Traditionally, breeding programs have focused on indirect measures of cow health and fitness, such as the length of productive life or SCC as an indicator of udder health (Martin et al., 2018). However, given that direct selection is more effective than indirect responses, recently many countries have implemented genetic evaluations for some health traits, including milk fever, retained placenta, metritis, displaced abomasum, ketosis, lameness, and clinical mastitis (Miglior et al., 2017; Cole and VanRaden, 2018).

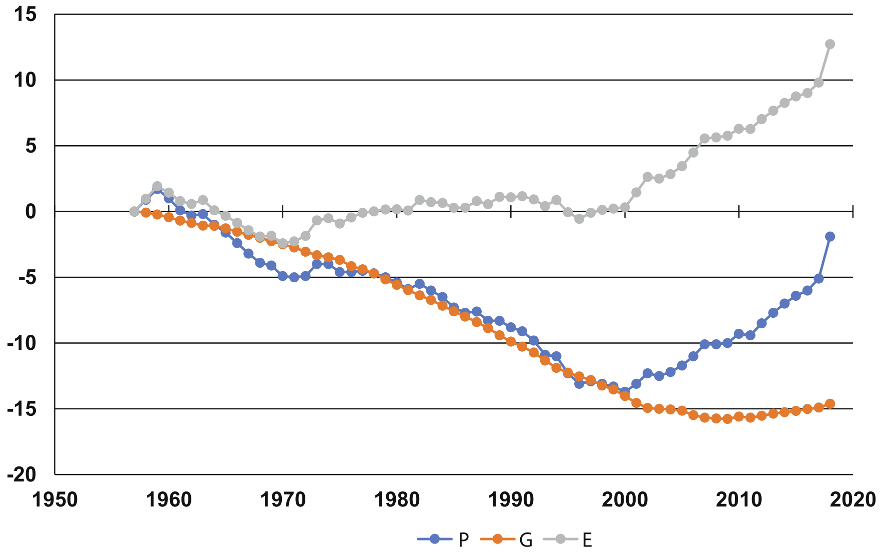
Heat stress is another factor negatively impacting dairy cattle performance and welfare, and consequently, causing huge economic losses and welfare issues to the dairy industry. Intense selection for increased production in recent decades has compromised the thermoregulatory competence of dairy cows (Aguilar et al., 2009, Santana et al., 2017). Indeed, production and thermotolerance are antagonistic traits because greater milk production leads to higher metabolic heat production, hence an increased susceptibility to heat stress (Tao et al., 2020). This is alarming as global temperatures trend upward and heat waves are expected to become more frequent and intense. There is a negative genetic relationship between milk production under thermoneutral conditions and milk production under thermo-stress conditions (Sigdel et al., 2019). This negative genetic correlation suggests that the continued selection for greater milk yield without considering the genetic merit of the animals for thermotolerance will result in increasing, even more, the harmful effects of heat stress on cow performance. Therefore, there is a critical need for breeding for thermotolerance (Nguyen et al., 2016), which is a heritable trait (Ravagnolo and Misztal, 2000; Nguyen et al., 2016). Recently, the Australian dairy industry introduced a genetic evaluation for thermotolerance which allows selection of animals that are more resistant to the detrimental effects of heat stress (Nguyen et al., 2016).

Can dairy farm intensification keep up with genetic progress?

Phenotypically, considerable gains in milk yield still seem achievable as suggested by the gap between mean production levels and maximum records in the recorded USA Holstein population (Fig. 5a). However relative gains of both measures decrease over time (Fig. 5b), similar to what has been observed for historical trends of major crop yields worldwide (Grassini et al., 2013). Although the phenotypic increase in average milk yield is well-supported by a continuous genetic trend, improvements in farm



(a)



(b)

Fig. 4. (a) Concomitant changes in milk production (lbs = pounds) and pregnancy rate (%) in US Holstein cattle in the last six decades. (b) Trends in phenotypic (P) average daughter pregnancy rate of the recorded US Holstein population, and its genetic (G) and residual (E) components. Values are reported relative to those from 1957. Data source: Council on Dairy Cattle Breeding website (July 2020; www.uscdcb.com).

environments in the past two decades have not kept up and may become a constraint (Fig. 6).

The modern high-producing dairy cow achieves greater levels of production per unit of digested feed, but higher rates of feed intake have apparently favored a long-term decline in digestive efficiency (Potts et al., 2017). As pointed by Vandehaar et al. (2016), the importance of the dilution of maintenance effect decreases with successive increments in milk yield so that the most productive herds are already close to milk production levels beyond which no further gain in efficiency would be expected.

As suggested by Clay et al. (2020), it is paramount to consider how the effects of intensification can occur synergistically (e.g., livelihoods and environment can be simultaneously improved or worsened) or as trade-offs (e.g., enhanced economic efficiency

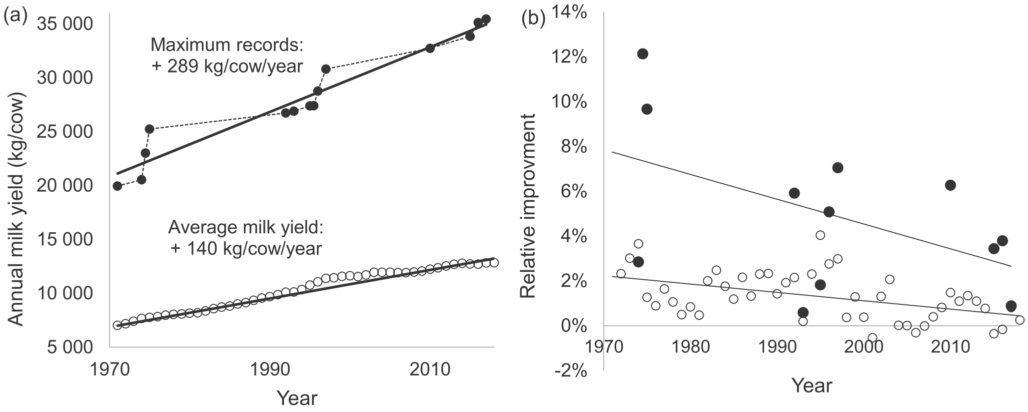


Fig. 5. Trends in average milk yield of the recorded US Holstein population compared to maximum individual records (a) and the associated relative improvements between successive measures (b). The comparison is only indicative, as data are not strictly comparable (e.g., different cow age, management). Data sources: maximum records: http://www.holsteinusa.com/holstein_breed/breedhistory.html, and average records: https://queries.uscdcb.com/eval/summary/trend.cfm?R_Menu=HO.m#StartBody.

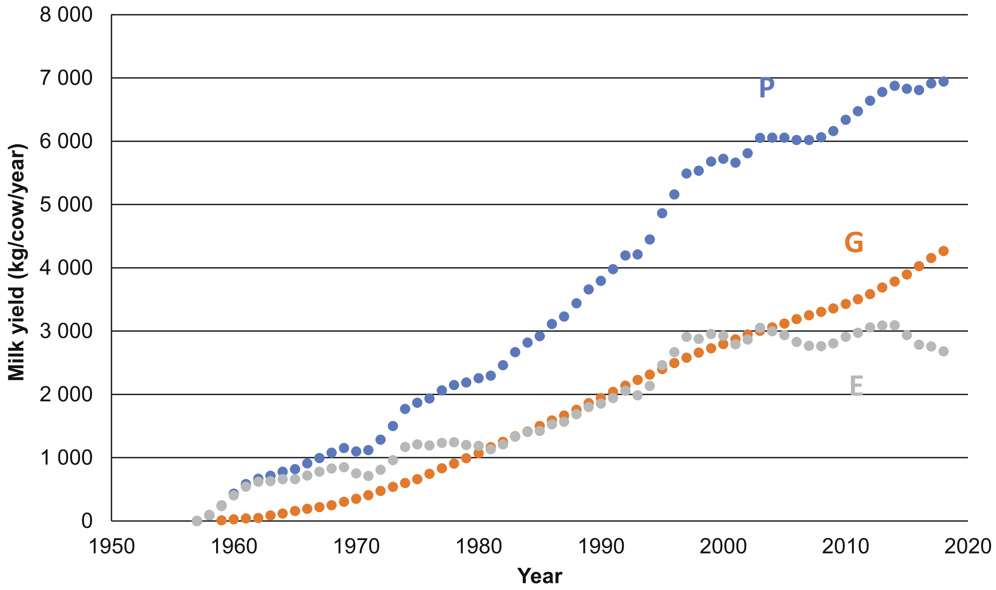


Fig. 6. Trends in phenotypic (P) average milk yield of the recorded US Holstein population (as reported in Fig. 5a from 1971), and its genetic (G) and residual (E) components. Values are reported relatively to those from 1957. Data source: https://queries.uscdcb.com/eval/summary/trend.cfm?R_Menu=HO.m#StartBody.

may come at the expense of human health; Clay et al., 2020). The larger adoption of precision technologies and accumulated knowledge in multiple scientific fields (e.g., nutrition, reproductive management, soil sciences, water management, agroecology, grassland management, ambiance control) also support the development of tools to enable optimal phenotypic expression of the genetic merit of animals raised in different dairy production systems.

Developments in dairy cattle genetic evaluations

Since domestication, the key traits under artificial selection (mainly based on phenotypic performance) were temperament (and other behavioral traits), physical and anatomical variables (e.g., coat color, body size), and milk production. With the methodological developments in the area of quantitative genetics, animal breeding, and phenomics, the array of traits targeted for improvement has expanded substantially over the past five to six decades as a response to the dynamic requirements of dairy producers, consumers, and society in general. As multi-trait selection became the norm in dairy breeding programs, the development of selection indexes played a major role in balancing the genetic merit of each individual for each trait under selection, based on their economic value or desired genetic gains (Byrne et al., 2016; Cole and VanRaden, 2018). Selection indexes have been refined over time to enable direct breeding emphasis toward specific production systems, market demands, or to address emerging production, environmental, or societal aspects of the dairy industry and society as a whole (Cole and VanRaden, 2018). Frequently, economic values in the breeding objectives are the key inputs to cost–benefit analysis and optimization of breeding schemes, but in some cases, it is challenging to define economic values for certain traits and therefore, selection indexes tend to be constructed based on desired gains or a blend of economic values and desired gains (Amer and Byrne, 2019). There are several national selection indexes (Cole and VanRaden, 2018) that differ based on the emphasis put in each trait category (production, reproduction, health, workability, efficiency, and body conformation). However, it is paramount to have more differentiated indexes to meet niche markets and alternative breeding goals (Phocas et al., 2016a and 2016b; Lopez-villalobos et al., 2018). Commercial breeding goals will continue to be refined regularly due to changes in production conditions, market requirements, and societal developments. Furthermore, as the biological background (including genetic relationships) of novel and traditional traits is uncovered and phenotyping technologies are commonly used, more efficient selection indexes will be proposed (Nieuwenhoven et al., 2013).

The success of genetic evaluation schemes has been made possible due to substantial advancements in statistical methods and computing resources. The development of methods have played a major role on enabling rapid genetic progress in the main dairy cattle populations. For detail reading of the genetic evaluation systems, please see: Weigel et al. (2017), Misztal et al. (2020), and Grosu et al. (2014). Nowadays, the majority of genetic evaluations for dairy cattle (as well as other livestock species) are based on the Mixed Model Equations (MME) and the Animal Model. In general, variance components (e.g., heritability estimates) are estimated based on likelihood (e.g., REML – Restricted Maximum Likelihood) and Bayesian methods. Globalization allowed the exchange of genetic material, such as semen and embryos, which required across-country genetic evaluations (MACE, Schaeffer, 2001). The discovery of major genes by molecular geneticists facilitated the selection of animals with favorable genotypes for some important traits. However, the success of marker-assisted selection was limited by the great distance between the causal mutations and genetic markers. Thus, even though advancements made over time were very important to ensure genetic progress, the use of genomic selection (Meuwissen et al., 2001) allowed rapid genetic progress in dairy cattle (Schaeffer, 2006). Recently, the genomic relationship matrix (VanRaden, 2008) has been combined with the traditional pedigree-based relationship matrix, in order to create a hybrid matrix that is used to simultaneously generate breeding values for genotyped and non-genotyped animals, a method known as single-step GBLUP (ssGBLUP, Misztal et al., 2009; Aguilar et al., 2010), which has become a gold standard for genomic evaluations in livestock.

Current research efforts have focused on developing and testing more computationally efficient algorithms and methods to facilitate the implementation of ssGBLUP in large datasets (e.g., Oliveira et al., 2019), as well as the development of alternative methods based on machine learning (Gengler, 2019). The use of alternative data sources such as whole-genome sequence information (not only additional SNP markers), structural variations, and high-throughput phenotyping (e.g., automated data recording systems), has also received a lot of attention and might contribute to increasing the rates of genetic progress in dairy cattle. However, the use of these alternative data sources is still incipient.

Genetic trends for traits under selection

Genetic selection has been very effective in improving various traits included in selection indexes in dairy cattle, as reviewed by Miglior et al. (2017) and Cole and VanRaden (2018). All traits under selection have been genetically modified over time (Fig. 7), with genetic gain rate depending on factors such as trait heritability and emphasis in the overall selection indexes. Furthermore, the implementation of genomic selection in the past decade has substantially contributed to increment the rates of genetic progress by increasing the accuracy of breeding values of young animals (Fig. 8), reducing the generation interval, and evaluating a larger number of selection candidates (in comparison to conventional progeny testing).

Potential contributions of genetic selection to more sustainable dairy farms

Genetic resources

The development and choice of genetic resources (e.g., breeds or lines) and breeding schemes (e.g., crossbreeding) implemented in the worldwide dairy industry depend on a plethora of factors such as the production systems (e.g., intensive, pastoral and grass-based systems, mixed farming-livestock, transhumance, and smallholders), geographical region, climatic conditions, management practices, cultural preferences, and market demands. In this context, certain breeds have evolved and become more adapted to specific regions, while others are more cosmopolitan and raised in a wider range of production systems (e.g., Holstein, Brown Swiss, Jersey, and their crosses).

Genomics information provides knowledge on specific alleles and haplotypes and therefore, can be used to more accurately assess genetic diversity levels, relatedness between individuals and populations, and presence/absence of deleterious mutations (e.g., Guarini et al., 2019). The wide use of reproductive technologies such as artificial insemination, coupled with short generation intervals (due to the implementation of genomic selection) can speed up the multiplication and transmission of deleterious alleles across populations. In this context, genomic information should be better used to manage genetic diversity in dairy cattle populations and remove deleterious mutations.

The maintenance of high genetic diversity in dairy cattle populations (within and across breeds) is crucial to prevent the situation in which a single (or few) breeds have to fit all dairy farming systems. In some countries, the conservation of local breeds has been done by using these populations for organic farming, development of special products for niche markets, and for new functions such as landscape and nature management (Oldenbroek, 2019). In general, small breeds are unfavored because they cannot take full advantage of genetic and genomic selection schemes (thus lower genetic progress per time unit) and there is a smaller investment from the artificial insemination market, as breeding companies tend to be more interested in larger breeds (Biscarini et al., 2015). This is a major challenge that needs to be addressed in the dairy industry. The maintenance of large numbers of local-breed animals will depend on the definition of their economic value in face of challenging and changing conditions such as climate change, greater diversification of production systems (e.g., organic, pasture-based, precision farming), and increase usage of by-products and alternative feed sources. Furthermore, several local breeds have cultural and social values to certain regions and are likely to be conserved as part of such traditions. It is very unlikely that a single breed can perform well across a wide range of production systems and environmental conditions. Furthermore, intensive selection in key dairy breeds have already caused fixation of certain alleles that might have undesirable effects related to fitness traits in low-input production systems. Therefore, local breeds are a reservoir of genetic material to be potentially transferred to the key dairy breeds (e.g., Holstein) through gene editing and crossbreeding schemes. As local breeds are already adapted to certain management and environmental challenges, it might be more economically feasible to genetically improve local breeds for greater performance in these systems than selecting cosmopolitan dairy breeds (e.g., Holstein) for better adaptation and welfare under harsher conditions.

Crossbreeding is not widespread in dairy cattle, in comparison to other livestock species (e.g., poultry and pigs), and therefore, within-breed genetic diversity is even more important. However, in developing countries and tropical regions, crossbreeding (especially between *Bos taurus taurus* and *Bos taurus indicus* breeds) has been used as an alternative to increasing productivity of local populations through the development of more productive and climatic adapted composite breeds [e.g. Brazilian Girolando (Canaza-Cayo et al., 2016)]. Recent studies have also investigated the role of crossbreeding to mitigate inbreeding depression and genetic diversity management (Dezetter et al., 2015) or on the performance and profitability of dairy herds (Dezetter et al., 2017).

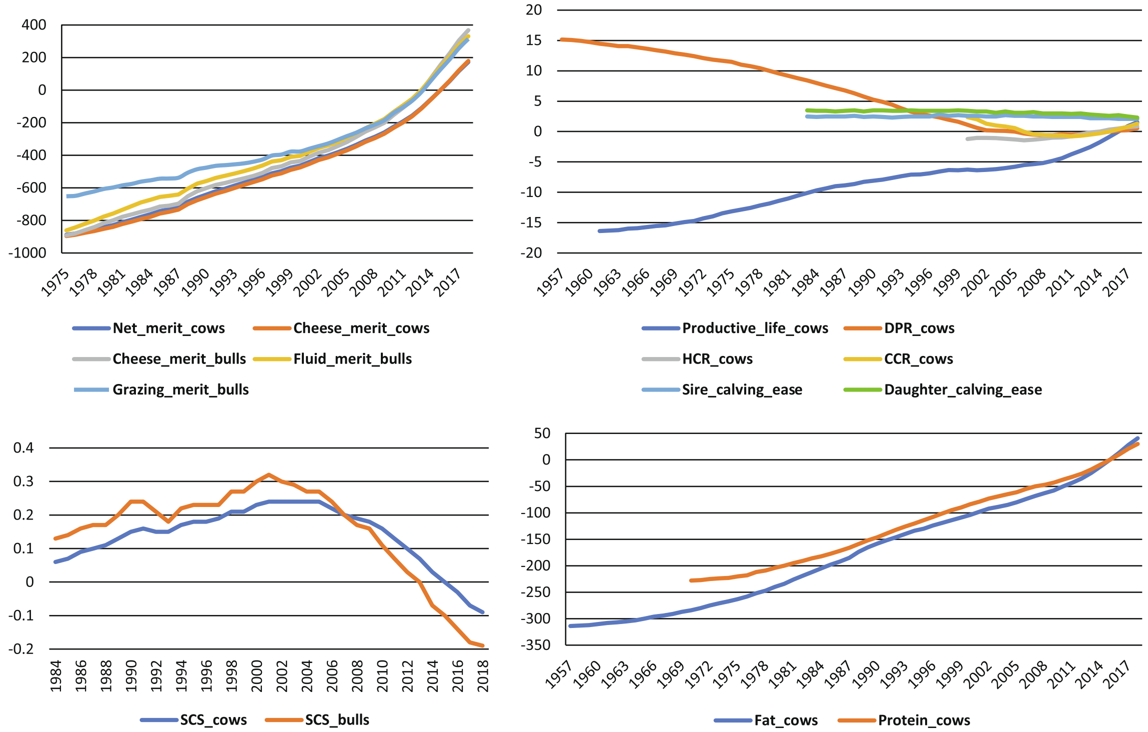


Fig. 7. Genetic trend (based on breeding values) for various selected traits in US Holstein cows and bulls, plotted by birth year. Data source: https://queries.uscdcb.com/eval/summary/trend.cfm. Net_merit_cows, Cheese_merit_bulls, Cheese_merit_bulls, Grazing_merit_bulls, and Fluid_merit_bulls represent selection index values for cows and bulls as defined by the Council on Dairy Cattle Breeding (CDCB, USA). Productive_life_cows: breeding value for productive life of cows, DPR_cows: breeding value for daughter pregnancy rate of cows, HCR_cows: heifer conception rate, CCR_cows: cow conception rate, Sire_calving_easy: breeding values for sire calving easy, Daughter_calving_ease: breeding value for daughter calving easy, SCS_cows and SCS_bulls: breeding value for somatic cell score of cows and bulls, Fat_cows and Protein_cows: breeding value of cows for fat and protein, respectively.

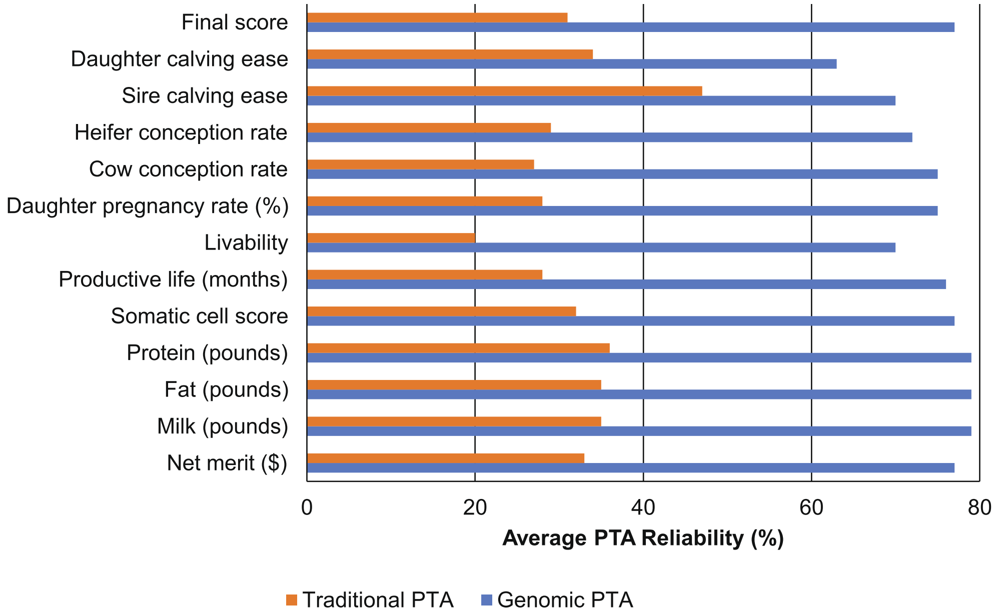


Fig. 8. Comparison of genomic and traditional PTA (Predicted Transmitting Ability) for US Holstein cattle (August, 2020). Data source: The Council on Dairy Cattle Breeding (https://queries.uscdcb.com/eval/summary/comparexml_menu.cfm).

Moving forward, optimal contribution selection (Meuwissen, 1997), which maximizes genetic gains under constrained levels of inbreeding, should be widely adopted in both numerically large and small breeds. A second alternative is to minimize inbreeding while maintaining a certain rate of genetic response (Colleau et al., 2004). These alternatives might be challenging as the dairy cattle breeding sector is mainly driven by private companies. In general, dairy farmers are becoming more informed of the negative consequences of inbreeding and are implementing mitigation alternatives (e.g., use of mating software and assistance of extension specialists). Furthermore, we believe that governmental agencies should reinforce the importance of maintaining genetic diversity by discouraging mating of close relatives or designing a payment system to motivate conservation of genetic diversity within and across breeds. Diversity metrics based on genomic information should be assessed across multiple dairy breeds and used for proper management of genetic resources. Lastly, considering the importance of high genetic diversity for future genetic progress and adaptation to changing and challenging environments, more public funds should be used to promote local genetic resources and financially support the conservation of rare or non-mainstream dairy breeds.

Genotype-by-environment interactions

In general, structured breeding programs have increased the genetic merit of dairy animals and have been accompanied by an improvement in the environmental conditions through management practices, both of which are needed for high productivity. However, there is a wide range of production systems (from extensive and low-input to intensive and precision-technology farms), and the best genotypes selected under certain conditions will not necessarily perform well in other environments or production systems, i.e., GxE (**genotype x environment**). Briefly, GxE interaction can be defined as a change in the response of genotypes to different environments or changes in the relative merit of genotypes in different environments (Rodríguez-Bermúdez et al., 2019; Mulder, 2017). Genotype-by-environment between environments leads to lower genetic gain if the selection is performed in a different environment (e.g., a nucleus), than in which the commercial animals are performing (Mulder, 2017). Selection for increased productivity has also led to greater environmental sensitivity (Rauw et al., 1998; Friggens et al., 2017) and therefore, it is expected that larger GxE effects will be observed when high-yielding dairy cows are raised in different production systems compared to those in which they were selected in (especially low-input systems, Dillon et al., 2003a and 2003b).

Over time, GxE was ignored in many instances, as the environments for intensive production are mainly controlled. However, considering the current challenges (e.g., higher average temperatures) and energy costs, there is a need to genetically select more resilient and robust animals (Mulder, 2017; Berghof et al., 2019). Several strategies have been sought to overcome these issues. First, breeding schemes can consider GxE in genetic and genomic evaluations to identify the most suitable genotypes for each condition. This can be done through the use of reaction norms using routinely recorded datasets such as milk yield and climatic variables or direct indicators of resilience and welfare (Berghof et al., 2019; Brito et al., 2020b). Different tools and approaches can be adopted to collect phenotypes to be used for genetic selection. For instance, precision technologies (e.g., activity sensors, feeding behavior recorders, automated milking robots, computer vision) can generate a wealth of data to maximize genetic progress for traits related to resilience and welfare, as reviewed by Berghof et al. (2019) and Brito et al. (2020b), respectively.

Secondly, local breeds can be used for the introgression of desirable alleles, crossbreeding with exotic breeds, and development of new composite breeds. When animals are genetically adapted to specific environmental conditions or production systems, they will tend to be more productive, have better welfare, and production costs will be lower. In addition to environmental conditions, a wide variety of production systems are becoming more common around the globe, including precision-technology-based dairy farms, organic, and agroecological production systems. Thus, different selection indexes need to be developed to select animals that perform well, have a better life (in terms of positive welfare, health, longevity), and are part of an environmentally and economically sustainable production system.

The role of local breeds toward increased dairy sustainability

In general, local breeds: (1) are more adapted to less intensive and suboptimal management practices and harsher environmental conditions such as high temperature and relative humidity, endo- and ectoparasites, higher altitudes, or lower-quality feed; (2) have greater fertility and longevity; and, 3) have lower incidence of metabolic diseases, hoof health issues, and reproductive disorders (e.g., Dillon et al., 2003a and 2003b; Walsh et al., 2007, 2008; Bedere et al., 2017a, 2017b and 2018). The large majority of these traits are already under selection (or in research stages) in Holstein (and other cosmopolitan breeds) breeding programs around the world. However, in addition to continue selecting for these traits in cosmopolitan dairy cattle breeding programs, considering the heritability of fitness traits (e.g., health, longevity, fertility), it might be more cost-effective to genetically improve the performance of local breeds while also avoiding deterioration of fitness traits, as already observed in breeds such as Holstein. In other words, the participation of local breeds in dairy production is expected to increase as their production levels are improved and adaptation and fitness are retained. On the other hand, Holstein (and other cosmopolitan dairy breeds) will be selected for increased fitness and adaptation with a reduced focus on milk yield. At the end, both breed groups will be more adapted to play an important role in specific production systems (e.g., precision farming and high-input vs low-input farming).

Novel breeding goals for long-term sustainability

The long-term sustainability of the dairy cattle industry depends on the development of balanced breeding goals to simultaneously improve animal health and welfare, productive efficiency, environmental impact, food quality and safety while minimizing the loss of genetic diversity. Genetic selection for some of these breeding goals have already been implemented around the world (e.g., Miglior et al., 2017; Cole and VanRaden, 2018) and certain countries have placed greater emphasis in these novel traits, especially in Europe. The wide availability of genomic tools provides a great venue to genetically improve traits that are difficult or expensive to measure (e.g., disease resistance, welfare, longevity, methane emissions) as well as to better manage genetic diversity (Meuwissen et al., 2020). The refinement of breeding programs to incorporate novel breeding objectives requires the development of high-throughput phenotyping technologies (and structured and continuous data recording streams), investigation of the genetic relationship between novel traits and those routinely recorded (and the potential consequences of selection for every single trait), the performance of large-scale genomic studies, especially genomic predictions and genome-wide association studies, and refinement of selection indexes to reflect improved knowledge of biology, new sources of data, and changing conditions in the environment and economy (Cole and VanRaden, 2018).

The greatest obstacle for including multiple traits in dairy cattle breeding programs has been the cost and difficulty to measure a large number of animals for close-to-biology traits, which usually lack well-defined phenotypes. The availability of precision technologies, that can be used across multiple production systems, is an opportunity to measure novel traits, especially resilience, welfare, and environmental efficiency (Brito et al., 2020b). Intensive selection for production traits combined with the intensification of dairy cattle production systems has resulted in animals that are at greater risk of behavioral, physiological, and immunological disorders (Barbat et al., 2010; Colditz and Hine, 2016; Friggens et al., 2017; Lawrence and Wall, 2014; Rauw et al., 1998, 2012; Star et al., 2008). Therefore, key groups of novel traits are: health (e.g., udder health, hoof health, metabolic disorders), fertility, feed efficiency, methane emissions, longevity, and overall resilience. Additional breeding goals or differential emphasis in selection indexes are required depending on the production system. For instance, major traits for agroecological dairy farming are: behavior (feeding on new resources, well-being indicators), overall resilience, reproduction, and nutrient efficiency. As we focus on increasing dairy sustainability, it will be crucial to evaluate the animals' efficiency to digest alternative feed sources (e.g., grasslands and forages, algae, food industry by-products, local crops). Furthermore, even animals with similar feed efficiency might still differ with regard to manure composition (e.g., nitrogen/phosphorous ratio), which will become increasingly important in order to mitigate the negative impact of animal production on the environment. For each group of traits, related variables might also be useful indicators (e.g., feeding behavior and feed efficiency). Depending on the production system adopted (e.g., beef-on-dairy, extensive production), beef traits (carcass, body size, meat quality) will also need to be genetically evaluated. Fertility and reproduction are of great importance in high-yielding dairy herds, but it is even more important in less specialized systems where milk production peak needs to overlap with the grasslands growing season.

Alternative options to intensive (high-input) dairy production systems: The role of genetic selection

There is a plethora of production systems being explored worldwide. As reviewed by Clay et al. (2020), sustainable intensification is related to increasing productivity while simultaneously decreasing the negative environmental effects of conventional farming practices and improving animal welfare. Secondly, agricultural multifunctionality provides an opportunity to derive diverse benefits from agroecosystems that extend beyond the production of food and fiber to include environmental services (e.g., carbon sequestration, biodiversity, and water quality) and maintenance of social-cultural processes. Moreover, agroecology emphasizes the context-specific nature of agroecosystems and considers how ecological principles can help achieve goals of sustainability and social equity (Clay et al., 2020). Prospective scenarios offer interesting insights for the development of current production systems as they address the multiple challenges of sustainability (e.g., impacts of diets on health, food security, climate change, biodiversity loss) in a systemic view. Achieving sustainability in its multiple dimensions is extremely ambitious and complex given that actions on a particular dimension may be detrimental to another dimension. In scenarios emphasizing profound transitions toward agroecological systems, there is a very large reduction in farm inputs and associated with a reduction in yield. In the case of dairy production systems, for instance, the TYFA model developed at European scale (Poux and Aubert, 2018) includes two typical dairy systems in 2050:

(i) "*a grass-fed system, in which the majority of fodder resources come from permanent grasslands, with an average level of productivity per cow of 5 000 kg of milk/year*" and,
(ii) "*a mixed system, in which permanent grasslands are combined with other fodder resources: temporary grasslands, cereals, and legumes (alfalfa, clover). The average production level is 7 000 kg of milk/year*".

Similarly, the Afterres2050 scenario developed at the French scale (Couturier et al., 2017) suggests the progressive replacement of high-input dairy systems (i.e., with milk yield average >10 000 kg/year/cow) by low-input systems with more moderate production levels. In both scenarios, the dairy herd replaced the beef herd and the less specialized dairy cow were also dual-purpose cows (milk and meat). The meat from culled cows and calves was considered to be less polluting than meat from a suckling herd (Puillet et al., 2012). This pattern can be improved by the use of female sexed semen for the renewal of the dairy herd and male sexed semen to produce well-conformed animals for meat production.

Rustic strains of Holstein-Friesian can be adapted for organic dairy herds as they are bred in pasture-based systems (as in New Zealand and Ireland; Rodríguez-Bermúdez et al., 2019). In the current organic dairy herds, no strategy seems to have been adopted massively and producers are still experimenting, using conventional breeds, as purebreds or crossing schemes, or local breeds (Rodríguez-Bermúdez et al., 2019). Nauta et al. (2009) showed that multifunctional organic farming (*vs* specialized organic dairy farming) could adopt local dairy breed as a commercial strategy for agritourism, and participate in a living gene-bank supported by subsidies from the European Commission.

In specialized organic dairy herds, crossbreeding could be increased. A large-scale experiment that studied several crosses for more than three generations has shown that Holsteins can be crossed with Montbeliarde, which is a dual-purpose breed with significant muscle development and good fertility. This cross can then be mated with Scandinavian Red, which has good health characteristics (Hazel et al., 2020, 2021). The rotational crossbreeding between these three breeds exploits well the complementarity across breeds. For farms that have climatic conditions that allow for year-round grazing, Montbeliarde could be replaced by Jersey to have more adapted animals for grazing systems. The rotational crossbreeding seems to be more rapid than selection in pure breeds, as it has the advantage of maintaining the heterosis effect and suppressing inbreeding. From a genetic evaluation point of view, evaluations maximizing the heterosis effect could be developed, as in various plants and non-ruminant breeding programs (González-Diéguez et al., 2020).

Conclusions

Remarkable achievements have been accomplished in the dairy cattle industry over the past decades, with a massive increase in milk productivity (in a limited number of breeds). Unfortunately, this progress has been accompanied by strong drawbacks, including loss of genetic diversity and deterioration of key biological mechanisms (e.g., health, resilience, robustness, welfare, longevity) in the most common dairy cattle breeds. Moving forward, the development of a more sustainable dairy cattle industry will require continued innovations in multiple areas, especially in genetics, strong involvement of all stakeholders (e.g., farmers, technical and scientific sectors, consumers, policy-makers), diversification of production systems, and great support from governments and private institutions toward experiencing and developing alternative production systems. There seems to be a consensus on the need to continue refining the current selection indexes and breeding goals to incorporate or give greater emphasis on traits related to animal welfare, health, resilience, longevity, and environmental efficiency. Novel phenotyping technologies, closer-to-biology traits, and genetic and genomic evaluation methods will continue to be developed and should be addressed to specific production systems. Finally, genetic selection of high-yielding dairy cattle will need to be part of more systemic approaches at the farm scale to favor profound transitions toward sustainable farming systems.

Ethics approval

Not applicable.

Data and model availability statement

None of the data were deposited in an official repository. All the data used in this review are publicly available in the tables and figures.

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Declaration of interest

None.

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