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Climate Adaptation of Tropical Cattle

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Abstract

There is sustained growth in the number of tropical cattle, which represent more than half of all cattle worldwide. By and large, most research in tropical areas is still focused on breeds of cattle, their particular advantages or disadvantages in tropical areas, and the tropical forages or feeds that could be usefully fed to them. A consistent issue for adaptation to climate is the heat of tropical environments. Changing the external characteristics of the animal, such as color and coat characteristics, is one way to adapt, and there are several major genes for these traits. However, further improvement in heat tolerance and other adaptation traits will need to use the entire genome and all physical and physiological systems. Apart from the response to heat, climate forcing through methane emission identifies dry season weight loss as an important if somewhat neglected trait in climate adaptation of cattle. The use of genome-estimated breeding values in tropical areas is in its infancy and will be difficult to implement, but will be essential for rapid, coordinated genetic improvement. The difficulty of implementation cannot be exaggerated and may require major improvements in methodology.

INTRODUCTION

Tropical agriculture faces many conflicting challenges. The tropics contain many countries that are still developing; they contain tropical forests, the lungs of the planet; and they are regions known for high biodiversity, including many exotic pests and diseases. Cattle agriculture in the tropics stares at the challenge of increasing productivity in the face of growing populations in these regions, but productivity has had to be harnessed to the needs of maintaining adaptation to the environment. Because productivity and adaptation to tropical environments have long been seen as antithetical, increased productivity has always been expected to come with the trade-off of reduced adaptation. As the effects of climate change have become obvious, additional factors have emerged to add to this traditional balancing act of productivity versus adaptation, namely, the bottom-line effects of these factors on climate forcing. Although these factors are elaborated in this review, two aspects of adaptation to the tropics are not covered. First, resistance or resilience to pests or diseases is not covered; this is an important topic that needs a review to itself, but more, as the immune system is involved it represents a great deal of added genetic complexity. Resistance or resilience represents an important suite of traits. Second, changes in the environment to suit maladapted cattle, such as the provision of shade or the spraying of high volumes of water into the air to change temperature or humidity, are not covered, as they are not adaptations of the animal to the environment.

CATTLE AND TROPICAL AREAS

Climatic adaptation of tropical cattle is a complex issue, and not only for semantic reasons. For instance, questions such as the number and variety of tropical cattle and the main production issues in the tropics are difficult to answer. There are many reasons for this, starting with the difficulty of defining a tropical area. For example, tropical agriculture does not occur only between the tropics of Cancer and Capricorn. Climate maps of the world show that tropical regions do not coincide with the area between the tropics, and there is nothing in particular that would limit tropical climatic regions to the tropics—see, for example, maps of the Köppen-Geiger climate classification (1, 2), in which tropical climatic and vegetation regions extend some distance outside the tropics in a nonuniform way. These maps also show that tropical climatic and vegetation regions are not uniform and vary substantially, including subtypes labeled as rainforest, monsoon, savannah, summer dry, and winter dry. The one constant is heat. One would expect that each one of these would have its own challenges requiring particular adaptations. Moreover, these maps do not recognize the subtropics as a climatic or vegetation area, even though it is a mainstay of discussion of cattle. To simplify matters, I call tropical climatic and vegetation regions tropical areas and use “between the tropics” to refer to areas that are defined strictly by the tropics of Cancer and Capricorn.

Tropical cattle are a diverse category and include cattle that either arose in the tropics, are composites of such tropical cattle and temperate cattle, or were temperate cattle that were translocated to the tropics and have been under natural or artificial selection there for many generations. Examples of cattle that arose in the tropics are breeds derived from *Bos taurus indicus*, usually shortened to *Bos indicus*. Most of these animals are derived from India in one way or another, whether translocated to Africa a thousand years ago or to the Americas or Australia in the last hundred years (3–6). They are clearly differentiated by possessing humps, which gives their other name, zebu cattle. Many composites have been generated, mostly through the Brahman breed, which is itself a composite, although usually possessing approximately 5% to 10% taurine ancestry. Taurine cattle (*Bos taurus taurus*, usually shortened to *Bos taurus*) entered Africa thousands of years ago and have adapted to tropical conditions there (4, 7), and these cattle are used either as purebreds or in composites either with other taurine breeds or with indicine breeds. Finally, taurine cattle were introduced to the Americas by the Portuguese and the Spanish hundreds of years ago and

have adapted to tropical conditions over that time (8). These are also used as purebreds or as composites, with either other taurine or indicine breeds.

The number of tropical cattle is hard to pin down. Global agricultural censuses occur every 10 years; the last, published in 2010 (9), was Census 2000, covering the period 1996 to 2005. The 2010 census has yet to be published because it refers to the time period from 2006 to 2015, and planning is under way for the 2020 census, which covers the years 2016 to 2025. The most recent Food and Agriculture Organization (FAO) statistics for numbers of cattle around the world were assembled in 2007 (10). Fortunately, the FAO keeps statistics updated on an annual basis, and the estimated head count of cattle for each country is made available (<http://faostat3.fao.org/home/E>, checked Dec. 9, 2015). Although this might appear to be easy to tally up, many countries lie across the tropics and have cattle inside and outside tropical areas, so a head count based on countries is going to be somewhat inaccurate. Nevertheless, in using these statistics and designating broad regions as either tropical, part tropical, or temperate, one sees that tropical cattle account for just over half the cattle worldwide. This total was greater than 805 million head in 2013; this number has been increasing steadily and would be expected to continue to grow in the decade ahead (**Figure 1**).

Any discussion of climatic adaptation of tropical cattle needs to keep in mind the challenges facing tropical agriculture in general. These challenges include changes in land use; intensification of farming practice; farming incentives; changes in food sources for the world, including an increase in animal sources of food and an increase in prepared and processed food; sustained and sustainable agricultural growth; minimization of the negative impacts on biodiversity; reduced vulnerability to income shocks; improved overall wealth; sparing of tropical forests; climate forcing having an impact on tropical crops and pastures; and failure of pest eradication, for example, that of rodents (11–18). Selecting cattle for the conditions of the past, such as low-input management systems, marginal or default conditions where cattle and other livestock are merely on the edge of plant-based agriculture, may not correspond to the direction in which tropical

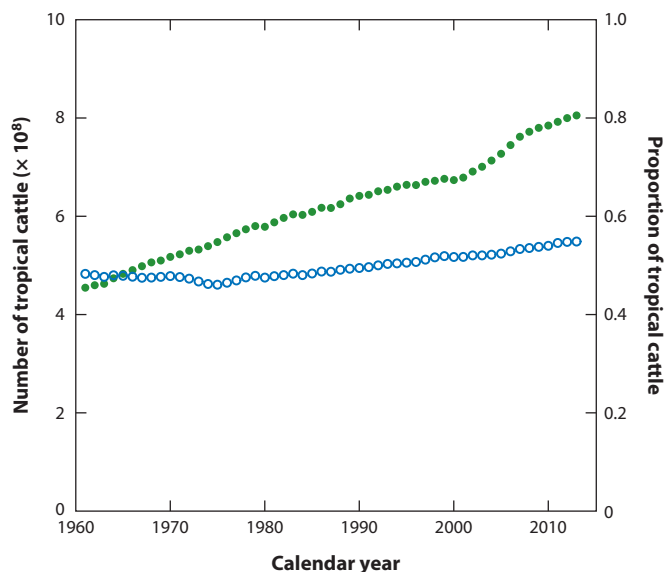


Figure 1

The approximate number of tropical cattle (*solid green circles*) and the proportion of tropical cattle (*open blue circles*) over the last four decades.

regions are heading or the needs of agriculturalists in those regions. Clearly, an agile mindset needs to be maintained, one where several options are held open to be taken advantage of as and when needed. In particular, adaptation, in the parlance of climate adaptation to climate change, is an activity that reduces the impact of climate change. This is especially important if those changes may not make a large difference now but may mitigate the effects of climate change, resulting in either the maintenance or increase of production in the face of climate change or in less decline than would have occurred in a business-as-usual approach (15).

TROPICAL CATTLE ADAPTATION

To get an idea of the main priorities in research in tropical adaptation of cattle, the phrase “Tropical Cattle Adaptation” was entered as a topic in ISI Web of Science on December 14, 2015. There were 115 results dating from 1993, 15 of which had nothing to do with tropical cattle. Owing to the limit of 150 references, only a selection of these could be included. One should note also that such a search will preferentially favor work written in English and may overlook work from researchers in, for example, South America, but many articles from Brazil and other tropical nations were included in the reference list. In the following analysis, a reference dealing with two or more categories was counted only once in the category it most suited. Of the 100, the main topics of the studies broke down as follows: There were 35 studies of breeds and breeding (19–24); 32 studies of feeds, nutrition, or pastures (25–29); 11 studies of parasites and disease resistance (30–34); 10 studies of genes or genomes (35–40); 8 studies of the environment, including mitigation, farming systems, and biofuels (41–45); and 4 studies of reproduction (46, 47). Of these 100 studies, there were 15 studies that took into account heat; 5 in which heat was the main focus; and 10 in which either heat was the minor focus or the traits studied were surrogates for heat, such as coat characteristics (48–51). In addition to the 4 main studies of reproduction, a further 2 studies examined reproduction as a minor aspect in other studies. The earliest study of genes or genomes captured by this search string dated from 2009 (52), although this would not be the first genetic study of tropical cattle adaptation. Two-thirds of studies concerned either breeding or feeding of cattle in a tropical environment. The cattle breeding studies were mainly about production, including growth of cattle in tropical environments, and nearly half of these focused to some extent on the heat of tropical environments. Although there have been some initial genome sequence studies of tropical cattle, of indicine breeds (37, 53–55), so far there has been little genome sequencing of indigenous or criollo breeds.

An examination of the breeds of cattle used in these studies shows the following themes. Of the 83 times breeds were identified, 18 (22%) referred to locally adapted tropical indigenous breeds, such as criollo cattle (56–59); 18 (22%) referred to modern or recently formed composites or crossbreeds between taurine and indicine cattle (60–64); 21 (25%) referred to improving or comparing adaptations of European taurine cattle from the developed world used in the tropics, chiefly the Angus (7) or Holstein (9) breeds (65–67); 21 (25%) referred to improving or comparing productivity in indicine breeds, chiefly the Brahman (12) or the Nelore (5); and 5 (6%) referred to studies of improved adapted breeds, of which 4 referred to the Senepol (68). Owing to differences in funding or breeds found in different parts of the world, these numbers or the differences between categories should not be overinterpreted. What these numbers illustrate are the main focus areas, namely, (*a*) the study of locally adapted purebreds with a long history in a particular area; (*b*) attempts to improve both productivity and adaptation in the tropics through various strategies, such as crossbreeding between taurine and indicine cattle, improving the adaptation of taurine cattle, or improving the productivity of indicine cattle; and (*c*) what appears to be a small emphasis on the study of taurine cattle that are adapted to the tropics and that have already undergone

genetic improvement. This last point is interesting because Senepol cattle have a gene, the Slick gene, that adapts them to the hot conditions of the tropics. Also worth noting is that established composite breeds, such as the Santa Gertrudis and Droughtmaster and others of that kind (69–71), did not feature much in that selection of the literature.

The issues associated with cattle in the tropics have been known for some time, and few new issues have arisen. For example, Bonsma (72) identified (*a*) heat, including radiation, temperature, and humidity; (*b*) feed, including feed quality and the ability to use the feed available; (*c*) resistance, including to parasites, especially ticks, and to photosensitivity, especially eye cancer and keratosis; and (*d*) the ability to avoid noxious plants, not only as a feed source but also the physical aspects of thorns and other plant defenses. He focused very strongly on (*a*) color and characteristics of hair and skin; (*b*) the ability of the animals to move great distances to forage; (*c*) birth weight of calves and the fecundity of animals; (*d*) milk production of cows in terms of the growth of calves; and (*e*) the longevity of breeding animals in the herd and the factors that affect this longevity, including the death rates of different breeds in tropical and subtropical areas. This might seem like ancient history, but these are still the issues that are discussed, and the genes underlying several of these important traits have now been identified, although for other traits, no start has yet been made.

There are strong differences between breeds in their heat tolerance and other characteristics (62, 73, 74). Animals of a breed often lie within narrowly defined ranges for characteristic colors and coat textures; size and overall shape; morphological features, such as ear length or wattles; a range of behavioral traits; density of sweat glands; and vascularization of the dermis, and some of these are thought to affect heat tolerance (75–78). Improvement in heat tolerance, therefore, requires a focus on not only visible traits but also physiological traits, traits that may be hard to perceive without in-depth measurement (79, 80).

Some of the heat-resistance traits are affected by major genes, which have been identified down to the nucleotide changes that cause the effects (Table 1). Most of these are genes affecting color,

Table 1 Genes for adaptation traits identified to the level of the gene

Trait	Specifics ^a	Gene	Type of mutation	Reference
Hair color	Red	<i>MC1R</i>	Coding c.310delG	81
Hair color	Roan	<i>KITLG</i>	Coding p.Ala227Asp	82
Hair color	Red	<i>COPA</i>	Coding p.Arg160Cys	83
Hair color	Grey	<i>MLPH</i>	Coding c.87_97del	84
Hair color	Color sided	<i>KIT</i>	Translocation to Bta29	85
Hair color	Dilution	<i>PMEL</i>	Coding p.Gly64Arg	86
Hair color	Dilution	<i>PMEL</i>	Coding p.Leu18del	87
Hair color	Dun	<i>TYRP1</i>	Coding p.His434Tyr	88
Hair color	Piebald	<i>KIT</i>	Complex genetics	89
Hair color	Piebald	<i>MITF</i>	Unknown	90
Coat type	Slick	<i>PRLR</i>	Coding p.Leu462*	91
Mature size	Hip height	<i>PLAG1</i>	Regulatory sequence	92

^aNote that genetic mutations resulting in albinism, black coat, and long hair (81, 91, 93) for which mutations have been identified were not included in the table, as it would be difficult to argue for an adaptive role for these traits in cattle in the tropics. There may be a role for the various partly colored mutations, such as piebald, especially if the variable coloring leaves large areas of white (94). Albinism, which is white, was excluded from the table because it would expose animals to sunburn, and tropical white cattle such as Brahman have black skins under the white hair. Mature size has impacts on several growth traits of importance, but the gene *PLAG1* is also associated with reproduction traits in tropical cattle (95), which may not be considered climate adaptation traits.

with dark colors being under a substantial disadvantage. Animals with black coloring need much more water to prevent overheating (78). However, owing to the substantial market penetration of black animals, with a premium paid for meat of these animals—chiefly owing to the Angus breed but to a lesser extent owing to marbling from the Wagyu breed—there is almost no going back from black coats. Coat type is a multifactorial trait with a complex scoring system (96), but at least one gene has been identified that causes a substantial change in coat type, generating a Slick phenotype that is accompanied by substantially improved heat tolerance (91, 97, 98). This heat tolerance has been shown to be transferable to the Holstein breed at least, although the background effects that affect the Slick phenotype have yet to be determined.

Gene editing of these allelic differences would be a fast way to include natural variation from one breed into another breed without affecting the adaptation to the environment or productivity of that breed in its management system. Recently, the mutation for the Celtic Poll allele of Angus breed cattle was gene edited into Holstein cattle, generating polled Holstein cattle that retained all the elite dairy productivity of the Holstein cattle (99). In a second example, the CD163 gene of pigs was knocked out using gene editing, resulting in animals that were completely resistant to porcine reproductive and respiratory syndrome virus (100). Given these extremely targeted changes, and the absence of transgenes in the resulting offspring, calls have been made for regulation to be focused on the gene-edited animal rather than on the method used to produce it (101).

Genetic analysis of composite taurine \times indicine animals shows that there are many alleles of moderate to large effect on adaptation to tropical conditions, called oligogenes. These alleles are not so large in their effects that they generate a discontinuous character, but they are large enough in size that they can be routinely detected even in moderate-sized samples. Examples are the effect of alleles at *PLAG1* on hip height, *CAPN1* and *CAST* on meat tenderness, and *DGAT1* on milk fat content (92, 102, 103). A genome-wide association study of 10 of these traits (39) found oligogenic alleles for all traits except the parasite- or disease-resistance traits, notably those of tick resistance and fly strike. Although this is encouraging for some adaptive traits, and although the study pointed to negative relationships between these oligogenic alleles and some of the traits, most of the total genetic variation was contained in polygenic effects. Interestingly, some of the oligogenic or major alleles were found in only one breed rather than all breeds. For some of these findings, one can be confident that these alleles were absent or had extremely low frequency in some of the breeds; for the color alleles, for example, the breeds had different colors, and the DNA testing showed a lack of genome-wide association study hits for those chromosomes where the color was missing from the breed. The negative relationships to traits for some of the alleles suggested that more of these studies should be performed, but they also showed that genetic progress will depend on genomic estimated breeding values (GEBV).

The use of GEBV has become a standard tool in the genetic selection of temperate cattle especially in the dairy industry (104, 105), but little to no progress has been made for tropical cattle (71). GEBV are now a standard tool in prediction of genetic merit in dairy cattle, and correlations between EBV and GEBV are very high (106, 107). Even in dairy cattle, though, prediction of GEBV for Jersey cattle can be low compared with that of Holstein, and prediction for crossbreed or composite animals suffers as well (71, 108). In beef cattle, more progress needs to be made, but GEBV are used in some breeds, especially the Angus (109, 110). The reason for this lower level of use in beef compared with dairy cattle is thought to be greater data sets in dairy cattle, automated methods of measuring trait values, and a narrower family base in Holstein cattle. Indeed, the prediction of New Zealand Holstein using Australian and North American Holstein suffers because the New Zealand Holstein contains some older lineages that are no longer present in Australia or North America (111) (B.J. Hayes, personal communication). For tropical cattle, there are additional challenges. First, the crossbreed and composite animals are

of more widely divergent starting breeds. One expects in that case the breeds may not have the same oligogenetic or major alleles segregating, as we saw for color alleles mentioned above; that the linkage disequilibrium between DNA markers and the quantitative trait loci may be different between breeds; and that the polygenic background might also be different. Second, it is rare for tropical cattle to be supported by the industrial infrastructure seen for temperate breeds. One expects that sampling of cattle will occur less and the sampling of breeds might be quite narrow, and so the construction of accurate GEBV could be a challenge. Obtaining accurate crossbred GEBV for tropical cattle might be an intractable problem without an advance in methodology. Without infrastructure, breeders might not use GEBV technology anyway. This would imply that breeders and producers would instead focus on breed definitions and breed differences in their choice of cattle because this would be the simple and reliable option open to them. But this approach may close off rapid, coordinated genetic progress.

It was hoped that GEBV would leapfrog the lack of uptake of conventional EBV, which shows poor uptake even in the tropical areas of developed countries (112), but the prospects appear grim at the moment and will require a great deal of effort. There is no doubt that DNA testing has been accepted for single-gene traits, such as the use of the Poll allele test in tropical cattle (113). The Slick allele test will also likely be used, and animals will continue to be selected on color and coat score. At the cattle stud level, parentage assignment is important for accurate selection, and DNA SNP arrays will continue to provide accurate parentage for animals in commercial herds. But GEBV for climate adaptability, including size, growth rate, and heat tolerance, would require large reference herds of animals set up to calibrate GEBV equations (114). Few countries in tropical areas have the infrastructure to do this, which means germ plasm improvement will be driven by those countries willing to make the investment. Nevertheless, given the issues of reduced resource availability, population increase, and the increased demand for produce from livestock, GEBV for important traits of tropical areas must not be ignored.

CATTLE EFFECTS ON CLIMATE

In discussing climatic adaptation of cattle, it is necessary to discuss the potential effects of cattle on radiative climate forcing. Anthropogenic climate forcing, including the effects of methane, appears to have occurred for the last 8,000 years (115). Methane and climate forcing are of particular relevance to tropical cattle owing to poor-quality forages as well as dry-season weight loss, as described below. Cattle and other ruminants produce methane as part of digestion (116), and methane is a short-lived gas in the atmosphere that has a large radiative forcing capability (117). Furthermore, manures lead to the production of a spectrum of nitrous oxides, which in their turn have effects on radiative forcing (118). Methane has an estimated lifetime of ~ 9.1 years in the atmosphere (117), and its global warming potential compared with carbon dioxide is reported from 21 to 56 (119, 120), with a ratio of 26.5 in the radiative efficiency of methane to carbon dioxide (117). These differences in global warming potential mean that one needs to be explicit in the conversion factors that one uses when comparing estimates. The atmosphere consists of more than 400 ppm of carbon dioxide, 1,823 parts per billion of methane, and 327 parts per billion of nitrous oxide (117), so there is approximately 219 times as much carbon dioxide as methane and approximately 1,223 times as much as nitrous oxide. The effects of carbon dioxide and methane have been compared with that of a wood stove versus a blowtorch in warming a room. The blowtorch, although fierce, has a smaller effect in warming the room until the number of blowtorches increases substantially. Nitrous oxide is of lesser concern for cattle production than methane partly because of the lower amount and partly because methane is a ruminant-specific item compared with other livestock types, but its lifetime in the atmosphere is ~ 123 years, and

it has a higher radiative efficiency than methane, so it cannot be ignored. (Proper handling of manures needs to occur for all livestock species owing to effects on air and water quality as well as the valuable phosphates contained in the manures, but this issue is outside the scope of climate adaptation of tropical cattle so it is not discussed further.) Methane levels have increased 250% since around 1750 (117). The effect of methane is significant; for example, in Australia, with new methods of estimation, cattle account for 44% of equivalents of carbon dioxide ($\text{CO}_2\text{-e}$) of agricultural emissions and 6.2% of total emissions (121), not all from methane, in a developed country of approximately 22 million people and 29 million cattle.

It seems highly likely that the total number of ruminants on the planet has increased since agriculture began. Currently, there are 75 million wild ruminants and approximately 3.5 billion domesticated ruminants, chiefly cattle, sheep, and goats (122), or approximately 1 for every 2 people. It is unlikely that the world contained 3.5 billion ruminants prior to agriculture. North America is estimated to have contained 25 to 40 million bison prior to 1800 (123, 124), and extrapolating that to the area of the earth that had native ruminants, to Africa, Asia, and Europe, would suggest numbers of the order of 194 million ruminants prior to agriculture, most of the species smaller than the Bovidae that currently dominate (122). Clearly, then, part of adaptation of cattle and other ruminants to climate must be the control of methane partly through genetic and nongenetic methods.

The amount of methane an animal produces is moderately heritable, and there are now attempts to select animals on the basis of methane produced. The level of heritability is low to moderate in several species and is related to residual feed intake (125–132), which may come as a surprise because the methane is produced by the quorum of protists in the rumen rather than by the individual itself. This suggests an interaction between the host's genetics and the microbial contents of the rumen. Measuring methane produced by an animal is tricky and time consuming, so attempts are being made to generate GEBV. There are also attempts being made to find easier ways of getting accurate methane measurements (116, 133).

On the nongenetic front, methane production is highly related to quality and composition of the feed (121, 134, 135). Poor-quality forage and periods of weight loss are associated with high relative methane production (136, 137). This is of importance to tropical cattle production because much of tropical forages and grasslands can be deficient in protein for large parts of the year and nitrogen supplementation often is needed (138–145). Indeed, I estimated that slightly more than half of all cattle were in tropical regions (**Figure 1**), and more than half of anthropogenic methane from cattle comes from tropical sources (146). Better-quality feeds and year-round growth would mitigate methane production because animals are grown to specific endpoints and not necessarily for specific lengths of time. If they reach the required endpoint early and with less methane produced, there would be a marked drop in methane production without a reduction in cattle numbers.

Dry-season weight gain is therefore a key trait for production in the tropics. Many tropical areas suitable for cattle have a hot dry and hot wet weather cycle. During the dry season, many grasses die back, leaving fiber-rich but protein-poor plant tissue above ground. There are clear patterns of weight gain followed by weight loss in the tropics (**Figure 2**). The data in **Figure 2** are previously published raw data from Beef Cooperative Research Centre experiments during the period 2000–2011 and consist of regular live-weight measurements of cattle over several years during wet and dry seasons (39, 62, 63). This figure shows periods when all cattle are gaining weight, when only some are gaining weight, or when all cattle appear to be losing weight. Dry-season weight loss has two important consequences: (*a*) If the wet season fails to arrive, this can lead to catastrophic loss, and (*b*) cattle off tropical pastures may come in waves, because slaughter after the dry season would result in loss of profit to producers. Selective breeding should be applied to produce animals that grow well on poor tropical forages and produce less methane.

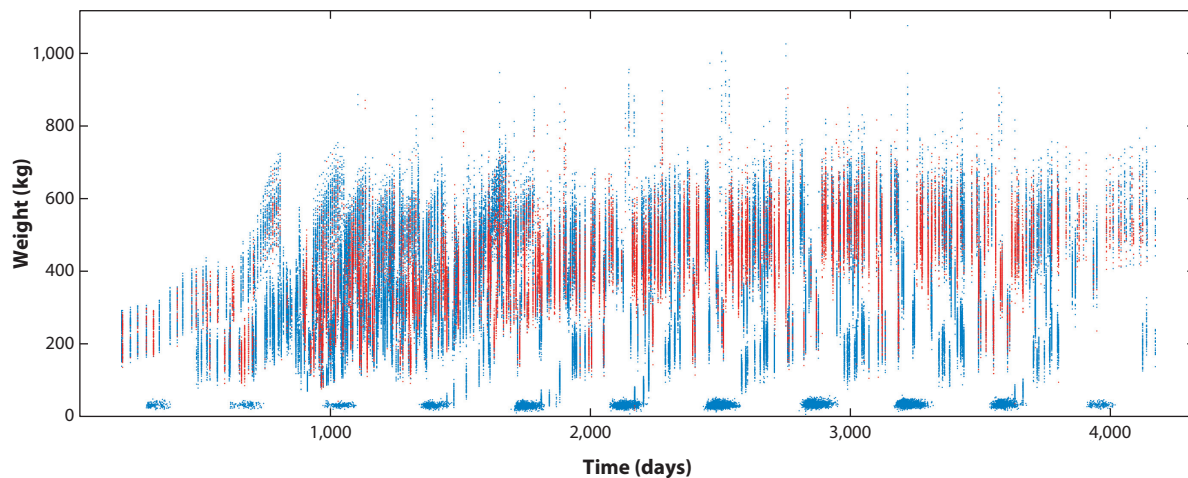


Figure 2

Weight gain (*blue*) or loss (*red*) of individual cattle grown in the tropics for cattle weighed serially at regular intervals over several years. Birth weights are shown as clusters of dots low down in the figure. When an animal has gained zero or more kilograms since the last weighing, its weight is shown in blue. If it has lost any weight, its weight is shown in red.

Growth or final weights in the tropics appear to have two components, one reflecting growth in the dry season and one reflecting growth in the wet season (61–63). Both of the components show relatively strong correlations to final weight, with genetic correlations above 0.4 (60). But although preweaning weight gain shows a correlation to wet-season weight gain, it showed little genetic correlation to dry-season gain in those data sets. In addition, wet- and dry-season gain show little correlation to each other, with a genetic correlation of $r \sim 0.2$ (60). This means that wet- and dry-season gain are effectively separate traits. Brahman breed animals showed lower wet-season gain and lower dry-season loss than tropical composite animals (62). This suggests that in very hard country, Brahman cattle may persist where composite cattle may not, even if they may not grow as quickly when conditions are favorable. Animals should therefore be selected for both dry- and wet-season weight gain; selection only for wet-season or for final weight would not necessarily improve dry-season performance unless it was specifically included in the selection index.

The measurement of methane on an animal basis is time consuming and difficult. Proxies would be welcome, and one proxy shows some promise. Interestingly, dairy milk fat components have been shown to have a relationship to methane produced by the animal (129, 147–150). These include the short-chain saturated fatty acids and some of the trans fatty acids. The rumen microorganisms are known to alter the fatty acid composition of the feed, generating a variety of conjugated linoleic acids that are affected by food source and changes in rumen pH (151). Methane is generated by only some of the rumen microorganisms, and so the potential exists for monitoring the long-term differences in rumen microorganisms through the fatty acids that are obtained from the rumen. The most convenient way to obtain this would be through milk fat. Estimating the composition of milk fat is a routine procedure, so one should not be astonished to find that differences in milk fat components show an R^2 of at least 0.67 and can be as high as 0.73 to the methane emitted by the animal (150). It goes without saying that fat associated with meat could be analyzed for these same fat components, so this indirect measurement of methane production is an opportunity to estimate methane production that needs to be verified.

Given the benefits of livestock production, one should ask what part of global methane production is due to cattle and other livestock versus other anthropogenic factors. The main sources of methane are natural wetlands, anthropogenic activity (livestock agriculture, rice cultivation, activity associated with fossil fuels, waste waters, and landfill), and biomass burning, which may be both natural and anthropogenic. It is estimated that 60–70% of global methane is due to anthropogenic activity (115, 117, 152). Globally, livestock contributes at least 2.45 Gt of CO₂-e, of which methane contributes 1.6 Gt of CO₂-e, with cattle accounting for 77% of the emissions (146). The entire anthropogenic emission of methane is 500 to 600 Tg per year; 1 Tg = 1 Mt, and after converting methane to carbon dioxide equivalents using a factor of 34, 500 Tg = 17 Gt of CO₂-e. An output of 1.6 Gt of CO₂-e owing to methane (146) is therefore between 9.4% and 11.4% of anthropogenic methane produced globally. All livestock produce more methane than does rice production, which contributes 0.96 Gt CO₂-e (153), a value that is slightly smaller than methane emissions for cattle alone. Comparison between these values is imprecise because they are calculated for different years, but they are sufficient to give a ranking for the importance of different sources of methane. Nevertheless, livestock provide many benefits to tropical areas that offset their methane production, such as nutritional security, reduction of poverty, and sustainability of the global food system (146).

CONCLUSION

There is still some way to go for improvement in tropical cattle adaptation. There has been progress in heat tolerance of cattle, with the identification of a few major alleles affecting color and coat characteristics. But there is still opportunity for further improvement in heat resistance at a physiological and structural level, which would have effects on water usage. Other traits that need improvement are growth traits, especially dry-season weight loss, which is also related to the quality of tropical pastures, water availability, and land use. These traits are important partly because of their relevance to methane production. At the moment, the genetics of tropical cattle focuses on breeds and breed characteristics on the one hand and DNA tests for single genes or to confirm parentage on the other hand. The focus on major genes would have required the introgression of genes from another breed and then serial backcrossing over many generations to recover the adaptedness that was lost. However, there is now the potential to change genes through gene editing in a highly precise way, a potential that has yet to receive approval from regulators for animals in the food chain, including for genes that affect climate adaptation. Nevertheless, most traits are multifactorial, and the genetic basis is unknown at the level of gene mutations. Therefore, improving dry-season gain or reducing methane emissions, or even making further improvements in heat tolerance, will require genetic selection focused on traits and on the use of all the genetic material, not just on a few genes. Achieving this will require the use of GEBV given the difficulties in measuring some of the traits, especially in tropical areas where infrastructure is poor. GEBV likely will first be used for traits that are well understood in temperate cattle, such as growth, once crossbreed GEBV become more accurate and stable. Heat tolerance and other adaptability traits will likely follow, given the great deal of interest in the potential for reduction in methane emissions. Clearly, then, the efforts to extend GEBV to tropical cattle need support owing to the large infrastructure needed to implement GEBV, including calibration herds, genome sequence, and crossbreed GEBV. Genetic improvement of tropical cattle has often proved to be difficult, compared with the strong productivity gains that have been made in temperate cattle. With the large number of tropical cattle and their large proportion relative to the total number of cattle, greater attention needs to be paid to this resource as the world struggles with the issues of sustainability and the feeding of a burgeoning global population.

SUMMARY POINTS

1. The number of cattle, and the proportion of global cattle, grown in tropical areas continues to rise.
2. Cattle adaptation in tropical areas still focuses largely on breeds of cattle and types of suitable feed.
3. DNA tests for tropical cattle are mainly for major genes and for parentage assignment and include traits such as coat color and texture, which are important for climate adaptation. Gene editing, if approved for animals in the food chain, would have applications in transferring genes conferring adaptability without necessarily reducing productivity of bloodlines, and vice versa.
4. As yet, DNA tests for GEBV have not reached commercial application for tropical cattle owing to a lack of predictive accuracy and infrastructure to implement GEBV.
5. As is well known, cattle produce a substantial amount of methane, which is reported here, and methods to measure this simply and accurately are urgently required so as to apply genetic selection.

FUTURE ISSUES

1. Genetic improvement of tropical cattle must move beyond the contemplation of breeds and breed characteristics.
2. The use of GEBV in tropical cattle will require improvements in methods of prediction for crossbreed cattle.
3. High-level genome sequence coverage of adapted or special breeds needs to be obtained before the animals become rare, because there is the possibility of discovering unique or unusual genes affecting adaptation to tropical areas. This could be combined with the use of phenotypic outliers to identify new or rare mutations that affect climate adaptation.
4. Dry-season weight loss may be the most important neglected trait of climate adaptation owing to the impact on methane emission relative to growth.
5. Cattle and other ruminants can use forage and fiber that are inedible for humans, but these food sources may be more methanogenic. Grain will not always be available as a feed source for cattle, so improved growth on poor substrates will be a key future issue.

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LITERATURE CITED

1. Kottek M, Grieser J, Beck C, Rudolf B, Rubel F. 2006. World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* 15:259–63
2. Peel MC, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* 11:1633–44
3. Sanders JO. 1980. History and development of zebu cattle in the United States. *J. Anim. Sci.* 50:1188–200
4. Hanotte O, Bradley DG, Ochieng JW, Verjee Y, Hill EW, Rege JEO. 2002. African pastoralism: genetic imprints of origins and migrations. *Science* 296:336–39
5. Gibbs RA, Taylor JF, Van Tassell CP, Barendse W, Eversole KA, et al. 2009. Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds. *Science* 324:528–32
6. McTavish EJ, Decker JE, Schnabel RD, Taylor JF, Hillis DM. 2013. New World cattle show ancestry from multiple independent domestication events. *PNAS* 110:E1398–406
7. MacHugh DE, Shriver MD, Loftus RT, Cunningham P, Bradley DG. 1997. Microsatellite DNA variation and the evolution, domestication and phylogeography of taurine and zebu cattle (*Bos taurus* and *Bos indicus*). *Genetics* 146:1071–86
8. Martinez AM, Gama LT, Canon J, Ginja C, Delgado JV, et al. 2012. Genetic footprints of Iberian cattle in America 500 years after the arrival of Columbus. *PLOS ONE* 7(11):e49066
9. Food Agric. Organ. 2010. *2000 world census of agriculture*. Rep., Food Agric. Organ., Rome, 246 pp.
10. Wint W, Robinson TP. 2007. *Gridded livestock of the world 2007*. Rep., Food Agric. Organ. Rome. 141 pp.
11. Bhagwat SA, Nogué S, Willis KJ. 2012. Resilience of an ancient tropical forest landscape to 7500 years of environmental change. *Biol. Conserv.* 153:108–17
12. Bhagwat SA, Nogué S, Willis KJ. 2014. Cultural drivers of reforestation in tropical forest groves of the Western Ghats of India. *Forest Ecol. Manag.* 329:393–400
13. Chávez AB, Broadbent EN, Zambrano AMA. 2014. Smallholder policy adoption and land cover change in the southeastern Peruvian Amazon: a twenty-year perspective. *Appl. Geogr.* 53:223–33
14. Hertel TW, Lobell DB. 2014. Agricultural adaptation to climate change in rich and poor countries: current modeling practice and potential for empirical contributions. *Energy Econ.* 46:562–75
15. Lobell DB, Tebaldi C. 2014. Getting caught with our plants down: the risks of a global crop yield slowdown from climate trends in the next two decades. *Environ. Res. Lett.* 9:074003
16. Renwick AR, Vickery JA, Potts SG, Bolwig S, Nalwanga D, et al. 2014. Achieving production and conservation simultaneously in tropical agricultural landscapes. *Agric. Ecosyst. Environ.* 192:130–34
17. Dinerstein E, Baccini A, Anderson M, Fiske G, Wikramanayake E, et al. 2015. Guiding agricultural expansion to spare tropical forests. *Conserv. Lett.* 8:262–71
18. Holmes ND, Griffiths R, Pott M, Alifano A, Will D, et al. 2015. Factors associated with rodent eradication failure. *Biol. Conserv.* 185:8–16
19. Fordyce G, James TA, Holroyd RG, Beaman NJ, Mayer RJ, O'Rourke PK. 1993. The performance of Brahman-Shorthorn and Sahiwal-Shorthorn beef cattle in the dry tropics of northern Queensland. 3. Birth weights and growth to weaning. *Aust. J. Exp. Agric.* 33:119–27
20. Shiota AM, Ferreira dos Santos S, Bueno de Mattos Nascimento MR, Ferreira Moura AR, Visona de Oliveira M, Ferreira IC. 2013. Physiological parameters, hair coat characteristics and thermal gradients in Nellore heifers in summer and winter in tropical environment. *Biosci. J.* 29:1687–95
21. Wolcott ML, Johnston DJ, Barwick SA. 2014. Genetic relationships of female reproduction with growth, body composition, maternal weaning weight and tropical adaptation in two tropical beef genotypes. *Anim. Prod. Sci.* 54:60–73
22. Porto-Neto LR, Barendse W, Henshall JM, McWilliam SM, Lehnert SA, Reverter A. 2015. Genomic correlation: harnessing the benefit of combining two unrelated populations for genomic selection. *Genet. Sel. Evol.* 47:84

23. Façanha DAE, Gomes da Silva R, Campos Maia AS, Guilhermino MM, De Vasconcelos AM. 2010. Annual variation of morphologic traits and hair coat surface temperature of Holstein cows in semi-arid environment. *Rev. Bras. Zootec.* 39:837–44
24. Sahagun R, Medina JHV, Ruiz IJ. 2009. Estimates of genetic and environmental parameters in tropical areas that influence the growth beef bovine F1. *J. Anim. Vet. Adv.* 8:2503–7
25. Baars RMT, Solano C, Baayen MT, Rojas J, 't Mannetje L. 1996. MIS support for pasture and nutrition management of dairy farms in tropical countries. *Comput. Electron. Agric.* 15:27–39
26. López A, Arroquy JI, Juárez Sequeira AV, García M, Nazareno M, et al. 2014. Effect of protein supplementation on tropical grass hay utilization by beef steers drinking saline water. *J. Anim. Sci.* 92:2152–60
27. Ramírez-Restrepo CA, O'Neill CJ, López-Villalobos N, Padmanabha J, McSweeney C. 2014. Tropical cattle methane emissions: the role of natural statins supplementation. *Anim. Prod. Sci.* 54:1294–99
28. Santos SA, de Campos Valadares Filho S, Detmann E, Diniz Valadares RF, de Mendes Ruas JR, de Mello Amaral P. 2011. Different forage sources for F1 Holstein × Gir dairy cows. *Livest. Sci.* 142:48–58
29. Magalhães KA, Valadares Filho SC, Detmann E, Diniz LL, Pina DS, et al. 2010. Evaluation of indirect methods to estimate the nutritional value of tropical feeds for ruminants. *Anim. Feed Sci. Technol.* 155:44–54
30. Bahbahani H, Hanotte O. 2015. Genetic resistance: tolerance to vector-borne diseases and the prospects and challenges of genomics. *Rev. Sci. Tech.* 34:185–97
31. Chevillon C, de Garine-Wichatitsky M, Barre N, Ducornez S, de Meeus T. 2013. Understanding the genetic, demographical and/or ecological processes at play in invasions: lessons from the southern cattle tick *Rhipicephalus microplus* (Acari: Ixodidae). *Exp. Appl. Acarol.* 59:203–18
32. Weir W, Karagenc T, Gharbi M, Simuunza M, Aypak S, et al. 2011. Population diversity and multiplicity of infection in *Theileria annulata*. *Int. J. Parasitol.* 41:193–203
33. Jiménez M, Martínez-Urtaza J, Chaidez C. 2011. Geographical and temporal dissemination of *Salmonella* isolated from domestic animal hosts in the Culiacan Valley, Mexico. *Microb. Ecol.* 61:811–20
34. Szabo MPJ, Olegario MMM, Santos ALQ. 2007. Tick fauna from two locations in the Brazilian savannah. *Exp. Appl. Acarol.* 43:73–84
35. Caldwell LC, Chase CC, Riley DG, Coleman SW, Phillips WA, et al. 2011. The influence of tropical adaptation on plasma concentrations of insulin-like growth factor-I in purebred and crossbred beef cattle. *J. Anim. Sci.* 89:4017–22
36. Porto-Neto LR, Jonsson NN, D'Occhio MJ, Barendse W. 2011. Molecular genetic approaches for identifying the basis of variation in resistance to tick infestation in cattle. *Vet. Parasitol.* 180:165–72
37. Liao XP, Peng F, Forni S, McLaren D, Plastow G, Stothard P. 2013. Whole genome sequencing of Gir cattle for identifying polymorphisms and loci under selection. *Genome* 56:592–98
38. Makina SO, Muchadeyi FC, van Marle-Koster E, Taylor JF, Makgahlela ML, Maiwashe A. 2015. Genome-wide scan for selection signatures in six cattle breeds in South Africa. *Genet. Sel. Evol.* 47:92
39. Porto-Neto LR, Reverter A, Prayaga KC, Chan EKF, Johnston DJ, et al. 2014. The genetic architecture of climatic adaptation of tropical cattle. *PLOS ONE* 9:e113284
40. Chan EKF, Nagaraj SH, Reverter A. 2010. The evolution of tropical adaptation: comparing taurine and zebu cattle. *Anim. Genet.* 41:467–77
41. Renaudeau D, Collin A, Yahav S, de Basilio V, Gourdière JL, Collier RJ. 2012. Adaptation to hot climate and strategies to alleviate heat stress in livestock production. *Animal* 6:707–28
42. Joyce LA, Briske DD, Brown JR, Polley HW, McCarl BA, Bailey DW. 2013. Climate change and North American rangelands: assessment of mitigation and adaptation strategies. *Rangel. Ecol. Manag.* 66:512–28
43. Murgueitio E, Calle Z, Uribe F, Calle A, Solorio B. 2011. Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. *Forest Ecol. Manag.* 261:1654–63
44. Lapola DM, Schaldach R, Alcamo J, Bondeau A, Msangi S, et al. 2011. Impacts of climate change and the end of deforestation on land use in the Brazilian legal Amazon. *Earth Interact.* 15:1–29
45. Puig CJ, Greiner R, Huchery C, Perkins I, Bowen L, et al. 2011. Beyond cattle: potential futures of the pastoral industry in the Northern Territory. *Rangel. J.* 33:181–94
46. Bényei B, Barros CCW. 2000. Effect of superovulation on performance of bovine embryo donors imported from temperate zone to tropical climate during the first two years of adaptation. *Arq. Bras. Med. Vet. Zootec.* 52:366–71

47. Bo GA, Baruselli PS, Martínez MF. 2003. Pattern and manipulation of follicular development in *Bos indicus* cattle. *Anim. Reprod. Sci.* 78:307–26
48. Hammond AC, Olson TA. 1994. Rectal temperature and grazing time in selected beef-cattle breeds under tropical summer conditions in subtropical Florida. *Trop. Agric.* 71:128–34
49. Bertipaglia ECA, da Silva RG, Cardoso V, Fries LA. 2007. Hair coat characteristics and sweating rate of Braford cows in Brazil. *Livest. Sci.* 112:99–108
50. Ribeiro ARB, Alencar MM, Freitas AR, Regitano LCA, Oliveira MCS, Ibelli AMG. 2009. Heat tolerance of Nelore, Senepol \times Nelore and Angus \times Nelore heifers in the southeast region of Brazil. *S. Afr. J. Anim. Sci.* 39:263–65
51. McManus C, Castanheira M, Paiva SR, Louvandini H, Fioravanti MCS, et al. 2011. Use of multivariate analyses for determining heat tolerance in Brazilian cattle. *Trop. Anim. Health Prod.* 43:623–30
52. Gautier M, Flori L, Riebler A, Jaffrezic F, Laloe D, et al. 2009. A whole genome Bayesian scan for adaptive genetic divergence in West African cattle. *BMC Genom.* 10:550
53. Barris W, Harrison B, McWilliam S, Bunch R, Goddard M, Barendse W. 2012. Next generation sequencing of African and Indicine cattle to identify single nucleotide polymorphisms. *Anim. Prod. Sci.* 52:133–42
54. Canavez FC, Luche DD, Stothard P, Leite KRM, Sousa-Canavez JM, et al. 2012. Genome sequence and assembly of *Bos indicus*. *J. Hered.* 103:342–48
55. Barendse W, McWilliam S, Bunch RJ, Harrison BE. 2015. Adaptive divergence in the bovine genome. *bioRxiv* doi:10.1101/022764
56. Riley DG, Chase CC, Coleman SW, Olson TA. 2007. Evaluation of birth and weaning traits of Romosinuano calves as purebreds and crosses with Brahman and Angus. *J. Anim. Sci.* 85:289–98
57. Coleman SW, Chase CC, Phillips WA, Riley DG, Olson TA. 2012. Evaluation of tropically adapted straightbred and crossbred cattle: postweaning gain and feed efficiency when finished in a temperate climate. *J. Anim. Sci.* 90:1955–65
58. Contreras G, Chirinos Z, Zambrano S, Molero E, Paez A. 2011. Morphological characterization and zoometric indexes of Criollo Limonero cows of Venezuela. *Rev. Fac. Agron. Univ. Zulia* 28:91–103
59. Maciel S, Okeyo AM, Amimo J, Scholtz MM, Naser FWC, Martins M. 2013. The effect of geographical region of birth on the reproductive performance of the Nguni in southern Mozambique. *S. Afr. J. Anim. Sci.* 43:S60–S63
60. Burrow HM. 2001. Variances and covariances between productive and adaptive traits and temperament in a composite breed of tropical beef cattle. *Livest. Prod. Sci.* 70:213–33
61. Burrow HM, Prayaga KC. 2004. Correlated responses in productive and adaptive traits and temperament following selection for growth and heat resistance in tropical beef cattle. *Livest. Prod. Sci.* 86:143–61
62. Barwick SA, Johnston DJ, Burrow HM, Holroyd RG, Fordyce G, et al. 2009. Genetics of heifer performance in “wet” and “dry” seasons and their relationships with steer performance in two tropical beef genotypes. *Anim. Prod. Sci.* 49:367–82
63. Barwick SA, Wolcott ML, Johnston DJ, Burrow HM, Sullivan MT. 2009. Genetics of steer daily and residual feed intake in two tropical beef genotypes, and relationships among intake, body composition, growth and other post-weaning measures. *Anim. Prod. Sci.* 49:351–66
64. Burrow HM. 2012. Importance of adaptation and genotype \times environment interactions in tropical beef breeding systems. *Animal* 6:729–40
65. Maia ASC, da Silva RG, Bertipaglia ECA. 2003. Haircoat traits in Holstein cows in tropical environments: a genetic and adaptive study. *Braz. J. Anim. Sci.* 32:843–53
66. Ojango JMK, Ducrocq V, Pollott GE. 2005. Survival analysis of factors affecting culling early in the productive life of Holstein-Friesian cattle in Kenya. *Livest. Prod. Sci.* 92:317–22
67. Koonawootrittriron S, Elzo MA, Thongprapi T. 2009. Genetic trends in a Holstein \times other breeds multibreed dairy population in central Thailand. *Livest. Sci.* 122:186–92
68. Flori L, Gonzatti MI, Thevenon S, Chantal I, Pinto J, et al. 2012. A quasi-exclusive European ancestry in the Senepol tropical cattle breed highlights the importance of the slick locus in tropical adaptation. *PLOS ONE* 7:e36133

69. Newman S, Reverter A, Johnston DJ. 2002. Purebred-crossbred performance and genetic evaluation of postweaning growth and carcass traits in *Bos indicus* × *Bos taurus* crosses in Australia. *J. Anim. Sci.* 80:1801–8
70. Schatz TJ, Ridley PER, La Fontaine DJM, Hearnden MN. 2007. Effects of genotype, sex and stocking rate on postweaning efficiency and value-adding potential at turnoff of weaners grazing improved pasture in the Douglas Daly region of the Northern Territory. *Aust. J. Exp. Agric.* 47:1272–76
71. Boerner V, Johnston DJ, Tier B. 2014. Accuracies of genomically estimated breeding values from pure-breed and across-breed predictions in Australian beef cattle. *Genet. Sel. Evol.* 46:61
72. Bonsma JC. 1949. Breeding cattle for increased adaptability to tropical and subtropical environments. *J. Agric. Sci.* 39:204–21
73. Johnston DJ, Reverter A, Burrow HM, Oddy VH, Robinson DL. 2003. Genetic and phenotypic characterisation of animal, carcass, and meat quality traits from temperate and tropically adapted beef breeds. 1. Animal measures. *Aust. J. Agric. Res.* 54:107–18
74. Prayaga KC, Corbet NJ, Johnston DJ, Wolcott ML, Fordyce G, Burrow HM. 2009. Genetics of adaptive traits in heifers and their relationship to growth, pubertal and carcass traits in two tropical beef cattle genotypes. *Anim. Prod. Sci.* 49:413–25
75. Turner H, Schleger A. 1960. The significance of coat type in cattle. *Aust. J. Agric. Res.* 11:645–63
76. Jian W, Duangjinda M, Vajrabukka C, Katawatin S. 2014. Differences of skin morphology in *Bos indicus*, *Bos taurus*, and their crossbreds. *Int. J. Biometeorol.* 58:1087–94
77. Behl R, Behl J, Joshi BK. 2010. Heat tolerance mechanisms in cattle status in zebu cattle: a review. *Indian J. Anim. Sci.* 80:891–97
78. Blackshaw J, Blackshaw A. 1994. Heat stress in cattle and the effect of shade on production and behaviour: a review. *Aust. J. Exp. Agric.* 34:285–95
79. Landaeta-Hernández A, Zambrano-Nava S, Hernández-Fonseca JP, Godoy R, Calles M, et al. 2011. Variability of hair coat and skin traits as related to adaptation in Criollo Limonero cattle. *Trop. Anim. Health Prod.* 43:657–63
80. München Alfonso EP, Barbosa da Silva MVG, dos Santos Daltro D, Stumpf MT, Dalcin VC, et al. 2016. Relationship between physical attributes and heat stress in dairy cattle from different genetic groups. *Int. J. Biometeorol.* 60:245–53
81. Klungland H, Vage DI, Gomez-Raya L, Adalsteinsson S, Lien S. 1995. The role of melanocyte-stimulating hormone (*MSH*) receptor in bovine coat color determination. *Mamm. Genome* 6:636–39
82. Seitz JJ, Schmutz SM, Thue TD, Buchanan FC. 1999. A missense mutation in the bovine *MGF* gene is associated with the roan phenotype in Belgian Blue and Shorthorn cattle. *Mamm. Genome* 10:710–12
83. Dorshorst B, Henegar C, Liao XP, Almen MS, Rubin CJ, et al. 2015. Dominant red coat color in Holstein cattle is associated with a missense mutation in the coatomer protein complex, subunit alpha (*COPA*) gene. *PLOS ONE* 10:e0128969
84. Li WB, Sartelet A, Tamma N, Coppieters W, Georges M, Charlier C. 2016. Reverse genetic screen for loss-of-function mutations uncovers a frameshifting deletion in the melanophilin gene accountable for a distinctive coat color in Belgian Blue cattle. *Anim. Genet.* 47:110–13
85. Durkin K, Coppieters W, Drögemüller C, Ahariz N, Cambisano N, et al. 2012. Serial translocation by means of circular intermediates underlies colour sidedness in cattle. *Nature* 482:81–U103
86. Oulmouden A, Julien R, Laforet M, Leveziel H. 2005. *Use of silver gene for the authentication of the racial origin of animal populations, and of the derivative products thereof.* WO Patent Appl. No. PCT/FR2004/001,952
87. Schmutz SM, Dreger DL. 2013. Interaction of *MC1R* and *PMEL* alleles on solid coat colors in Highland cattle. *Anim. Genet.* 44:9–13
88. Berryere TG, Schmutz SM, Schimpf RJ, Cowan CM, Potter J. 2003. *TYRP1* is associated with dun coat colour in Dexter cattle or how now brown cow? *Anim. Genet.* 34:169–75
89. Fontanesi L, Tazzoli M, Russo V, Beever J. 2010. Genetic heterogeneity at the bovine *KIT* gene in cattle breeds carrying different putative alleles at the spotting locus. *Anim. Genet.* 41:295–303
90. Fontanesi L, Scotti E, Russo V. 2012. Haplotype variability in the bovine *MITF* gene and association with piebaldism in Holstein and Simmental cattle breeds. *Anim. Genet.* 43:250–56
91. Littlejohn MD, Henty KM, Tiplady K, Johnson T, Harland C, et al. 2014. Functionally reciprocal mutations of the prolactin signalling pathway define hairy and slick cattle. *Nat. Commun.* 5:5861

92. Karim L, Takeda H, Lin L, Druet T, Arias JAC, et al. 2011. Variants modulating the expression of a chromosome domain encompassing *PLAG1* influence bovine stature. *Nat. Genet.* 43:405–13
93. Schmutz SM, Berryere TG, Ciobanu DC, Mileham AJ, Schmitz BH, Fredholm M. 2004. A form of albinism in cattle is caused by a tyrosinase frameshift mutation. *Mamm. Genome* 15:62–67
94. Brenig B, Beck J, Floren C, Bornemann-Kolatzki K, Wiedemann I, et al. 2013. Molecular genetics of coat colour variations in White Galloway and White Park cattle. *Anim. Genet.* 44:450–53
95. Hawken RJ, Zhang YD, Fortes MRS, Collis E, Barris WC, et al. 2012. Genome-wide association studies of female reproduction in tropically adapted beef cattle. *J. Anim. Sci.* 90:1398–410
96. Schleger A, Turner H. 1960. Analysis of coat characters of cattle. *Aust. J. Agric. Res.* 11:875–85
97. Olson TA, Lucena C, Chase CC, Hammond AC. 2003. Evidence of a major gene influencing hair length and heat tolerance in *Bos taurus* cattle. *J. Anim. Sci.* 81:80–90
98. Mariasegaram M, Chase CC, Chaparro JX, Olson TA, Brenneman RA, Niedz RP. 2007. The slick hair coat locus maps to chromosome 20 in Senepol-derived cattle. *Anim. Genet.* 38:54–59
99. Carlson DF, Lancto CA, Zang B, Kim E-S, Walton M, et al. 2016. Production of hornless dairy cattle from genome-edited cell lines. *Nat. Biotechnol.* 34:479–81
100. Whitworth KM, Rowland RRR, Ewen CL, Tribble BR, Kerrigan MA, et al. 2016. Gene-edited pigs are protected from porcine reproductive and respiratory syndrome virus. *Nat. Biotechnol.* 34:20–22
101. Carroll D, Van Eenennaam AL, Taylor JF, Seger J, Voytas DF. 2016. Regulate genome-edited products, not genome editing itself. *Nat. Biotechnol.* 34:477–79
102. Grisart B, Coppieters W, Farnir F, Karim L, Ford C, et al. 2002. Positional candidate cloning of a QTL in dairy cattle: identification of a missense mutation in the bovine *DGAT1* gene with major effect on milk yield and composition. *Genome Res.* 12:222–31
103. Barendse W, Harrison B, Hawken R, Ferguson D, Thompson J, et al. 2007. Epistasis between calpain 1 and its inhibitor calpastatin within breeds of cattle. *Genetics* 176:2601–10
104. Hayes BJ, Bowman PJ, Chamberlain AJ, Goddard ME. 2009. Invited review: genomic selection in dairy cattle: progress and challenges. *J. Dairy Sci.* 92:433–43
105. VanRaden PM, Van Tassell CP, Wiggans GR, Sonstegard TS, Schnabel RD, et al. 2009. Invited review: reliability of genomic predictions for North American Holstein bulls. *J. Dairy Sci.* 92:16–24
106. Winkelman AM, Johnson DL, Harris BL. 2015. Application of genomic evaluation to dairy cattle in New Zealand. *J. Dairy Sci.* 98:659–75
107. Ma P, Lund MS, Nielsen US, Aamand GP, Su G. 2015. Single-step genomic model improved reliability and reduced the bias of genomic predictions in Danish Jersey. *J. Dairy Sci.* 98:9026–34
108. Kemper KE, Reich CM, Bowman PJ, vander Jagt CJ, Chamberlain AJ, et al. 2015. Improved precision of QTL mapping using a nonlinear Bayesian method in a multi-breed population leads to greater accuracy of across-breed genomic predictions. *Genet. Sel. Evol.* 47:29
109. Chen L, Schenkel F, Vinsky M, Crews DH, Li C. 2013. Accuracy of predicting genomic breeding values for residual feed intake in Angus and Charolais beef cattle. *J. Anim. Sci.* 91:4669–78
110. Boerner V, Johnston D, Wu XL, Bauck S. 2015. Accuracy of Igenity genomically estimated breeding values for predicting Australian Angus BREEDPLAN traits. *J. Anim. Sci.* 93:513–21
111. MacLeod IM, Bowman PJ, vander Jagt CJ, Haile-Mariam M, Kemper KE, et al. 2016. Exploiting biological priors and sequence variants enhances QTL discovery and genomic prediction of complex traits. *BMC Genom.* 17:144
112. Bortolussi G, McIvor JG, Hodgkinson JJ, Coffey SG, Holmes CR. 2005. The northern Australian beef industry, a snapshot. 2. Breeding herd performance and management. *Aust. J. Exp. Agric.* 45:1075–91
113. Mariasegaram M, Harrison BE, Bolton JA, Tier B, Henshall JM, et al. 2012. Fine-mapping the *POLL* locus in Brahman cattle yields the diagnostic marker CSAFG29. *Anim. Genet.* 43:683–88
114. Horton BJ, Banks RG, van der Werf JHJ. 2015. Industry benefits from using genomic information in two- and three-tier sheep breeding systems. *Anim. Prod. Sci.* 55:437–46
115. Ruddiman WF. 2003. The anthropogenic greenhouse era began thousands of years ago. *Clim. Change* 61:261–93
116. Hill J, McSweeney C, Wright ADG, Bishop-Hurley G, Kalantar-zadeh K. 2016. Measuring methane production from ruminants. *Trends Biotechnol.* 34:26–35

117. Arndt DS, Blunden J, Willett KW. 2015. State of the climate in 2014. *Bull. Am. Meteorol. Soc.* 96:S1–S267
118. Fowler D, Pilegaard K, Sutton MA, Ambus P, Raivonen M, et al. 2009. Atmospheric composition change: ecosystems-atmosphere interactions. *Atmos. Environ.* 43:5193–267
119. Lelieveld J, Crutzen PJ, Dentener FJ. 1998. Changing concentration, lifetime and climate forcing of atmospheric methane. *Tellus Ser. B Chem. Phys. Meteorol.* 50:128–50
120. Robertson GP, Paul EA, Harwood RR. 2000. Greenhouse gases in intensive agriculture: contributions of individual gases to the radiative forcing of the atmosphere. *Science* 289:1922–25
121. Charmley E, Williams SRO, Moate PJ, Hegarty RS, Herd RM, et al. 2016. A universal equation to predict methane production of forage-fed cattle in Australia. *Anim. Prod. Sci.* 56:169–80
122. Hackmann TJ, Spain JN. 2010. Invited review: ruminant ecology and evolution: perspectives useful to ruminant livestock research and production. *J. Dairy Sci.* 93:1320–34
123. Halbert ND, Gogan PJP, Hiebert R, Derr JN. 2007. Where the buffalo roam: the role of history and genetics in the conservation of bison on US federal lands. *Park Sci.* 24:22–29
124. Kolipinski M, Borish S, Scott A, Kozlowski K, Ghosh S. 2014. Bison: yesterday, today, and tomorrow. *Nat. Areas J.* 34:365–75
125. Robinson DL, Goopy JP, Hegarty RS, Oddy VH, Thompson AN, et al. 2014. Genetic and environmental variation in methane emissions of sheep at pasture. *J. Anim. Sci.* 92:4349–63
126. de Haas Y, Windig JJ, Calus MPL, Dijkstra J, de Haan M, et al. 2011. Genetic parameters for predicted methane production and potential for reducing enteric emissions through genomic selection. *J. Dairy Sci.* 94:6122–34
127. Goopy JP, Robinson DL, Woodgate RT, Donaldson AJ, Oddy VH, et al. 2016. Estimates of repeatability and heritability of methane production in sheep using portable accumulation chambers. *Anim. Prod. Sci.* 56:116–22
128. Lassen J, Lovendahl P. 2016. Heritability estimates for enteric methane emissions from Holstein cattle measured using noninvasive methods. *J. Dairy Sci.* 99:1959–67
129. Lassen J, Poulsen NA, Larsen MK, Buitenhuis AJ. 2016. Genetic and genomic relationship between methane production measured in breath and fatty acid content in milk samples from Danish Holsteins. *Anim. Prod. Sci.* 56:298–303
130. Pinares-Patino CS, Hickey SM, Young EA, Dodds KG, MacLean S, et al. 2013. Heritability estimates of methane emissions from sheep. *Animal* 7:316–21
131. Robinson DL, Goopy JP, Donaldson AJ, Woodgate RT, Oddy VH, Hegarty RS. 2014. Sire and liveweight affect feed intake and methane emissions of sheep confined in respiration chambers. *Animal* 8:1935–44
132. Waghorn GC, Hegarty RS. 2011. Lowering ruminant methane emissions through improved feed conversion efficiency. *Anim. Feed Sci. Technol.* 166–67:291–301
133. Bishop-Hurley GJ, Paull D, Valencia P, Overs L, Kalantar-zadeh K, et al. 2016. Intra-ruminal gas-sensing in real time: a proof-of-concept. *Anim. Prod. Sci.* 56:204–12
134. Beauchemin KA, Kreuzer M, O'Mara F, McAllister TA. 2008. Nutritional management for enteric methane abatement: a review. *Aust. J. Exp. Agric.* 48:21–27
135. Doreau M, van der Werf HMG, Micol D, Dubroeuq H, Agabriel J, et al. 2011. Enteric methane production and greenhouse gases balance of diets differing in concentrate in the fattening phase of a beef production system. *J. Anim. Sci.* 89:2518–28
136. Kurihara M, Magner T, Hunter RA, McCrabb GJ. 1999. Methane production and energy partition of cattle in the tropics. *Br. J. Nutr.* 81:227–34
137. McCrabb GJ, Hunter RA. 1999. Prediction of methane emissions from beef cattle in tropical production systems. *Aust. J. Agric. Res.* 50:1335–39
138. Archimede H, Eugene M, Magdeleine CM, Boval M, Martin C, et al. 2011. Comparison of methane production between C3 and C4 grasses and legumes. *Anim. Feed Sci. Technol.* 166–67:59–64
139. Ash A, Hunt L, McDonald C, Scanlan J, Bell L, et al. 2015. Boosting the productivity and profitability of northern Australian beef enterprises: exploring innovation options using simulation modelling and systems analysis. *Agric. Syst.* 139:50–65
140. Johnson CR, Reiling BA, Mislevy P, Hall MB. 2001. Effects of nitrogen fertilization and harvest date on yield, digestibility, fiber, and protein fractions of tropical grasses. *J. Anim. Sci.* 79:2439–48

141. Hill JO, Coates DB, Whitbread AM, Clem RL, Robertson MJ, Pengelly BC. 2009. Seasonal changes in pasture quality and diet selection and their relationship with liveweight gain of steers grazing tropical grass and grass-legume pastures in northern Australia. *Anim. Prod. Sci.* 49:983–93
142. Panjaitan T, Quigley SP, McLennan SR, Swain AJ, Poppi DP. 2014. Digestion of forages in the rumen is increased by the amount but not the type of protein supplement. *Anim. Prod. Sci.* 54:1363–67
143. Poppi DP, McLennan SR. 1995. Protein and energy utilization by ruminants at pasture. *J. Anim. Sci.* 73:278–90
144. Ribeiro GO, Teixeira AM, Velasco FO, Faria WG, Pereira LGR, et al. 2014. Production, nutritional quality and *in vitro* methane production from *Andropogon gayanus* grass harvested at different maturities and preserved as hay or silage. *Asian-Aust. J. Anim. Sci.* 27:330–41
145. Sampaio CB, Detmann E, Paulino MF, Valadares SC, de Souza MA, et al. 2010. Intake and digestibility in cattle fed low-quality tropical forage and supplemented with nitrogenous compounds. *Trop. Anim. Health Prod.* 42:1471–79
146. Herrero M, Havlik P, Valin H, Notenbaert A, Rufino MC, et al. 2013. Biomass use, production, feed efficiencies, and greenhouse gas emissions from global livestock systems. *PNAS* 110:20888–93
147. Chilliard Y, Martin C, Rouel J, Doreau M. 2009. Milk fatty acids in dairy cows fed whole crude linseed, extruded linseed, or linseed oil, and their relationship with methane output. *J. Dairy Sci.* 92:5199–11
148. Dijkstra J, van Zijderveld SM, Apajalahti JA, Bannink A, Gerrits WJJ, et al. 2011. Relationships between methane production and milk fatty acid profiles in dairy cattle. *Anim. Feed Sci. Technol.* 166–67:590–95
149. Mohammed R, McGinn SM, Beauchemin KA. 2011. Prediction of enteric methane output from milk fatty acid concentrations and rumen fermentation parameters in dairy cows fed sunflower, flax, or canola seeds. *J. Dairy Sci.* 94:6057–68
150. van Engelen S, Bovenhuis H, Dijkstra J, van Arendonk J, Visker M. 2015. Short communication: genetic study of methane production predicted from milk fat composition in dairy cows. *J. Dairy Sci.* 98:8223–26
151. Griinari JM, Baumann DE. 2000. Biosynthesis of conjugated linoleic acid and its incorporation into meat and milk in ruminants. In *Advances in Conjugated Linoleic Acid Research*, Vol. 1, ed. MP Yurawecz, MM Mossoba, JKG Kramer, MW Pariza, GJ Nelson, pp. 180–200. Champaign, IL: Am. Oil Chem. Soc.
152. Bousquet P, Ringeval B, Pison I, Dlugokencky EJ, Brunke EG, et al. 2011. Source attribution of the changes in atmospheric methane for 2006–2008. *Atmos. Chem. Phys.* 11:3689–700
153. Yan XY, Ohara T, Akimoto H. 2003. Development of region-specific emission factors and estimation of methane emission from rice fields in the East, Southeast and South Asian countries. *Glob. Change Biol.* 9:237–54

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Errata

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