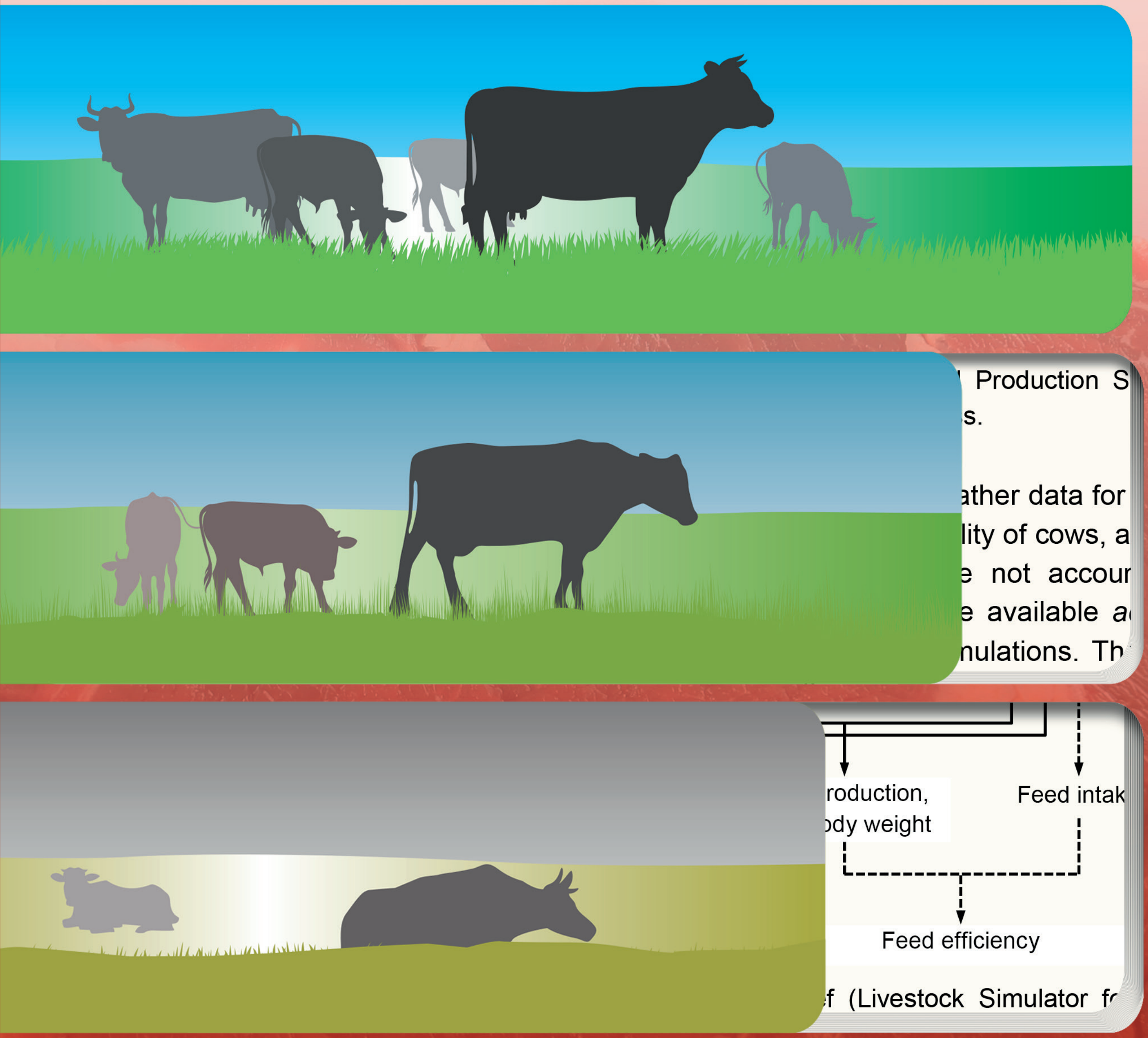
A generic method to analyse yield gaps in feed-crop livestock systems



Aart van der Linden

Propositions

1. Sustainable intensification requires benchmarking of livestock production and feed production together.
   (this thesis)

2. To increase production of animal-source food, yield gap mitigation in feed crops is more effective than yield gap mitigation in livestock.
   (this thesis)

3. Sustained evolution is more viable than revolution to enhance sustainable agricultural development.

4. Science cannot mitigate the gap between useful and meaningful.

5. The current emphasis on multi-disciplinary research makes discipline-oriented scientists concerned of being perceived as narrow-minded.

6. The demand for societal impact of research leads to distorted claims in the media and eventually to distrust in science.

Propositions belonging to the thesis, entitled

‘A generic method to analyse yield gaps in feed-crop livestock systems.’

Aart van der Linden

Wageningen, 28 March 2017

A generic method to analyse yield gaps in feed-crop livestock systems

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Abstract

Global livestock production is expected to increase in future decades, and expansion of the agricultural area for feed production is not desired. Hence, increasing livestock production per unit agricultural area is essential. The bio-physical scope to increase production of livestock systems with the corresponding feed crop production (feed-crop livestock systems) could not be assessed generically at the start of this research. In crop production, however, crop models based on concepts of production ecology are widely applied to assess the bio-physical scope to increase actual production. The difference between the biophysical scope and actual production is referred to as the yield gap. The objectives of this thesis were 1) to develop a generic framework to assess the scope to increase production in feed crop-livestock systems based on concepts of production ecology, 2) to develop a generic livestock model simulating potential (*i.e.* maximum theoretical) and feed-limited livestock production, and 3) to apply this framework and model to feed-crop livestock systems, and conduct yield gap analyses.

Concepts of production ecology for livestock were specified in more detail. Feed efficiency at herd level was a suited benchmark for livestock production only, and production of animal-source food per hectare for feed-crop livestock systems. Application of the framework showed that the yield gap was 79% of the potential beef production of a cow-calf system, and 72% of a cow-calf-fattener system in the Charolais region of France. The model LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle) was developed to simulate potential and feed-limited production of beef cattle using input data about animals' genotype, climate, and feed quality and availability. The model consists of sub-models describing thermoregulation, feed intake and digestion, and energy and protein utilisation. Model evaluation under different agro-ecological conditions indicated live weight gain was estimated fairly well (15.4% deviation from measured values). LiGAPS-Beef was coupled with crop growth models to simulate potential and resource-limited production of twelve grass-based beef production systems in the Charolais region. Resource-limited production combines feed-limited production of cattle and water-limited production of feed crops. Yield gaps were on average 85% of potential live weight production per hectare, and 47% of resource-limited production. Yield gaps were attributed to feed quality and quantity limitation (41% of potential production), water-limitation in feed crops (31%), the combination of sub-optimal selling or slaughter weights, culling rates, calving dates, age at first calving, and stocking densities (9%), and the combination of prolonged calving intervals and calf mortality (2%). Improved grassland management and an earlier start of the grazing season may increase live weight production per hectare. Furthermore, the resource-limited production of bulls was simulated to increase by 6-14% from 1999-2006 up to 2050 due to climate change.

From the results of this thesis, it can be concluded that 1) a generic framework using concepts of production ecology is available now to assess the bio-physical scope to increase production in feed-crop livestock systems per unit area; 2) the mechanistic model LiGAPS-Beef simulates potential and feed-limited production of beef cattle fairly well; 3) combining LiGAPS-Beef with crop growth models allows to quantify yield gaps in feed-crop livestock systems, and to analyse these yield gaps. The method described in this thesis can be used subsequently to identify options to mitigate yield gaps, and to increase livestock production per unit area, which may contribute to sustainable intensification of agriculture.

Contents

Chapter 1

General Introduction

1.1 Background

The human population is expected to increase from 7.4 billion people in 2016 to 9.7 billion in 2050 (UN, 2015). Higher incomes and urbanisation allow people to buy a larger variety of foods, which results in shifts towards more affluent diets that contain more animal-source food (ASF) (Smil, 2002a, Tilman *et al.*, 2011, Tilman and Clark, 2014). The combined effects of population increase, urbanisation, and economic growth will most likely increase the global demand for food by 60% between 2012 and 2050 if current trends continue (OECD/FAO, 2012). The projected increase in global demand for ASF is especially large for meat and eggs, but milk production keeps pace with the growth of the global population (Fig. 1.1).

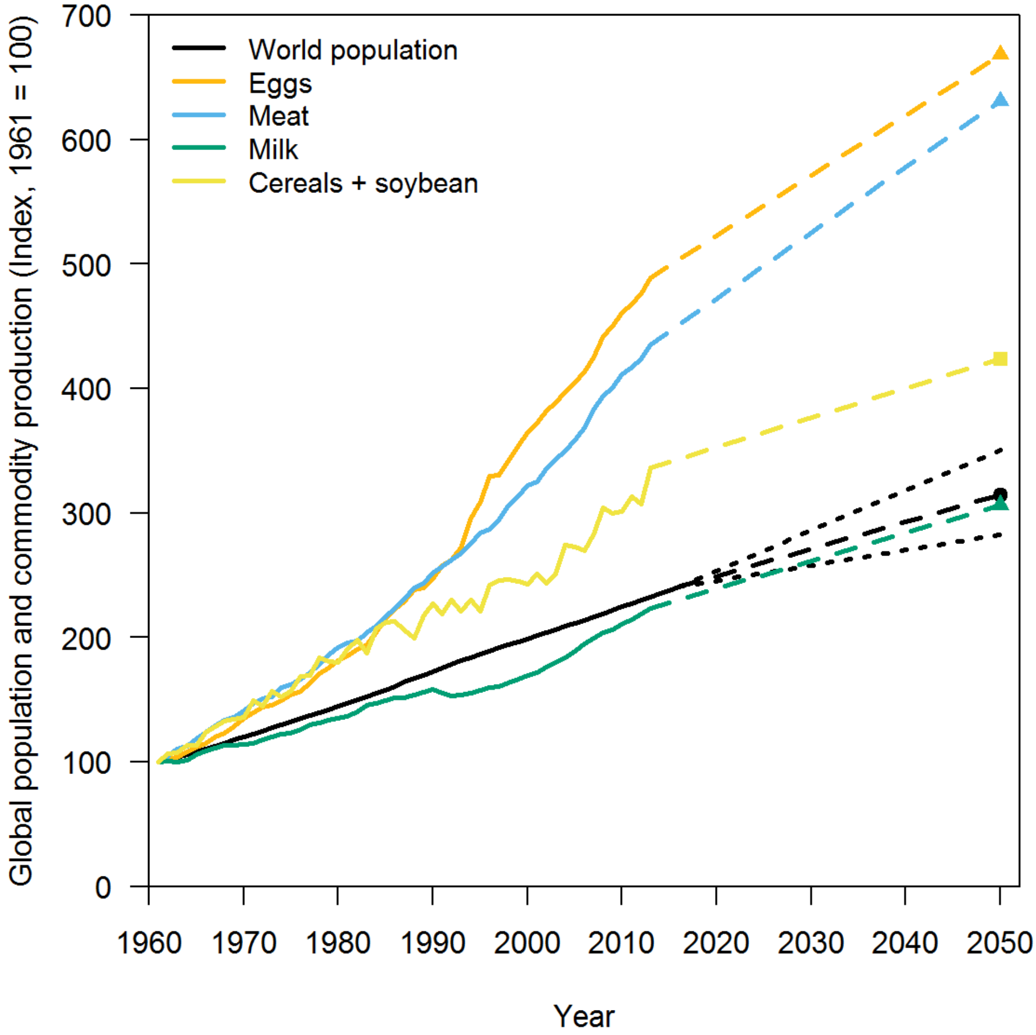

Figure 1.1 Development of the world population and production of agricultural commodities from 1961 to 2050. Population data up to 2016 are from GeoHive (2016), and projections (dashed lines) are from the United Nations (UN, 2015). The dotted lines indicate the upper and lower estimates of the world population towards 2050. Production data of commodities up to 2013 are from FAO (2015), and projections from Bruinsma (2009) and Alexandratos and Bruinsma (2012).

Currently, more than 800 million people are undernourished, and more than two billion people suffer from micronutrient deficiencies (Kumssa *et al.*, 2015). Realising food security for 9.7 billion people in 2050 is a challenge that goes beyond the production of enough food (Godfray *et al.*, 2010). Food security is defined as a situation when all people at all times have physical, social, and economic access to sufficient, safe, and nutritious food that meets their dietary needs and food preferences for an active and healthy life. The four dimensions of food security are food availability; access to food; food utilization and its nutritional quality; and stability of food security over time (FAO, 2013). Food availability entails the production of food, and is a necessary precondition for the other three dimensions of food security. Within the multi-faceted subject of food security, this thesis focusses on food production.

Meeting the additional demand for food in future decades can be achieved by reducing the demand for food and the corresponding arable land, expanding agricultural land, mitigating yield gaps on existing land, and preventing the current production potential to be lost (Fig. 1.2) (Keating *et al.*, 2014). Reducing the demand for food can be achieved by reducing food waste, which amounts 30-40% of the food produced globally (Godfray *et al.*, 2010). Reducing the proportion of ASF in diets reduces the demand for feed crops and the corresponding arable land, that then can be used to cultivate human food crops (Cassidy *et al.*, 2013, Eisler *et al.*, 2014, Van Kernebeek *et al.*, 2016, Van Zanten *et al.*, 2016a).

The projected expansion in agricultural land area is approximately 7% between 2005 and 2050, which is only a fraction of the projected increase for food (Alexandratos and Bruinsma, 2012). Most of the land potentially suited for crop production is currently pasture or nature area (Alexandratos and Bruinsma, 2012). Expansion of arable land or intensively managed pastures at the expense of natural pasture or nature involves a loss of biodiversity, ecosystems services, and natural landscapes. This strategy to increase food production, therefore, is widely acknowledged as undesired (Tilman *et al.*, 2011, Garnett *et al.*, 2013, Kuyper and Struik, 2014). Expanding fish production from non-land based aquaculture can contribute to an increased food supply too. Since most of the world's fish stocks are fully fished or even overfished, the total supply of fish from capture fisheries and aquaculture is expected to keep pace with the increasing world population (Bene *et al.*, 2015). The vast majority of the future increase in food production is thus likely to be derived from land-based agriculture, and should preferably not be derived from land expansion. This implies that the food production per unit area has to be increased. Now, the question raises to what extent the actual food production per unit area can be increased. The theoretical scope to increase food production per unit area is the yield gap. The yield gap is defined as the difference between the potential (*i.e.* maximum theoretical) yield and the actual yields in farmers' fields (Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013). The need for mitigating yield gaps on existing land is widely acknowledged in the current debate about food security (Garnett *et al.*, 2013, Godfray and Garnett, 2014).

Preventing the loss of production potential can contribute substantially to meeting the global food demand (Keating *et al.*, 2014). Future food production can be undermined by climate change (Parry *et al.*, 2004), land degradation (Gibbs and Salmon, 2015), and an increasing scarcity of inputs for agriculture (Steinfeld *et al.*, 2006, Cassidy *et al.*, 2013). While agriculture is affected by the loss of production potential, the sector is also one of the main contributors to climate change and environmental degradation (Tilman *et al.*, 2001, Steinfeld *et al.*, 2006).

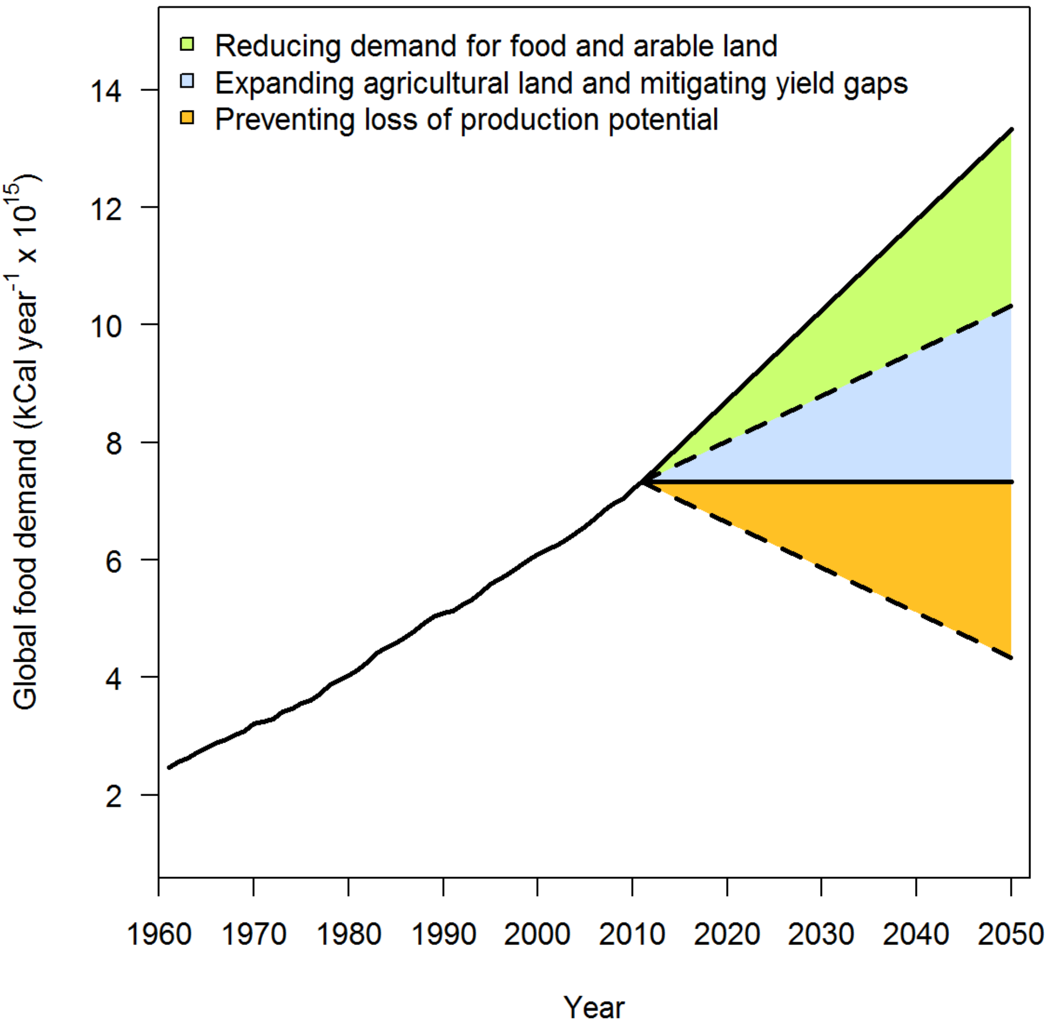

Figure 1.2 Historic demand for food at global level from 1960 to 2011, and a conceptual representation of the additional food demand up to 2050. The hypothetical effects of reducing the demand for food and arable land, expanding agricultural land and mitigating yield gaps, and preventing loss of production potential are each represented as a wedge. The horizontal line indicates the current food production. Data on global food demand are from FAO (2015). Figure adapted from Keating *et al.* (2014).

1.2 Sustainable intensification

Within the strategies to meet global food demand, this thesis focusses mainly on mitigation of yield gaps on existing agricultural land. Mitigating yield gaps should preferably coincide with less negative impacts on the environment to sustain the production potential. Increasing food production per unit of land with less pressure on the environment is defined as sustainable intensification (Garnett *et al.*, 2013, Godfray and Garnett, 2014). Sustainable agriculture is defined as practices that meet the current and future societal needs for food and fibre, for ecosystem services, and for healthy lives. These practices maximize the net benefit to society when all costs and benefits are considered (Tilman *et al.*, 2002). Intensification is defined as increasing output per unit of resource input, which refers especially to land, but also to other resources (Pretty *et al.*, 2011, Struik *et al.*, 2014).

The need to apply a broad range of tools and strategies for sustainable intensification is widely acknowledged (Garnett and Godfray, 2012, Garnett *et al.*, 2013, Godfray and Garnett, 2014). Many authors noted and discussed the ambiguity and trade-offs between the terms sustainable and intensification (Garnett and Godfray, 2012, Garnett *et al.*, 2013, Pretty and Bharucha, 2014, Struik *et al.*, 2014). Sustainable intensification is debated, since subjective choices are inevitable to balance sustainability and intensification (Struik *et al.*, 2014). Nevertheless, sustainable intensification is generally regarded as a major strategy to contribute to global food security. This strategy can be implemented simultaneously with other strategies contributing to food security, such as reducing food waste and altering dietary patterns (Garnett and Godfray, 2012).

Sustainable intensification can refer to increasing plant-derived food or ASF per unit of land. Crop production, or yield, is an output of cropping systems. Crop production is defined as the amount of crop product, and is generally expressed as dry matter (DM) produced per unit of land area and per unit of time (*e.g.* t DM ha^{-1} $year^{-1}$). Crop productivity is defined as the amount of crop product divided by the amount of an input for crop production (*e.g.* kg DM per m^3 water or kg fertilizer). Since land used for crop production can be regarded as an input, crop production can be regarded as a special case of crop productivity (Van Noordwijk and Brussaard, 2014). Next to crop production systems, the concept of sustainable intensification is applied to livestock production systems and aquaculture (Thornton, 2010, Pretty *et al.*, 2011, Campbell *et al.*, 2014, Eisler *et al.*, 2014, FAO, 2016). Livestock production is defined as the output of animal product from a livestock system. Livestock production can be expressed as the weight of ASF per animal per year, or as the weight of ASF per hectare per year. The amount of animal product per unit of feed input (*i.e.* feed efficiency) is generally indicated as livestock productivity, and not as livestock production. In this thesis, however, feed efficiency is indicated also as livestock production, since crop production is expressed per unit of input (land area) as well.

Increasing livestock production per unit of land can be achieved by increasing the feed efficiency (*e.g.* kg ASF per kg DM intake), which has been a priority for livestock research in the past. Feed efficiency can be improved by breeding, as shown by historic developments (Havenstein *et al.*, 2003, Hayes *et al.*, 2013, Zuidhof *et al.*, 2014). Breeding can also contribute to livestock breeds that are better adapted to high temperatures and low quality feed (Hayes *et al.*, 2013). Improving animal nutrition can contribute to sustainable intensification of livestock also. Future nutritional research will likely focus on using new industrial by-products as feed, next to crop breeding for better feed quality (Thornton, 2010). Another entry point for sustainable intensification in livestock production is the prevention of animal diseases, which decrease animal welfare, feed efficiency, and profitability, and increase the impact of livestock production on the environment.

1.3 Assessing the scope for sustainable intensification

The consensus on the necessity of sustainable intensification in crop and livestock production urges the assessment of the scope to increase production for different regions in the world. This scope for intensification of agricultural systems can be assessed with empirical and mechanistic methods.

1.3.1 Empirical methods to assess the scope for sustainable intensification

Empirical methods to benchmark agricultural production are based on observed data. One of the empirical methods is benchmarking the average production realised by farmers against the highest production levels observed (for example the top decile farmers). The scope to increase production is the difference between this benchmark and the average production on farms (Hoang, 2013, Stuart *et al.*, 2016). This straightforward method has been applied often in cropping systems (Waddington *et al.*, 2010, Laborte *et al.*, 2012, Tanaka *et al.*, 2015, Stuart *et al.*, 2016). Alternatively, the average actual production can be benchmarked against the highest production levels obtained in field experiments and yield contests (Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013, Sadras *et al.*, 2015).

Another empirical method is benchmarking the actual production against the best-practice production with the actual inputs. The actual production divided by the best-practice production with the actual inputs is also referred to as the technical efficiency. The technical efficiency can be determined with stochastic frontier analysis for particular farms or farm types. The technical efficiency has been assessed for cropping systems (Vasco Silva *et al.*, 2016), livestock systems (Temoso *et al.*, 2016), and crop-livestock systems (Henderson *et al.*, 2016). In addition, the best-practice production with the actual inputs in crop-livestock systems can be simulated with farm models that redesign the farm configuration (Cortez-Arriola *et al.*, 2014). In general, empirical benchmarking accounts for the current constraining factors to agricultural production in their entirety, so the bio-physical, economic, social, environmental, cultural, legislative, and ethical constraints are all taken into account. Empirical benchmarking thus allows to assess the feasible scope to increase production under the current conditions, given the constraints in their entirety.

Empirical benchmarking of agricultural production, however, has four major drawbacks. Firstly, the empirical methods are location-specific, so their results can only be applied to similar farming systems under similar agro-ecological conditions. Large amounts of experimental data are required to benchmark agricultural production empirically under different agro-ecological conditions, which is time-consuming and costly. Secondly, empirical benchmarking accounts for the current constraints to production in their entirety, including the bio-physical, economic, social, environmental, cultural, legislative, and ethical ones. The bio-physical potential for agricultural production in a specific region is determined by the genotypes of crops and animals, the climate, and the soil type, which are each relatively fixed for long periods of time. Crop and animal genotypes, for example, can only be changed gradually by breeding programmes occupying multiple years or even decades (De Wit, 1986). The economic, social, cultural, legislative, and ethical constraints for agricultural production affect farm management, and consequently what fraction of the bio-physical potential is actually realized. Unlike the conservative bio-physical potential, the current constraints for agricultural production may be very different from the ones in 2050, due to economic and societal developments. For example, price fluctuations can alter economic constraints on the short term, and new legislation can change legislative constraints abruptly. Hence, using the current yields of the best farmers to estimate the scope for intensification in 2050 may have limited value. Thirdly, the scope for intensification under future scenarios (*e.g.* climate change, improved farm design) cannot be assessed via empirical benchmarks, as these are based on measurements from the present and past. Fourthly, explaining the gap between the empirical benchmark and the average production is not straightforward, since constraining factors are lumped, and considered in their entirety. Empirical benchmarking hardly allows to distinguish the most constraining factors causing the yield gap separately of each other. Consequently, identifying improvement options to intensify production may not be straightforward. In conclusion, empirical benchmarks should be complemented by other methods to assess the scope for sustainable intensification in different farming systems and under different agro-ecological conditions, to anticipate on the increasing global demand for food towards 2050.

1.3.2 Concepts of production ecology to assess the scope for sustainable intensification in crop production systems

The drawbacks of empirical methods can be overcome by using mechanistic models to benchmark agricultural production, which are based on concepts of production ecology. Concepts of production ecology integrate basic information on bio-physical

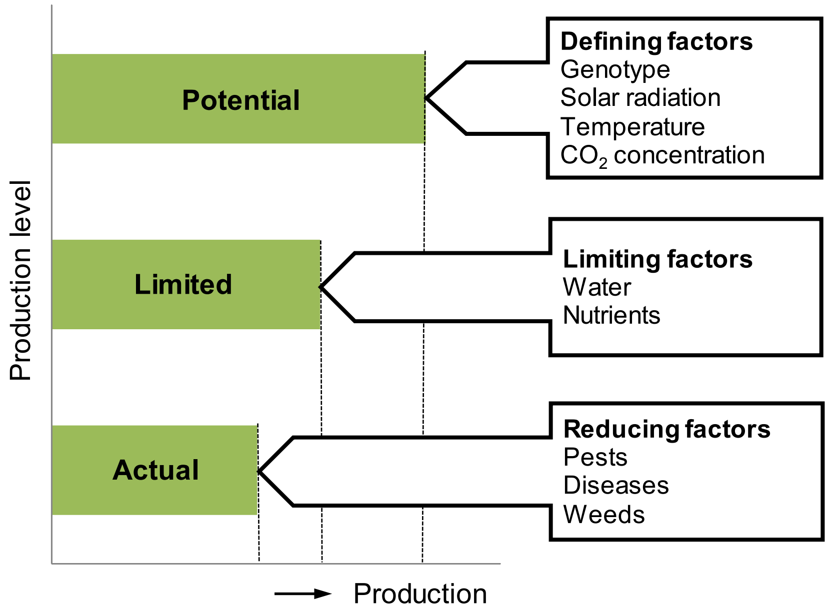

Figure 1.3 Potential, limited, and actual production levels in crop production systems with their corresponding growth defining, limiting, and reducing factors respectively. Adapted from Van Ittersum and Rabbinge (1997).

processes to get insight in the feasible and efficient input-output combinations of agricultural systems. This approach allows to estimate production levels that are feasible from a bio-physical perspective. Concepts of production ecology are mainly used in crop sciences, but van de Ven *et al.* (2003) argued that these concepts can be applied to livestock sciences as well. Concepts of production ecology distinguish potential, limited, and actual production levels, with their corresponding growth defining, growth limiting, and growth reducing factors respectively (Fig. 1.3).

Potential crop production is the theoretical maximum production from a bio-physical perspective, and is defined by the crop genotype, solar radiation, temperature, and CO_2 concentration (Fig. 1.3). Crop management is assumed to be ideal under potential production. Besides selection of a well-adapted crop species and cultivar (*i.e.* genotype) and a favourable sowing date, the defining factors for crops grown in the open field cannot be influenced by farmers. Limited crop production is determined by water and/or nutrient supply, which can be managed by farmers through irrigation and fertilization. Actual crop production is the production farmers realise in practice. The factors that lead to actual crop production (on top of the limiting factors) are pests, diseases, and weeds (Van Ittersum and Rabbinge, 1997, Evans and Fischer, 1999). Intensifying crop production can be achieved by yield protecting measures to control the reducing factors, and by yield increasing measures to mitigate the limiting factors (Van Ittersum and Rabbinge, 1997). Hence, concepts of production ecology provide a generic and theoretical framework that disentangles the main bio-physical factors affecting crop production.

For irrigated conditions, the difference between the potential and actual yields is named the yield gap, while for rainfed conditions the yield gap is defined as the difference between the water-limited yield and actual yield (Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013). The potential and water-limited crop production levels required to estimate yield gaps are simulated with crop growth models that are based on concepts of production ecology, whereas actual crop production is measured on farms. The yield gap reflects the theoretical scope to increase production from a bio-physical perspective. The degree to which limiting and reducing factors affect production depends on economic, social, cultural, legislative, and ethical factors. In practice, farmers may increase production at most to 75-85% of the potential or water-limited production, as shown for farms in north-west Europe and parts of the United States. Increasing production beyond this level is generally not cost-effective, not feasible in practice, or not environmentally wise (Cassman *et al.*, 2003, Van Ittersum *et al.*, 2013). The exploitable yield gap is subsequently defined as the difference between 75-85% of the potential or water-limited production and the actual production. Analysis of the yield gap can contribute to insight in how to increase the actual production. Yield gap analysis is a useful method to identify the major factors constraining production, to prioritize agricultural research, to evaluate scenarios, and to provide input for models assessing food security and land use (Van Ittersum *et al.*, 2013).

Mechanistic crop growth models are widely used in crop sciences to simulate potential and limited production levels (Bouman *et al.*, 1996, Jones *et al.*, 2003, Keating *et al.*, 2003, Van Ittersum *et al.*, 2003). In general, these crop growth models are dynamic and deterministic. Mechanistic crop growth models integrate effects of defining and limiting factors on the bio-physical processes in crops. Hence, crop growth models allow to identify the factors constraining growth in specific phases of the growing season. As mechanistic crop growth models simulate bio-physical processes generically, crop growth models can be applied to a wide variety of climates and cropping systems. Such crop growth models also allow to simulate crop production under future scenarios, such as climate change (Asseng *et al.*, 2013). In addition, effects of improved management options on crop yield, water use, and nutrient use can be simulated.

The theoretical framework provided by concepts of production ecology, and the crop growth models based on these concepts, have proven to be effective in identifying constraining factors for crop growth, and have contributed to identifying improvement options. Crop production of Sahelian rangelands, for example, was shown to be limited by phosphorus availability in the first part of the growing season, and by nitrogen in the second part, instead of water, as was generally acknowledged.

Hence, increasing nitrogen and phosphorus application could mitigate the yield gap in Sahelian rangelands (Breman and De Wit, 1983). Wheat production in southern Australia was considered to be predominantly limited by water, but application of concepts of production ecology showed that yields were often below the water-limited yield in some sites, which suggested that nitrogen and phosphorus were limiting yields (French and Schultz, 1984). A yield gap analysis for irrigated rice in the Philippines demonstrated that an increased nitrogen application at key phases could further increase production (Kropff *et al.*, 1993). Recent examples of yield gap analyses consider chickpea (Soltani *et al.*, 2016), rice (Singh *et al.*, 2015, Espe *et al.*, 2016), wheat (Deihimfard *et al.*, 2015, Hochman *et al.*, 2016), potato (Svubure *et al.*, 2015), sugar cane (Marin *et al.*, 2016), and the tropical grass *Miscanthus* (Strullu *et al.*, 2015). Hence, yield gap analysis based on concepts of production ecology has been extensively and successfully applied to different crops in different locations across the globe.

1.4 Knowledge gaps and objectives

1.4.1 Concepts of production ecology in livestock systems

As application of concepts of production ecology in cropping systems has led to quantification of yield gaps and has contributed to yield gap mitigation, a similar approach could be effective and successful in livestock systems. Potential, limited, and actual livestock production were described similarly to crop production, as well as the growth defining, limiting, and reducing factors. Growth defining factors for livestock production are the genotype and the climate surrounding the animal (Fig. 1.4).

Growth limiting factors are drinking water, feed quality, and feed quantity (Van de Ven *et al.*, 2003). Limited production is referred to as feed-limited production also, as the availability of drinking water is often not limiting livestock production. The growth reducing factors are animal diseases and stress (Van de Ven *et al.*, 2003). Van de Ven *et al.* (2003) also broadly quantified and illustrated potential and feed-limited production levels for cattle in the Netherlands and West-Africa. Defining and limiting factors were assumed to affect cattle production, but the effects of these factors on production were not quantified. Hence, estimating the potential and feed-limited production generically for different cattle production systems was not fully accomplished. When applying the concepts of production ecology and sustainable intensification to livestock, it should be kept in mind that boundless intensification towards potential or feed-limited production at the expense of animal welfare is not acceptable. Sustainable intensification certainly needs to be accompanied by acceptable levels of animal welfare (Garnett *et al.* 2013).

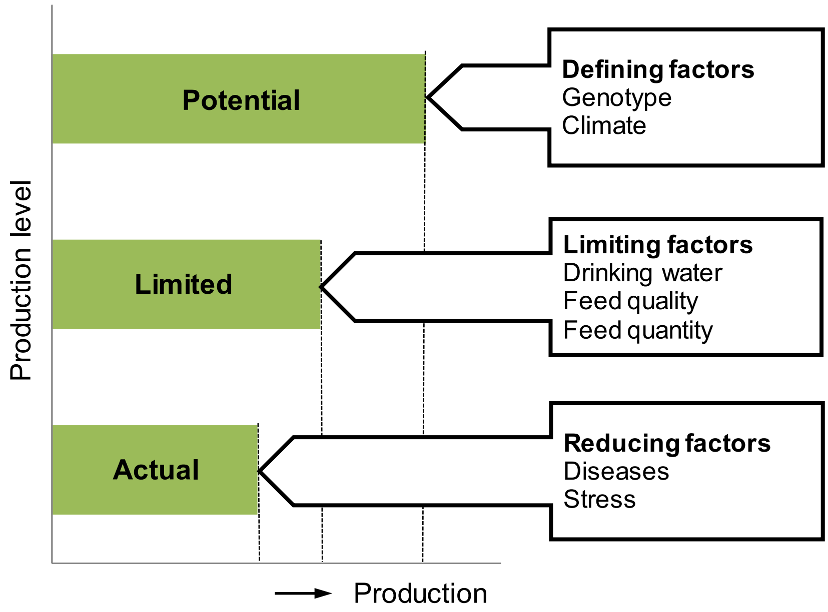

Figure 1.4 Potential, limited, and actual production levels in livestock systems with their corresponding growth defining, limiting, and reducing factors respectively. Adapted from Van de Ven *et al.* (2003).

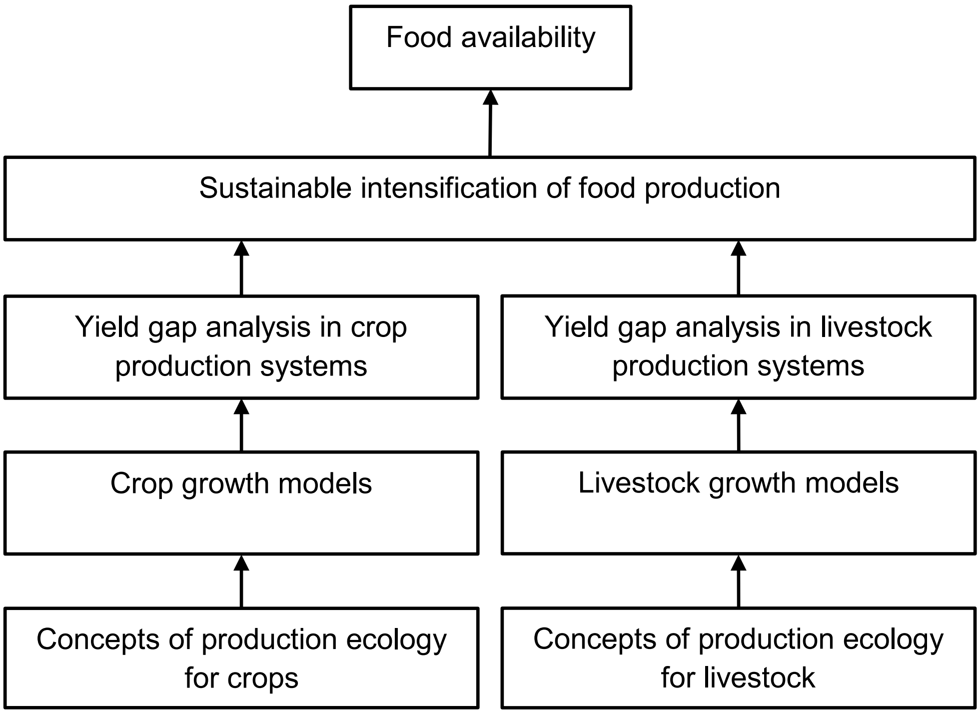

Figure 1.5 Schematic overview of how applying concepts of production ecology in crops and livestock can contribute to sustainable intensification and an improved food availability.

The potential and feed-limited production of livestock may be quantified generically with livestock growth models. The aim of such livestock models is to assess yield gaps in livestock production, and to identify constraining factors for livestock growth (yield gap analysis) in different farming systems under a wide range of agro-ecological conditions. After yield gap analysis, improvement options can be explored to sustainably intensify livestock production, which contributes to an increased food production and availability (Fig. 1.5). A livestock model must meet several criteria to assess yield gaps and to allow yield gap analysis:

- The model must be mechanistic and contain sufficient detail to simulate the effects of the genotype, climate, feed quality, and available feed quantity on livestock growth and production under different agro-ecological conditions. Simulating the effects of the defining and limiting factors, and their interactions, are required to identify the most constraining factors for livestock production.
- In line with concepts of production ecology for livestock, information about the genotype, climate, feed quality, and available feed quantity should be model inputs. Since feed quality and quantity determine feed intake, intake is a model output. Hence, models requiring feed intake as an input, or calculating feed input empirically, do not comply with concepts of production ecology. This suggests that many of the available animal models do not comply to concepts of production ecology, because they usually need feed intake as an input (Jones *et al.*, 2016). The total feed intake predicted by a model complying to concepts of production ecology allows to calculate the livestock production per unit of agricultural land area, using the DM yield of the feed crops consumed.
- The model must simulate livestock production at herd or flock level, which allows to keep track of the total feed intake required for livestock production. Hence, simulating the performance of specific animals within a herd (*e.g.* productive or reproductive), or specific phases in their life cycle only, is not sufficient to assess the scope to increase livestock production per hectare.
- Given the increasing global demand for food, the ASF produced should preferably be model output. For example, simulating live weight of animals kept for meat production is less precise than simulating the production of meat, because the carcass percentage and the fraction of edible meat in the carcass may vary under different agro-ecological conditions, and among different farming systems.
- The model must simulate all relevant outputs of ASF fully, and not partially. This implies that herds or flocks kept for dairy production produce meat also, through slaughter of culled animals, and male animals not used for dairy production.

The bio-physical scope for increasing livestock production has not been assessed with mechanistic models, let alone that yield gap analysis was conducted. The only existing model based on concepts of production ecology is LIVSIM (LIVestock SIMulator), which simulates the effect of feeding strategies on milk production of dairy cattle in the Central Highlands of Kenya (Rufino *et al.*, 2009). LIVSIM neglects, however, the influence of climate. Moreover, the body composition of cows was not simulated with LIVSIM, so beef production from culled cows could not be assessed. Hence, LIVSIM did not fully meet the aforementioned criteria for a livestock model that can assess the scope to increase livestock production generically.

Dozens of mechanistic livestock models have been published. Although descriptions of mechanistic livestock models other than LIVSIM do not refer explicitly to concepts of production ecology as defined by Van de Ven *et al.* (2003), many of them include elements of these concepts (*e.g.* Moughan *et al.*, 1987; Wellock *et al.*, 2004). After a review of scientific literature, 32 mechanistic, dynamic livestock models were investigated whether they could meet the aforementioned criteria to assess the scope to increase livestock production generically (Appendix 1A). Parameters representing different genotypes or breeds are included in most models (88%). Less than half of the models (41%) includes the effects of climate on livestock production. Approximately half of the models including the effect of climate used an empirical method, so most of the livestock models apply to the climate conditions they have been calibrated for. All models simulate energy flows in animals to represent feed quality, and most of them include protein flows too (91 %). One model did not simulate feed intake, since digested nutrients were used as input. Feed intake is predicted based on the available feed quantity in 38% of the models, which complies to the concepts of production ecology. Other livestock models require feed intake as an input, calculate feed intake empirically, or calculate feed intake backwards, from a given production level.

About half of the livestock models simulates livestock production at herd or flock level (52%), whereas a minority of the models simulates the production of ASF (26%). These models were generally more complex than the others at animal level, as body composition, and the lipid and protein content of the ASF were simulated. Models tended to simulate either ASF production from individual animals, or live weight production from herds, whereas the combination of ASF production from herds was only found in two models (Appendix 1A). All in all, no single model could fully meet the criteria to assess the bio-physical scope to increase livestock production readily, and to identify constraining factors for growth under a wide range of agro-ecological conditions (Appendix 1A). In conclusion, a mechanistic livestock model to quantify yield gaps and to conduct yield gap analysis generically was not available at the start of this research.

1.4.2 Concepts of production ecology in feed-crop livestock systems

Feed from arable land or grassland is an input for livestock systems. The majority of farms across the globe can be classified as mixed crop-livestock systems, where crop and livestock production occur on the same farm (Van de Ven *et al.*, 2003, Herrero *et al.*, 2010). Livestock systems importing feed require off-farm land for feed production, and the production of feed crops and livestock can be regarded as geographically separated. Whether or not crop and livestock production occur on the same farm and the same location, livestock production is inherently associated with the production of feed crops and food crops (by-products). Hence, all livestock systems are part of a feed-crop livestock system, which includes livestock and all feed crops required for livestock production. Estimating potential and feed-limited livestock production analogously to potential and water-limited crop production would allow to assess the potential and limited production per unit area for feed-crop livestock systems. Subsequently, the actual production of a feed-crop livestock system can be benchmarked against its potential or limited production. Limiting production for feed-crop livestock systems follows from a combination of water-limited crop production and feed-limited livestock production, which is also referred to as resource-limited production in this thesis. Using concepts of production ecology would thus allow to assess yield gaps for feed-crop livestock systems too.

After assessing and analysing yield gaps, improvement options can be identified to mitigate yield gaps in feed-crop livestock systems. The nexus between feed and livestock production is highly relevant for future food production, because about one-third of the global arable land is used for feed production (Herrero *et al.*, 2013). Mitigating yield gaps in feed-crop livestock systems might decrease the use of arable land for feed crops, which leaves more arable land available for food crops (Van Kernebeek *et al.*, 2016, Van Zanten *et al.*, 2016a, Van Zanten *et al.*, 2016b). Currently, assessing yield gaps generically is not possible for feed-crop livestock systems, since appropriate methods to assess yield gaps in the livestock component of these systems generically are not available.

1.4.3 Objectives

To allow for a quantitative benchmarking of the opportunities to increase livestock production per unit of feed input and per unit of land, the objectives of this thesis are to:

- Develop a generic framework to assess the scope to increase production of feed-crop livestock systems, based on concepts of production ecology.
- Develop a generic livestock model to simulate potential and feed-limited livestock production, based on concepts of production ecology.
- Apply the generic framework and livestock model to a range of feed-crop livestock systems, and conduct yield gap analyses.

The objectives of this thesis are implemented for beef cattle. The main reason for selecting beef cattle is that beef can be the only ASF output from beef production systems, whereas some other livestock types and species (e.g. dairy cattle or laying hens) have multiple ASF outputs (milk and meat, or eggs and meat). Having one ASF output facilitates modelling and avoids allocation of feed input to multiple ASF outputs. Beef cattle were selected for their considerable economic importance also.

Beef is the third agricultural commodity in terms of production value ($185 billion in 2012), after milk and rice (FAO, 2015). In addition, beef cattle are ruminants, which digest fibrous feeds that cannot be digested by humans. Cattle production can potentially contribute, therefore, to ASF production without much competition for arable land between the production of feed crops and the production of human food crops (Schader *et al.*, 2015, Van Kernebeek *et al.*, 2016, Van Zanten *et al.*, 2016b). I will discuss, however, the applicability of the framework and model to other livestock types and species as well in the General Discussion (Chapter 7, Section 5.3).

1.5 Outline of the thesis

To address the first objective of this thesis, the concepts of production ecology for livestock are developed further in Chapter 2, building on the work of Van de Ven *et al.* (2003). In addition, this chapter provides a simple calculation method for potential livestock production, with an illustration for Charolais beef cattle in France. The calculations account for the defining factor genotype only, assuming that climate did not affect beef production. A generic, mechanistic, and dynamic model simulating potential and feed-limited production of beef cattle is presented in Chapter 3 (Fig. 1.6). This model is named LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle). LiGAPS-Beef accounts for the cattle

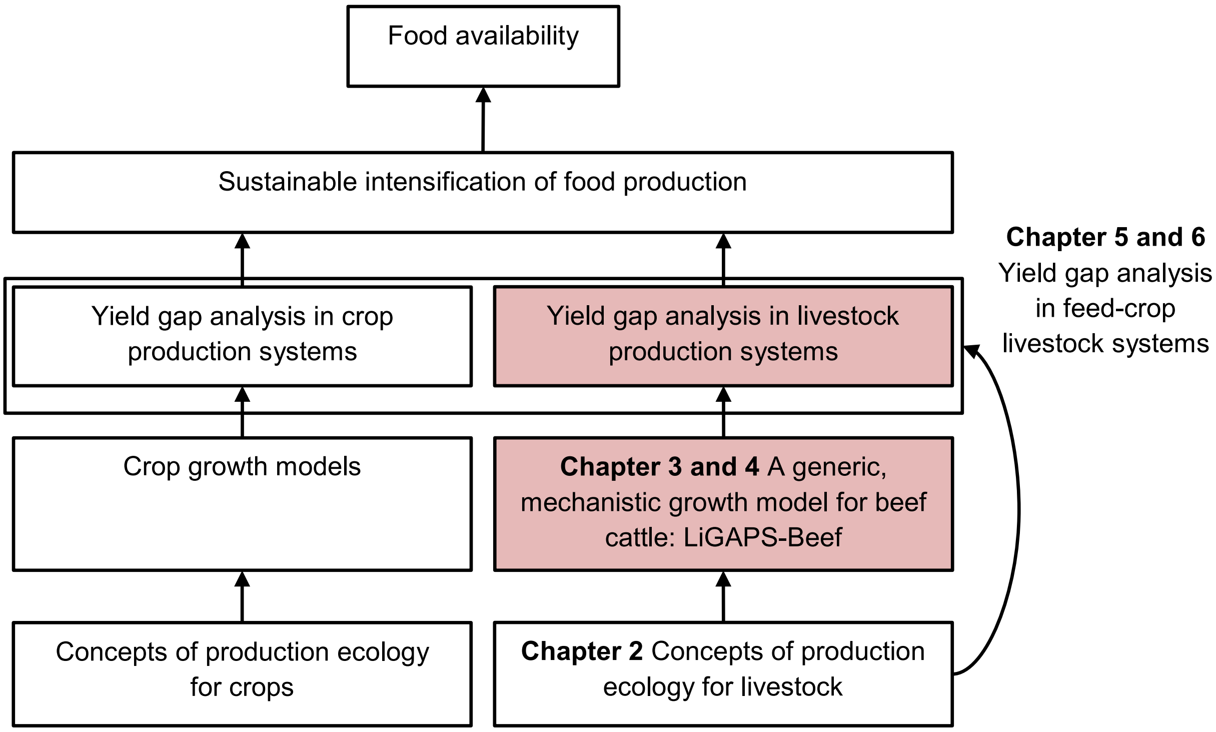

Figure 1.6 Overview of the chapters and structure of this thesis. Livestock growth models to assess the scope to increase livestock production generically, and to conduct yield gap analysis (indicated in red) were not available at the start of this research. LiGAPS-Beef = Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle

genotype, climate, feed quality, and feed quantity, and allows to estimate potential and feed-limited beef production in different beef production systems across the globe. The model is illustrated for beef production systems in France and Australia. In Chapter 4, the model LiGAPS-Beef is evaluated with data from different beef production systems in Australia, Uruguay, and the Netherlands. Chapter 3 and 4 thus address the second objective of the thesis, *i.e.* developing a generic model to simulate potential and feed-limited livestock production, based on concepts of production ecology (Fig. 1.6).

The objective of Chapter 5 is to estimate the scope to increase production in feed-crop livestock systems (Fig. 1.6), which is illustrated for a case of grass-based beef production in the Charolais area of France. LiGAPS-Beef has been combined with a mechanistic grass growth model for perennial ryegrass (*Lolium perenne* L.), which is based on concepts of production ecology also. This allows simulation of potential and resource-limited production for grass-based beef farms with Charolais cattle. Actual production in these systems was benchmarked against potential and resource-limited production, and yield gaps were analysed. In Chapter 6, the advantage of mechanistic models to simulate future scenarios is exploited. This chapter investigates the resource-limited beef production of Charolais bulls under climate change in 2050, and includes an analysis of the current yield gap. Chapter 7 contains the General Discussion, where the main results from the preceding chapters are discussed, and new applications of the generic framework and LiGAPS-Beef are explored. New applications are spatially mapping yield gaps of beef production systems, extension of LiGAPS-Beef to cattle kept for multiple purposes, and extension of the model to other livestock species. Other applications discussed are assessing food-feed competition and quantifying sustainability indicators. The last part of the General Discussion lists the main conclusions of this thesis.

Chapter 2

A framework for quantitative analysis of livestock systems using theoretical concepts of production ecology

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Abstract

In crop science, widely used theoretical concepts of production ecology comprise a hierarchy in growth defining, limiting, and reducing factors, which determine corresponding potential, limited, and actual production levels. These concepts give insight in theoretically achievable production, yield gaps, and yield gap mitigation. Concepts of production ecology have been demonstrated to be applicable to livestock science, but so far they have not been used quantitatively for livestock production. This paper aims to define theoretical concepts of production ecology for livestock systems in more detail, to express livestock production in suitable units, and to provide a framework to analyse production levels for livestock systems and feed-crop livestock systems.

Growth defining (genotype and climate), growth limiting (feed quality and quantity), and growth reducing factors (diseases and stress) in livestock production are described analogous to the growth factors in crop production. Management practices, such as housing, feeding, culling, and slaughter are specified. From the perspective of a livestock system, production is expressed per animal, per unit of animal body mass, and per unit of feed intake, whereas from the perspective of a feed-crop livestock system, production is recommended to be expressed in kg livestock product ha^{-1} $year^{-1}$.

The quantitative framework is illustrated for Charolais cattle (*Bos taurus* subsp.) in two beef production systems in France, differing in feeding strategies. System A produces heavier calves than system B, whereas cattle in system B are fed a higher fraction of concentrates in the diet compared with system A. Potential beef production was similar for systems A and B, and estimated to be 152 kg beef $animal^{-1}$ $year^{-1}$ and 251 g beef kg^{-1} live weight $year^{-1}$, while there was a minor difference when expressed per unit of feed intake (54.5 vs 54.8 g beef kg^{-1} dry matter (DM)). Actual livestock production was lower for system A than for system B (24.9 vs 31.2 g beef kg^{-1} DM). Potential production per unit area was again similar for systems A and B (631 vs 634 kg beef ha^{-1} $year^{-1}$), while actual production was much lower for system A than for system B (133 vs 180 kg beef ha^{-1} $year^{-1}$). The yield gap at feed-crop livestock system level was 79% of potential production for system A and 72% for system B. We conclude that the framework is effective to reveal the scope to increase production and resource use efficiency in livestock production.

2.1 Introduction

Variation in production among farming systems is, amongst others, caused by multiple biophysical factors. Quantifying the contribution of biophysical factors to production of farming systems could contribute to an explanation of current production levels and reveal options to increase production. In crop production, relevant biophysical factors are subdivided in three groups: growth defining, growth limiting, and growth reducing factors (Evans, 1993, Van Ittersum and Rabbinge, 1997). Growth defining factors determine potential growth and potential production. Growth defining and limiting factors together determine limited growth and limited production. All three groups of biophysical factors jointly determine actual growth and actual production, which is the crop production level observed in farmers' fields. This hierarchy in biophysical growth factors is well-known in crop production, and acknowledged as theoretical concepts of production ecology (Van Ittersum and Rabbinge, 1997, Van de Ven *et al.*, 2003).

These theoretical concepts of production ecology, also referred to as production ecological concepts, have been widely and successfully applied to crop production (Bouman *et al.*, 1996, Van Ittersum *et al.*, 2003). Today's crop production across the world can be benchmarked against potential or water-limited production. Differences between these benchmarks and actual production levels are referred to as yield gaps (Van Ittersum and Rabbinge, 1997, Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013). Yield gap analysis, based on production ecological concepts, enables the identification of constraints to agricultural production.

There are many examples in the literature where biophysical constraints to crop production were identified and yield gaps were mitigated after application of the production ecological concepts (Breman and De Wit, 1983, French and Schultz, 1984, Kropff *et al.*, 1993). Farmers in Australian cropping systems, for example, perceived water as the single most important factor limiting wheat yields. It was shown, however, that water-limited production was not achieved in some sites, because nitrogen and phosphorus limited crop yield (French and Schultz, 1984).

Improvement options, based on biophysical analysis of yield gaps, may not be implemented due to socio-economic, environmental, ethical, or cultural constraints. Socio-economic constraints can be labour availability, input prices and output prices. In addition, environmental regulations to restrict nutrient and pesticide use may affect production (Rabbinge and Van Latesteijn, 1992). In livestock systems, regulations on animal welfare and their underlying ethics also set boundaries to production (Croney and Millman, 2007). Increasing production per animal can be associated with negative effects on animal welfare, which stresses the need of an ethical framework that disbars some options for livestock production (Garnett *et al.*, 2013). Hence, putting an improvement into practice requires both yield gap analysis and analysis of specific non-biophysical constraints (Van de Ven *et al.*, 2003, Van Ittersum *et al.*, 2013, Oosting *et al.*, 2014).

Although yield gap analysis is commonly applied to cropping systems, it is not applied to livestock systems, to our knowledge. Van de Ven *et al.* (2003) already demonstrated that a similar set of production ecological concepts used in crop production can be used also in livestock production. They broadly quantified potential and limited levels of livestock production, but separate effects of genotype, climate, feed quantity, and feed quality on production were not quantified. So far, no framework is available and applicable for quantification of livestock systems that includes the effect of defining, limiting, and reducing factors on livestock production. This paper aims, therefore, to provide such a framework to analyse and quantify livestock production, based on production ecological concepts. The framework is illustrated quantitatively by assessing actual and potential production of Charolais beef cattle in France.

Livestock production will be quantified from the perspective of a livestock system and a feed-crop livestock system. A livestock system includes livestock production at herd level, and feed crops are an external input. A feed-crop livestock system includes livestock production and the corresponding feed crop production. All land necessary for feed crop production is part of a feed-crop livestock system, no matter whether feed is produced in the same geographical location as the animals, or in a different location.

2.2 Materials and methods

2.2.1 Concepts and methodology

Defining the production ecological concepts for livestock

Analogous to the production ecological concepts used in crop production (Fig. 2.1 A) (Van Ittersum and Rabbinge, 1997, Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013), Van de Ven *et al.* (2003) identified growth defining, limiting, and reducing factors in livestock production (Fig. 2.1B). Growth defining factors in animal production are animal genotype, also referred to as animal breed, and climate. Growth of animals can be affected negatively by climate under cold (Delfino and Mathison, 1991) and hot conditions (Blackshaw and Blackshaw, 1994, McGovern and Bruce, 2000). Like in crops, genotype × climate interactions are observed in livestock (Burrow, 2012). Potential production is achieved when drinking water and feed supply are not limiting production, and diseases and stress are fully controlled (Van de Ven *et al.*, 2003).

Drinking water and feed are growth limiting factors to livestock production (Fig. 2.1 B). Feed limitation is differentiated in feed quantity limitation and feed quality limitation (Van de Ven *et al.*, 2003). If feed intake does not supply sufficient energy,

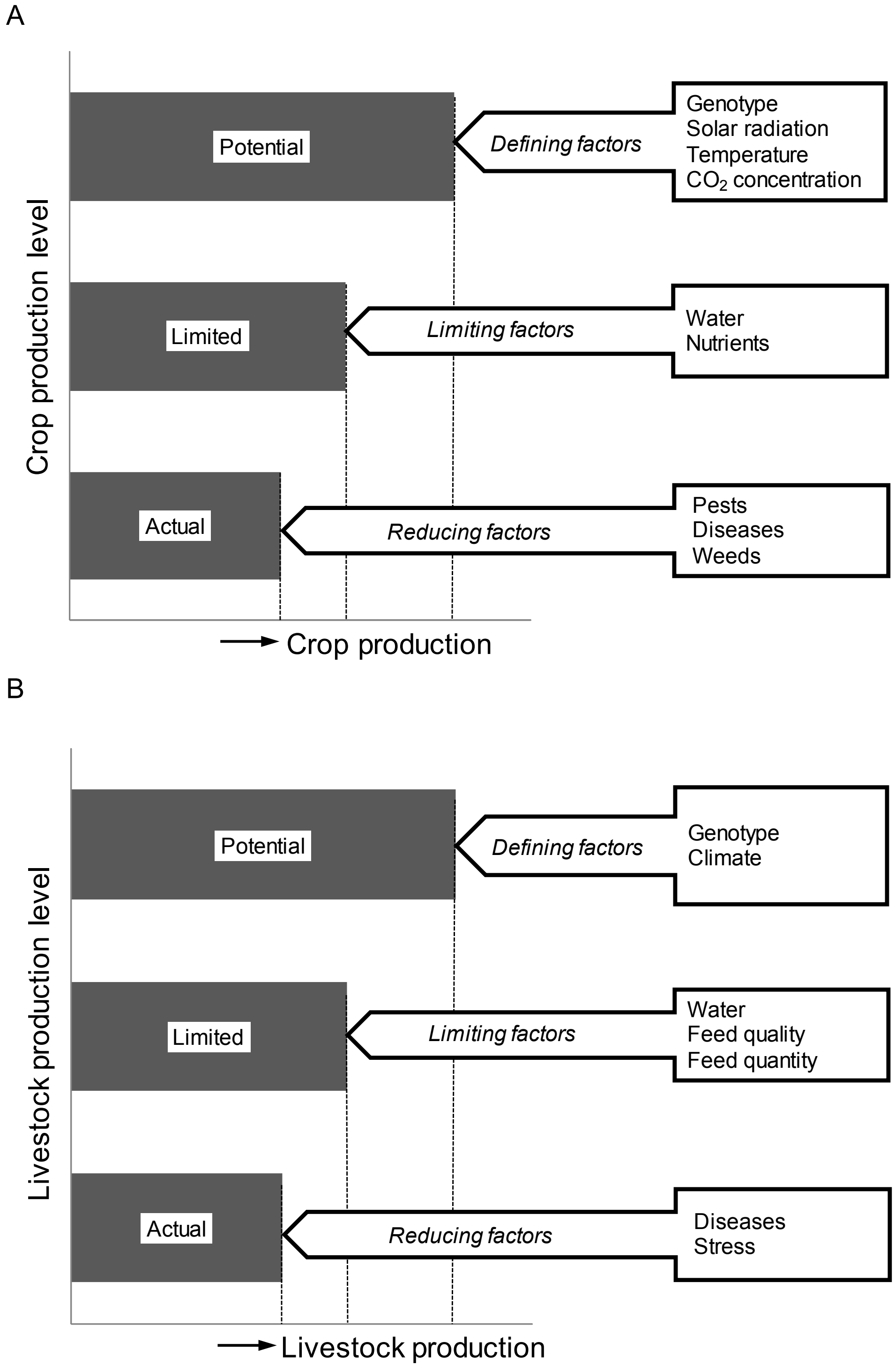

Figure 2.1 Potential, limited, and actual crop production levels with their corresponding growth defining, limiting, and reducing factors in cropping systems (A) and livestock systems (B). Source: Van Ittersum and Rabbinge (1997) and adapted from Van de Ven *et al.* (2003).

protein, essential amino acids, fibre, or other nutrients, growth is below its potential level and production becomes feed limited. Feed quality affects the heat production after feeding (West, 1999). In addition, feed limitation can negatively affect fertility (Veerkamp, 1998). Diseases and stress are reducing factors in livestock systems.

Pain and suffering associated with diseases and stress can lead to sub-optimal animal welfare. Stress occurs if animals are not able to fulfil their needs to an adequate extent (Curtis, 1987). Stress, as a reducing factor, is defined as sub-optimal fulfilment of animal needs that reduces livestock production due to other factors than climate, feed, and drinking water, as these are already included in the other production levels.

Livestock management under potential production

Potential production of crops is defined by a given genotype and the climate (Van Ittersum and Rabbinge, 1997). It is achieved under best management practices, although this is not a precise description (Cassman, 1999). Climate is a defining factor in crop production, because it cannot be manipulated by management under field conditions. Climate is also considered a defining factor for crops cultivated in greenhouses, because a greenhouse is fixed for a period of investment, contrary to the variable yield increasing factors (*i.e.* water and nutrients) which can be managed almost instantly in crops. Animals housed indoors are equivalent to crops in greenhouses. Hence, potential production in livestock can be assessed for outdoor conditions and in stables. We define potential livestock production for a given genotype and a given (indoor) climate. Climate does not affect growth or production if an animal is in the thermo-neutral zone.

Under potential production, feed quality is optimal and feed is available in non-limiting quantities (Van de Ven *et al.*, 2003). The diet formulated under potential production should provide energy and nutrients required by animals according to their physiological state. Additional requirements to the diet differ between animal species. Maturation and harvest time of annual crops is determined by the genotype and the climate. Desired product quality and highest product quantity are often reached simultaneously at harvest time. Slaughter age of animals kept for meat production can be determined by meat quality and feed efficiency (FE, meat produced per unit of feed DM intake). In addition, social, economic, and cultural factors can affect slaughter age (Scoones, 1992, Budisatria *et al.*, 2008). Under potential production, livestock mortality is only caused by genetic and climatic factors. Livestock mortality solely related to genetic and climatic factors, however, is hard to assess. Culling of reproductive animals affects the average number of offspring per reproductive animal. Causes for culling are numerous and interrelated. It is hard to investigate separate effects of genotype, climate, feed quality, and feed quantity on culling probabilities.

Units for expressing production

To quantify livestock production levels based on production ecological concepts, we first investigate units used to express crop production, and subsequently derive analogous units for livestock production, and for production of feed-crop livestock systems.

Units for crop production

Crop production is usually expressed in tons of dry or fresh product per hectare per year, or per growing season. A crop is considered a population of uniform plants that interact and compete with each other for solar radiation, water, and nutrients. Crop growth can be described by an exponential growth phase, a linear growth phase, and a senescence phase (Goudriaan and Monteith, 1990). Under potential production, incoming solar radiation is the main determinant of crop growth: the relation between intercepted solar radiation and crop growth tends to be linear (Monteith and Moss, 1977). Given the relatively short duration of the exponential growth phase and senescence phase under potential production, solar radiation (an input of the system) drives crop production to a greater extent than the aboveground crop biomass and leaf area index (states of the system). Similarly, water (an input of the system) drives crop production generally to a greater extent than root biomass (a state of the system) under water-limited production (Musick *et al.*, 1994). Application of a limiting nutrient (an input of the system) drives crop production to a greater extent than root biomass (a state of the system), if no other factors are limiting (Van Keulen, 1982, Vos, 2009).

We define a system where output is more determined by system input than by system states as an input-based system. The alternative is a state-based system, where system output is more determined by system states than system input. Input rates determine crop growth to a larger extent under potential and limited crop production than system states. Crop production systems, therefore, are predominantly input-based. Solar radiation, water, and nutrient input can all be expressed per hectare per year. Potential and limited crop production are accordingly expressed input-based, in kg DM ha^{-1} year^{-1}. Crop production can also be expressed as state-based, for example, in kg product per plant per year. This is not a useful measure, as this expression does not take into account competition among plants in a crop. Another option is to express crop production state-based as crop product per kg of average biomass over a year or growing season. Such state-based expressions are, to our knowledge, not used in the literature, nor deemed useful for production ecology.

Units for livestock production

Livestock production can be represented similarly to crop production. Under potential production, feed supply satisfies nutritional requirements of animals (Van de Ven *et al.*, 2003), and competition for feed is absent. By definition, animal characteristics (states of the system) determine production to a larger extent than the feed quantity (an input of the system). Potential livestock production is thus state-based, contrary to potential crop production. Feed quality limitation and feed quantity limitation can occur simultaneously. As under feed quality limitation feed quantity is not limiting, competition for feed is absent, and production is state-based. Production under feed quantity limitation is, by definition, input-based. In conclusion, livestock production can be expressed both state-based and input-based. We express, therefore, livestock production in both ways in the following section.

Livestock production can be expressed state-based *per animal* per year. This is calculated as total herd production per year divided by the total number of animals in a herd. In addition, production can be expressed state-based *per productive animal* per year, excluding reproductive animals. Livestock production can also be expressed state-based in kg animal product *per kg body weight* per year. This is calculated by dividing total herd production per year by the total livestock weight of all animals present in the herd or flock. Similarly, production can be expressed per tropical livestock unit (TLU) per year (Van de Ven *et al.*, 2003). Another state-based expression of livestock production is the biomass-food productivity (Steinfeld and Opio, 2009), defined as annual protein production from a herd or flock divided by the total weight of the herd or flock. Livestock production can be expressed in kg animal product *per kg metabolic body weight* per year, which is referred to as the Kleiber ratio (Kleiber, 1947). This is calculated by dividing total herd production per year by the total metabolic body weight of all animals present in the herd. The Kleiber ratio takes into account that energy requirements for maintenance are linearly related to metabolic body weight. Hence, the Kleiber ratio can be used as a proxy for FE (Scholtz *et al.*, 1990). Input-based livestock production is expressed as system output (animal products) divided by system input (feed). Thus, livestock production can be expressed input-based as g animal product kg^{-1} DM feed intake, also referred to as FE. The reciprocal of FE is the feed conversion ratio (FCR), expressed as kg DM feed kg^{-1} animal product.

Units for production of feed-crop livestock systems

The feed-crop livestock system includes livestock production and all corresponding feed crop production. Hence, all livestock systems are part of a feed-crop livestock system. A system where livestock and crop production take place at the same geographical location is referred to as a mixed crop-livestock system. The majority of farming systems in the world are mixed crop-livestock systems (Van de Ven *et al.*, 2003, Herrero *et al.*, 2010, Udo *et al.*, 2011, Oosting *et al.*, 2014). Landless livestock systems can be regarded as a part of feed-crop livestock systems in which the livestock and the crop component are geographically separated. Combining feed crop and livestock systems would enable to analyse resource use required for livestock products, under potential and limited production levels for different agricultural systems around the globe. Feed-crop livestock systems do not produce food crops, but exclusively feed crops required for livestock production.

To calculate production of feed-crop livestock systems, input-based production of the cropping system and the livestock system are multiplied (Eq. 1). This results in the production of the feed-crop livestock system, expressed in kg animal product ha^{-1}

year^{-1}. If feed is a by-product of the crop, a fraction of the cropland can be allocated to the by-product by economic allocation, physical allocation (*e.g.* mass), and system expansion methods (ISO, 2006). An advantage of using input-based production for both crops and livestock is that production of feed-crop livestock systems can be calculated easily (Eq. 1). Production of a feed-crop livestock system, therefore, is expressed best input-based, in kg animal product ha^{-1} year^{-1}.

$$(1) \qquad \underbrace{\frac{\text{kg DM feed}}{\text{ha} \times \text{year}}}_{\text{Feed crop production}} \times \underbrace{\frac{\text{kg animal product}}{\text{kg DM feed}}}_{\text{Livestock production}} = \underbrace{\frac{\text{kg animal product}}{\text{ha} \times \text{year}}}_{\text{Feed-crop livestock production}}$$

2.2.2 Application to Charolais production in France

The theory presented in section 2.1 was applied to two beef production systems with Charolais (*Bos taurus* subsp.) cattle in France. Potential and actual production were calculated for beef cattle (state-based and rate-based), for feed crops (rate-based, per ha), and for production of feed-crop livestock systems (rate-based, per ha). This enabled to compute relative yield gaps for cattle, feed crops, and feed-crop livestock systems.

Calculation of potential beef production

To compute potential production in our example case, beef cattle were assumed to be permanently in the thermo-neutral zone, independent whether they were housed outdoors or indoors. This implies climate did not negatively affect animal performance and hence, potential beef production was determined only by cattle genotype. Because the contribution of genotype, climate, and feed limitations to mortality is hard to separate, we ignored mortality rates in the computation of potential production. Potential production is the production level where FE at herd level is highest.

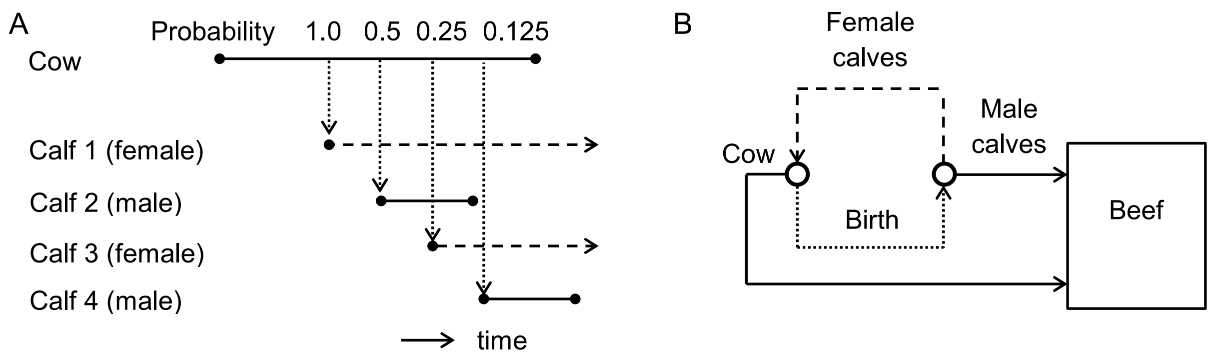

Figure 2.2 (A) Cow and male calf life spans (solid lines) in a livestock cycle. Probabilities for having one, two, three, or four calves per cow are indicated. Replacement calves (dashed lines) are not part of the livestock cycle. Dotted lines indicate birth. Male and female calves are in random order, and only four out of the maximum eight calves per cow are indicated. (B) Beef production from cows and male calves under potential production. Solid lines indicate beef production, the dashed line indicates replacement, and the dotted line birth.

The smallest possible herd consisted of one reproductive animal and its offspring, minus replacement offspring, and was referred to as a herd unit. Replacement offspring was part of another herd unit (Fig. 2.2 A). Total life span in the herd unit was the sum of the life span of the cow and the calves not used for replacement (Fig. 2.2 A). Similarly, total beef production in this herd unit consisted of beef production from the cow and the calves not used for replacement (Fig. 2.2 A). As the number of replacement calves equals the number of cows slaughtered, also the number of herd units terminated equals the number of herd units initiated in a herd (Fig. 2.2 B).

To assess potential production, all cows were assumed to give birth to a first calf, to reach a calving interval of one year (Jouven *et al.*, 2008), and the culling rate was 50% per year after birth of the first calf. Hence, each cow gives, on average, birth to one female calf and one male calf. A herd unit consisted, on average, of one cow and one male calf in the French beef production systems. Cows are assumed to have a maximum age until which production can be maintained. It was assumed that cows can have a maximum of eight calves. Given the calving interval and weaning age, reproductive cows were maximum ten years old at culling (Table 2.1). Only a fraction of the cows reached this maximum age, due to culling. FE at herd level increases with increasing culling rate, because growth rate of cows decreases after the first calf is born, and subsequently total beef production at herd level increases with increasing culling rate. Slaughter weight of the male calf was set equal to the slaughter weight resulting in highest FE at herd level. This implies that the male calf is slaughtered at an age when its FE equals the FE of the reproductive cow. Reproductive bulls were assumed to comprise a small portion of the reproductive herd, and were neglected in this example.

The dynamics of total body weight (TBW) of productive and reproductive cattle in both beef production systems were based on breed and sex-specific Gompertz curves. Empty body weight (EBW) was assumed to be 89% of TBW. Gompertz curves were used to calculate beef production per kg TBW, or per kg metabolic body weight, also referred to as $EBW^{0.75}$. Average TBW for an individual animal in the herd unit was calculated as the sum of daily TBWs divided by its slaughter age in days. Average TBW in a livestock herd was calculated as the sum of daily TBWs of all animals in a herd unit, divided by the sum of their slaughter ages in days. A similar approach was adopted for average metabolic body weight.

The protein fraction in the TBW was similar for cows and male calves, but lipid faction was assumed to be higher for cows than for male calves. Net energy (NE) required for growth of body tissue was higher for cows than for male calves (Table 2.2). NE requirement for maintenance and physical activity was proportional to the $EBW^{0.75}$ (Table 2.2).

Table 2.1. General parameters used to calculate potential production of Charolais beef cattle.

Parameter	Value	Unit	Reference
Age at first calving	2.34	years	
Calving interval	1	year	Jouven *et al.*, 2008
Weaning age	210	days	Jenkins and Ferell, 1992
Culling rate[a]	50	% year^{-1}	
Maximum calf number	8		
Maximum age at weaning eighth calf[b]	9.94	years	
Heat increment of feeding	0.27	MJ MJ^{-1} ME	
ME content wheat	13.0	MJ kg^{-1} DM	Kolver, 2000
ME content hay	9.7	MJ kg^{-1} DM	Kolver, 2000
ME content diet	11.8	MJ kg^{-1} DM	
Potential production wheat	9.8	kg DM ha^{-1} year^{-1}	Global Yield Gap Atlas, 2015
Potential production grass	21.7	kg DM ha^{-1} year^{-1}	De Koning and Van Diepen, 1992
Potential production hay[c]	17.4	kg DM ha^{-1} year^{-1}	
Potential production diet	11.6	kg DM ha^{-1} year^{-1}	
Fraction carcass	0.55		
Fraction beef in carcass	0.82		

[a] Culling rate applies after birth of the first calf.
[b] Only a fraction of the cows reaches maximum age, due to culling.
[c] Hay making involves a 20% dry matter loss.
DM = dry matter; ME = metabolisable energy

Total NE requirements consist of NE requirements for maintenance, physical activity during grazing, growth, gestation, and lactation. Heat increment of feeding is defined in this paper as energy required for rumination, digestion, and absorption of feed. Heat increment of feeding is also referred to as diet-induced thermogenesis, thermic effect of feeding, and specific dynamic action (Secor, 2009). NE requirements plus heat increment of feeding equated metabolisable energy (ME) requirements.

We assumed that if beef cattle were fed a diet of wheat (65%) and good quality hay (35%) *ad libitum*, all nutritional requirements to sustain potential growth were met, and sufficient fibre was provided to sustain good rumen functioning (Mertens, 1997). Heat increment of feeding was estimated at 0.27 MJ MJ^{-1} ME for the wheat-hay diet under potential production. ME content of the diet was 11.8 MJ ME kg^{-1} DM (Table 2.1). Total ME requirements were calculated from NE requirements, and were converted to DM wheat and hay. DM losses during hay making were assumed to be 20%. Potential production of the diet was 11.6 t DM ha^{-1} year^{-1}, including DM losses during hay making (Table 2.1). Land use for wheat and hay was fully allocated to feed production. Total feed intake and beef production enabled calculation of FE of Charolais cattle. Production of feed-crop livestock systems was calculated by multiplying the potential production level of the diet and the FE of cattle (Eq. 1).

Table 2.2 Breed and sex-specific parameters used to calculate potential production of Charolais beef cattle.

Parameter	Unit(s)	Male	Female	Reference
Birth weight	kg	48.1	45.9	Simčič *et al.*, 2006
Mature TBW	kg	1300	950	
Protein fraction in TBW		0.21	0.21	
Lipid fraction in TBW		0.30	0.40	
NE requirement growth	MJ kg^{-1} TBW	25.3	30.6	Emmans *et al.*, 1994; Owens *et al.*, 1995
NE requirement maintenance	kJ kg $EBW^{-0.75}$ day^{-1}	311	311	Ouellet *et al.*, 1998; NRC, 2000
NE requirement physical activity	kJ kg $EBW^{-0.75}$ day^{-1}	60	60	Brosh *et al.*, 2006; Brosh *et al.*, 2010
NE requirement gestation	GJ $calf^{-1}$	2.91	2.78	based on Fox *et al.*, 1988
NE requirement milk production	GJ $calf^{-1}$	4.21	4.21	based on Moe and Tyrell, 1975

EBW = empty body weight; NE = net energy; TBW = total body weight

Table 2.3 Farm characteristics of systems A and B (Réseaux d'Elevage Charolais, 2012).

Farm characteristic	System A[a]	System B[a]
LW production (t $year^{-1}$)	85.5	61.1
Grassland area (ha)	280	130
Grassland with one cut hay (ha)	113	64
Hay production (t DM $year^{-1}$)	460	283
Hay production (t DM ha^{-1} $year^{-1}$)	4.1	4.4
Area arable crops (ha)	0	150
Concentrates fed (t FM $year^{-1}$)	87	190
Dry matter fraction concentrates[b]	0.85	0.85
Slaughter weight males (kg $animal^{-1}$)	460[c]	430[d]
Slaughter weight females (kg $animal^{-1}$)[e]	435[c]	413[d]
Reproductive cows	215	92
Mortality repr. cows (% $year^{-1}$)	10	9
Culling repr. cows (% $year^{-1}$)	7	6
Grazing period (days $year^{-1}$)	260	240

[a] System A corresponds to farm type 11111 and system B corresponds to farm type 31041 described by Réseaux d'Elevage Charolais (2012)
[b] Assumed dry matter fraction
[c] Slaughter weight is given as live weight
[d] Slaughter weight is given as carcass weight
[e] Weighted average
DM = dry matter; FM = fresh matter; LW = live weight

Calculation of actual beef production

Beef production was investigated in two different systems, A and B, which are actually present in the Charolais basin of France, and described by Réseaux d'Elevage Charolais (2012). The two systems were selected because of their difference in feeding strategies: the fraction of concentrates in the diet was relatively low in system A and relatively high in system B compared to other beef production systems in the Charolais basin of France. Under actual production, cattle in system A were mainly fed on fresh grass and hay, and supplemented with some concentrates. Concentrates were an external input for system A, as this farming system has no on-farm land to cultivate arable crops (Table 2.3). Concentrates were partly produced on farm in system B, and the remainder was an external input. Off-farm land required for concentrate production, although geographically separated from the beef production system, was regarded as a part of the feed-crop livestock system. The off-farm land area required for concentrate production was hence added up to the on-farm land area required for concentrate production and on-farm pasture area to calculate the total land area required for feed production. Slaughter weights of male and female calves were higher in system A than in system B (Table 2.3). Cattle were housed in stables during winter, and were grazing outside for the other part of the year. Most calves were born in spring, and weaned in autumn (Jarrige, 1989). The grazing period in system A was 20 days longer than in system B (Table 2.3).

The following assumptions were made to calculate actual feed production in systems A and B. Concentrates consumed by cattle consisted of wheat only. Average wheat production in France was 6.9 t DM ha^{-1} $year^{-1}$ in the period 2003-2012 (FAO, 2015). Intake during grazing in the Charolais basin was 4.8 t DM grass ha^{-1} $year^{-1}$ for permanent grassland (Veysset *et al.*, 2005). If permanent grassland was cut once for hay production, hay production was 4.1 t DM ha^{-1} $year^{-1}$ for system A and 4.4 t DM ha^{-1} $year^{-1}$ for system B (Table 2.3), and intake during grazing after hay production was 1.9 t DM grass ha^{-1} $year^{-1}$ (Veysset *et al.*, 2005). Actual grass production in systems A and B was similar, although hay production in system A was greater than in system B (Table 2.3).

Grass intake at farm level was calculated from the area under permanent grassland, the area under one-cut-hay, and the corresponding grass DM intake per ha per year. Losses during hay making were assumed to be 20% of DM. Hay intake was calculated from the area under one-cut-hay and hay DM production per ha per year, corrected for DM losses during hay making. Concentrates were assumed to consist of wheat with a DM fraction of 0.85. The land area required for concentrate production was calculated as concentrate DM intake divided by wheat DM production per ha. DM losses of hay and concentrates during feeding were neglected. Total DM intake was the sum of grass, hay, and concentrate intakes. Land area required for feed production was the sum of the grassland area (Table 2.3) and area for concentrate production.

Live weight production in systems A and B was adopted from Réseaux d'Elevage Charolais (2012) (Table 2.3). Carcass fraction and beef fraction in the carcass (Table 2.1) were assumed to be similar under actual production and potential production. Beef production was calculated as live weight production multiplied by the carcass fraction and the beef fraction in the carcass. Actual FE was calculated as beef production divided by DM intake. Actual production of the feed-crop livestock system was calculated as beef production divided by the land area required for feed crops. Yield gaps for cattle, feed crops, and the feed-crop livestock system were calculated as potential minus actual production (Van Ittersum *et al.*, 2013). The relative yield gap was computed as the yield gap divided by potential production.

2.3 Results

When male calves were slaughtered at a weight of 925 kg TBW, FE was highest at herd level. Potential beef production per herd unit was 827 kg (Table 2.4). State-based potential beef production was similar for systems A and B. Input-based potential beef production was approximately similar for systems A and B (Table 2.5).

Table 2.4 Age, TBW, and beef production at slaughter, and average total body weight, and average metabolic body weight of Charolais cattle under potential production.

	Number of animals	Age at slaughter (years)	TBW at slaughter (kg)	Beef at slaughter (kg)	TBW_{avg} (kg)	$EBW^{0.75}{}_{avg}$ ($kg^{0.75}$)
Cow	1.0	3.9[a]	908	410	638	114
Male calf[b]	1.0	1.5	925	417	520	97
Livestock cycle	2.0	5.5	1833	827	604[c]	109

[a] Slaughter age is lower than the maximum of 9.9 years, due to culling
[b] On average one male calf per herd unit, excluding replacement calves
[c] Weighted average cow and male calf based on slaughter age
$EBW^{0.75}{}_{avg}$ = average metabolic body weight; TBW_{avg} = average total body weight

Table 2.5 Potential and actual beef production of Charolais beef cattle in France. Production is expressed state-based and input-based.

Expression	Production level	Expressed per	System A	System B	Unit
State-based[a]	Potential livestock	animal	152	152	kg beef animal^{-1} year^{-1}
	Potential livestock	kg TBW	251	251	g beef kg TBW^{-1} year^{-1}
	Potential livestock	kg $EBW^{0.75}$	1389	1389	g beef kg $EBW^{-0.75}$ year^{-1}
Input-based[a]	Potential livestock	kg DM intake	54.5	54.8	g beef kg^{-1} DM feed
	Potential feed crop	hectare	11.6	11.6	t DM ha^{-1} year^{-1}
	Potential feed-crop livestock	hectare	631	634	kg beef ha^{-1} year^{-1}
	Actual livestock	kg DM intake	24.9	31.2	g beef kg^{-1} DM feed
	Actual feed crop	hectare	5.33	5.76	t DM ha^{-1} year^{-1}
	Actual feed-crop livestock	hectare	133	180	kg beef ha^{-1} year^{-1}

[a] For explanation of state-based and input-based expression of production, see section 2.1.3.
$EBW^{0.75}$ = metabolic body weight; TBW = total body weight

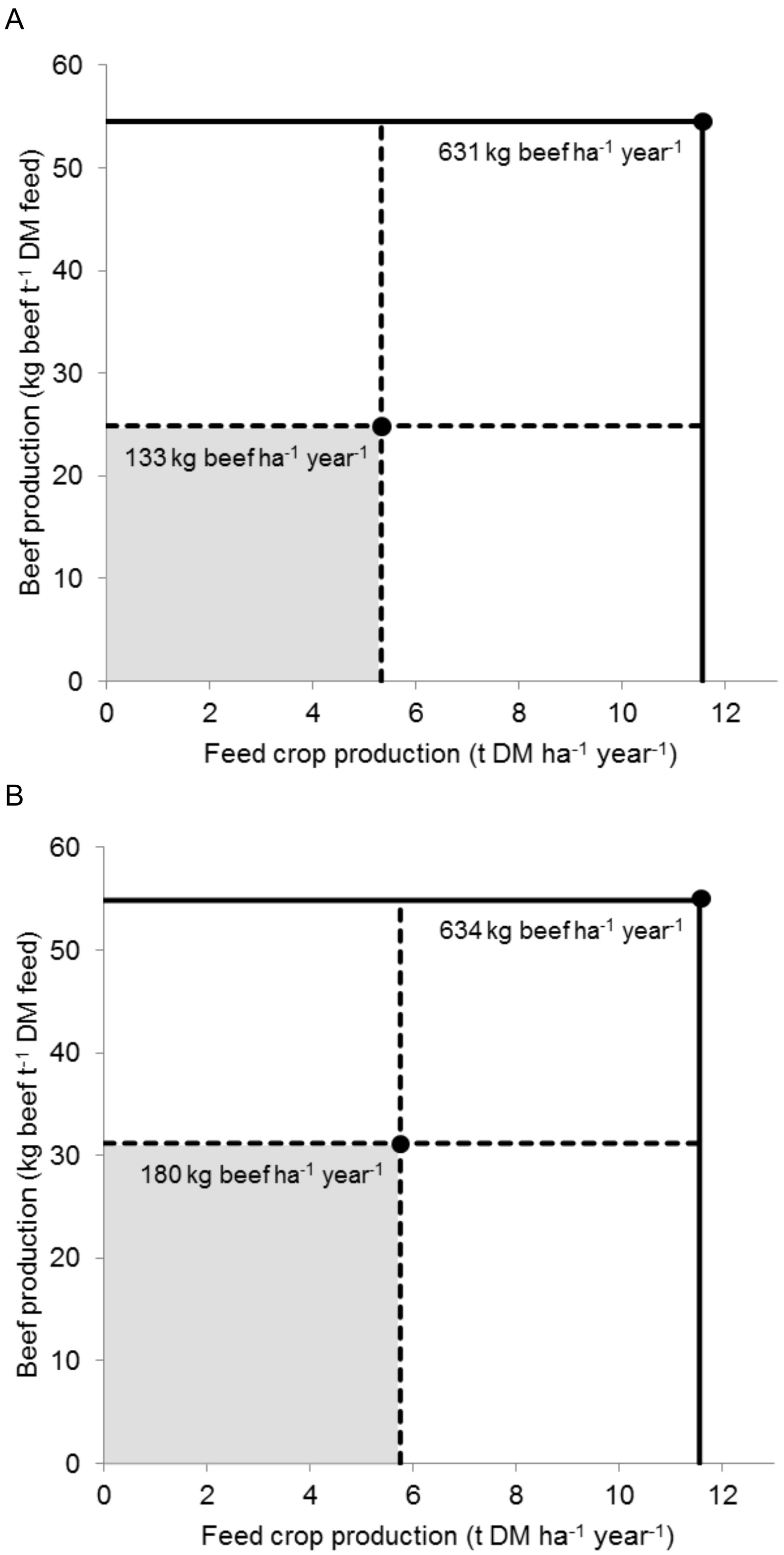

Figure 2.3 Potential and actual production in system A (left) and B (right). Dashed lines indicate actual feed crop and livestock production. Solid lines indicate potential feed crop and livestock production. The grey area enclosed by dashed lines indicates actual production of the feed-crop livestock system; the area enclosed by solid lines indicates potential production of the feed-crop livestock system. DM = dry matter.

Table 2.6 Relative yield gaps (as % of potential production) for livestock production, feed crop production, and production of feed crops and livestock in systems A and B, expressed on a dry matter (DM) basis and a metabolisable energy (ME) basis.

Expression yield gap	DM basis		ME basis	
System	A	B	A	B
Livestock (%)	54.4	43.1	45.2	34.6
Feed crop (%)	53.9	50.2	61.6	56.7
Feed-crop livestock (%)	79.0	71.7	79.0	71.7

Potential production of feed (65% wheat; 35% hay) was 11.6 t DM ha^{-1} $year^{-1}$ in France, requiring 77% of the land area for wheat, and 23% for hay. Actual feed production in system A was lower than in system B (Table 2.5). Production of feed-crop livestock systems was 631 kg beef ha^{-1} $year^{-1}$ for system A and 634 kg beef ha^{-1} $year^{-1}$ for system B under potential production (Table 2.5, Fig. 2.3). Actual beef production in system A was 133 kg beef ha^{-1} $year^{-1}$ and 180 kg beef ha^{-1} $year^{-1}$ in system B (Table 2.5, Fig. 2.3). Actual livestock production in system A was 46% of potential production, implying a relative yield gap of 54%. The relative yield gap in system B was 43% of potential production. The relative yield gap for feed crops was 54% in system A and 50% in system B (Table 2.6). The relative yield gap was 79% in system A and 72% in system B (Table 2.6). Expressed in land use, this corresponded to an actual land use of 75 m^2 year kg^{-1} beef in system A and 56 m^2 year kg^{-1} beef in system B, compared to a potential land use of 16 m^2 year kg^{-1} beef in both systems.

It should be noted that the proportion of wheat (65%) in the feed under potential production was higher than under actual production in system A (4.8%) and system B (18.3%). The ME content of feed under potential production was 20.2% higher than the ME content of feed under actual production in system A, and 15.0% higher than in system B. Expressing feed production and intake on an ME basis instead of a DM basis decreased the relative yield gap for livestock and increased the relative yield gap for feed crops. The relative yield gap for feed-crop livestock systems was not different on an ME or DM basis (Table 2.6).

2.4 Discussion

2.4.1 Application of production ecological concepts to livestock production

We applied theoretical concepts from crop production to livestock production and defined these concepts in more detail than previously done, especially with regard to housing, feeding, slaughter age, and culling. In addition, we explored ways to express production of livestock systems and feed-crop livestock systems. This resulted in a framework that was used to quantify production levels of livestock systems and feed-crop livestock systems. Subsequently, this framework was illustrated for beef production systems in France.

The framework presented in this paper was illustrated for beef production, where most of the production comes from the calves, but we assume this approach can be applied to all livestock species kept for meat production. There is also scope to apply the framework to animals kept for milk production. Animals producing milk are reproductive animals, and their offspring is not the main product, but may be used for replacement or other purposes. Instead of having a fixed (NE requirement for) milk production, as in the present case (Table 2.2), milk production of dairy cows should be variable, and influenced by growth defining, limiting, and reducing factors. Application of the framework to livestock species producing multiple products, however, is more complex. In addition to beef, cattle produce milk, hides, and manure, which is used as fuel or fertilizer in tropical areas. Moreover, cattle supply services, such as transportation and draught power. Some of those products and services are interchangeable (*e.g.* draught power and beef production), which complicates determination of a potential or limited production level based on biophysical considerations.

In our example, cattle under potential production were fed exclusively wheat (65%) and hay (35%), while simultaneously NE for physical activity was required during the grazing period. Both feeds can be fed year-round in a stable without NE requirements for grazing. The climate, although neglected in this paper, is partly an indoor climate, and partly an outdoor climate in the French beef production systems. We have chosen, therefore, to calculate NE for physical activity under potential production for the period cattle were exposed to outdoor climate conditions. We have chosen a diet consisting of wheat and hay under potential production, which is able to satisfy the nutritional requirements of beef cattle. Nutritional requirements for maintenance, growth, gestation, and lactation are variable over the lifetime of an animal, implying that different diets may be optimal in different life stages. Adaptation of diets may further reduce the land use for beef production, but was not explored in this paper. The beef production systems in the example included reproductive cattle. Livestock reproduction and production can occur in different systems too, for example, in egg production (Dekker *et al.*, 2011), broiler production (Leinonen *et al.*, 2012, Leinonen *et al.*, 2014), and in beef production (Ogino *et al.*, 2007, Beauchemin *et al.*, 2010, Pelletier *et al.*, 2010). Yet, we propose to account for reproductive animals when assessing production levels if the proportion of feed intake of reproductive animals in a herd unit is a significant part of total intake (*e.g.* in beef cattle).

Animal welfare was not taken into account under potential and actual production in the example. Principles of good animal welfare are included in the ‘five freedoms’: (1) freedom from thirst, hunger, and malnutrition, (2) freedom from discomfort, (3) freedom from pain, injury, and disease, (4) freedom to express normal behaviour, and (5) freedom from fear and distress (Webster, 2001). Mitigation of feed deficiencies, diseases, and stress might improve both animal production and welfare. Other strategies might increase animal production but reduce animal welfare. Location-specific synergies and trade-offs between animal production and welfare (Garnett *et al.*, 2013) have to be addressed in a post-model analysis.

2.4.2 Potential and actual beef production for two Charolais beef production systems

State-based potential production per animal was 152 kg beef animal^{-1} year^{-1} in systems A and B (Table 2.5), which is equivalent to 0.42 kg beef animal^{-1} day^{-1}. This corresponds to a live weight gain (LWG) of 0.92 kg animal^{-1} day^{-1}. It should be noted that this is an average LWG at herd level, which includes cows. Average LWG of male calves was 1.56 kg animal^{-1} day^{-1} from birth to slaughter at 1.5 years of age. Charolais male calves, fed *ad libitum* on a high concentrate diet, were reported to have an average LWG of 1.38 kg animal^{-1} day^{-1} between five months and 1.5 years of age (Pfuhl *et al.*, 2007), which is close to the calculated LWG under potential production. Because the diet was fed *ad libitum* and had a high ME and protein content, cattle in the experiment of Pfuhl *et al.* (2007) may have resembled potential production.

Because the grazing period in system A is twenty days longer than in system B, slightly more NE for physical activity is required in system A. As a result, FE under potential production is not exactly the same in systems A and B (Table 2.5). The additional NE for physical activity in system A also results in a slightly lower potential production compared to system B (Table 2.5), but the difference is very small.

Maximum FE reported in European and North American beef production systems is little below 100 g LW kg^{-1} DM at herd level (Smil, 2002b). This corresponds to a FE of 45 g beef kg^{-1} DM, assuming a carcass fraction of 55% and a beef fraction in the carcass of 82%. The maximum FE actually obtained in Europe and North America is less than the FE under potential production (54-55 g beef kg^{-1} DM), and much higher than the FE under actual production in systems A (25 g beef kg^{-1} DM) and B (31 g beef kg^{-1} DM).

For feed-crop livestock systems, relative yield gaps were 79% in system A and 72% in system B (Table 2.6), which implies that there is substantial scope to increase production, from a bio-physical perspective. Average crop yields tend to plateau at 75%-85% of potential or water-limited production, because increasing production further is generally not economically profitable or practically feasible (*i.e.* the exploitable yield gap) (Van Ittersum *et al.*, 2013). It is interesting to note that maximum FE under actual production in Europe and North America (45 g beef kg^{-1} DM) is also approximately 80% of FE under potential production.

Assuming that production in both the crop *and* livestock sub-system can be increased up to 80% of potential production, the plateau for production of feed-crop livestock systems would be 64% of potential production, which corresponds to a relative yield gap of 36%. The exploitable yield gap at feed-crop livestock system level thus would be 43% of potential production for system A and 36% for system B. The plateau might be reached at a lower percentage in systems A and B for economic reasons, as additional premiums prevail to extensive, grass-based beef farms in France (Veysset *et al.*, 2005). Yield gap mitigation might, therefore, not be economically profitable in the two French beef production systems. Yield gaps in this study were calculated from the difference between potential and actual production. Hence, yield gaps will decrease if limited crop and livestock production are set as benchmarks for actual production.

Expressing livestock production on an ME basis corrects for differences in ME content of feeds under potential and actual production. Expressing livestock production on an ME basis decreased yield gaps compared to production on a DM basis (Table 2.6), as ME content of feed under actual production was lower than under potential production. For the same reason, yield gaps for feed crops increased on a ME basis compared to a DM basis (Table 2.6). Production of feed-crop livestock systems is, however, not different on an DM basis and ME basis (Table 2.6), as multiplication of feed crop and livestock production cancels out units of feed mass (Eq. 1) and ME.

De Vries and de Boer (2010) reported an actual land use of 49 m^2 year kg^{-1} beef for suckler systems, using economic allocation of farm outputs. Nguyen *et al.* (2010) reported 43 m^2 year kg^{-1} beef for suckler systems in the European Union. Land use under actual beef production in systems A and B (75 and 56 m^2 year kg^{-1} beef $year^{-1}$) is thus higher than land use reported in De Vries and de Boer (2010) and Nguyen *et al.* (2010). Differences may be explained by different production levels of feed crops, feeding strategies, and herd management. In addition, cropland is partly allocated to by-products in the studies of De Vries and de Boer (2010) and Nguyen *et al.* (2010), while all land was allocated to feed production in this paper.

2.4.3 Modelling potential and limited livestock production

Quantification of potential and limited livestock production may be facilitated by the use of models. Such models need to be dynamic to simulate a full herd unit. Ideally, livestock models are generic and applicable to a wide range of livestock species, breeds, climates, housing types, and diets, and require a limited number of input parameters. Empirical models, in contrast to mechanistic models, are not generic, and can be applied only under conditions similar to those the model was calibrated for. Quantification of potential and limited livestock production hence requires mechanistic models that integrate information on genotype, climate, feed quality, and feed quantity with sufficient level of detail.

There are many dynamic livestock models available to simulate growth and production of chicken (King, 2001), pigs (Whittemore and Fawcett, 1976, Van Milgen *et al.*, 2008), and cattle (Hoch and Agabriel, 2004, Tedeschi *et al.*, 2004, Bryant and Snow, 2008). These models contain information on the effects of defining and limiting growth factors on livestock growth and production. To our knowledge, the current livestock models either do not simulate the full life cycle of animals, or lack specific growth factors, or include growth factors empirically. Hence, development of mechanistic, dynamic livestock models, suited for quantification of potential and limited production levels, can be based on the available models, but requires substantial additional steps.

2.4.4 Applications and future research

Feed crop and livestock growth models, based on production ecological concepts, can be combined (Eq. 1). Land use for livestock products under potential and limited production can subsequently be assessed, and compared to the actual land use for beef, pork, chicken, milk and egg production (De Vries and De Boer, 2010). Expressing production of feed-crop livestock systems in product per unit land area, and the reciprocal, land area per unit product, is already well-established in life cycle assessment (De Vries and De Boer, 2010). Expressing both food crop and livestock production (from feed-crop livestock systems) per unit land area provides scope to calculate the number of people that can be nourished from one hectare with a specific diet, and enables to assess the effect of dietary changes (Cassidy *et al.*, 2013).

Agricultural systems are characterised by input-output combinations (Van Ittersum and Rabbinge, 1997). Models based on production ecological concepts allow assessment of alternative production possibilities, their corresponding input-output combinations, and resource use efficiency. Exploring alternatives contributes to optimization of agricultural systems design and indicates which corresponding management decisions could be taken (Van de Ven *et al.*, 2003). Targets for livestock production levels can be defined and a so called target oriented approach can be used. This enables to investigate what level of inputs is necessary to realise target production levels (Van Ittersum and Rabbinge, 1997).

Given the increasing demand for food, caused by a growing population and economic development, increasing agricultural production from existing arable land is one of the strategies to meet future food demand and to contribute to food security (Tilman *et al.*, 2011). To prioritize agricultural development and interventions, regions with a high yield gap can be identified by applying production ecological concepts (Van Ittersum *et al.*, 2013). Besides contributing to yield gap mitigation, production ecological concepts can be used to explore resource use efficiency of agricultural inputs. Application of production ecological concepts might, therefore, reveal options to increase production of livestock systems and feed-crop livestock systems in a sustainable way.

2.5 Conclusions

This paper presents a framework to quantify potential production in livestock systems, in analogy to the production ecological concepts for cropping systems. Combining production ecological concepts in both cropping and livestock systems provides scope to assess production levels of feed-crop livestock systems per unit of land area. The framework was illustrated for potential and actual beef production from Charolais cattle in two farming systems (A and B) in France, which have different feeding strategies under actual production. Results showed that yield gaps are larger in system A (low concentrate diet) than in system B (high concentrate diet) for livestock production and production at feed-crop livestock system level. The yield gap was 79% of potential production per unit area in system A and 72% in system B, implying scope to increase production, from a bio-physical perspective. The framework has thus shown its effectiveness in assessing potential and actual production of different livestock production systems, and thus their yield gaps. Moreover, the framework may enable development of mechanistic livestock growth models that integrate effects of genotype, climate, feed quality, and feed quantity at a sufficient level of detail. Applying theoretical concepts of production ecology to livestock provides a benchmarking method to assess and quantify yield gaps in livestock production. Subsequent yield gap analysis can identify biophysical constraints to production, and contribute to further optimization in the design of agricultural systems.

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Chapter 3

LiGAPS-Beef, a mechanistic model to explore potential and feed-limited beef production 1. Model description and illustration

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Abstract

The expected increase in global demand for livestock products calls for insight into the potential to increase actual production levels across the world. This insight can be obtained by using theoretical concepts of production ecology. These concepts distinguish three production levels for livestock: potential (*i.e.* theoretical maximum) production, which is defined by genotype and climate only; limited production, which is defined by feed quantity and quality; and actual production. The objective of this paper is to present a mechanistic, dynamic model allowing simulation of potential and limited production for beef cattle. This model, named LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle), integrates sub-models regarding thermoregulation, feed digestion, and energy and protein utilisation in a novel way. Growth of beef cattle is simulated at animal and herd level, based on energy and protein flows. The model is designed to be generically applicable to beef production systems across the world. Main model inputs are: breed-specific parameters, weather data, information about housing, and data regarding feed quality and quantity. Main model outputs are: average daily weight gain, feed intake, and feed efficiency at animal and herd level. Measured heat production in experiments and simulated heat production by the thermoregulation sub-model were generally in agreement. Measured metabolisable energy (ME) contents corresponded to simulated ME contents by the feed digestion sub-model (R^2-adj. = 0.86 and 0.91). Model use was illustrated for beef production with Charolais and Brahman × Shorthorn cattle in France and Australia, both at animal and at herd level. Simulations showed that feed efficiency (FE) of Charolais cattle at herd level, under potential and feed-limited production (*ad libitum,* grass-based diet), was higher in France (74 and 49 g beef kg^{-1} DM) than in Australia (52 and 0 g beef kg^{-1} DM). Brahman × Shorthorn cattle had a slightly higher FE in Australia than in France under potential production (67 and 64 g beef kg^{-1} DM), whereas this was reversed for feed-limited production (41 and 46 beef kg^{-1} DM). These results indicate that the FE is highest for breeds adapted to local climatic conditions. Further model evaluation is required to assess whether LiGAPS-Beef estimates cattle growth accurately, which is reported in a companion paper (Van der Linden *et al.*, 2017b).

Implications

The model LiGAPS-Beef presented in this paper simulates potential (*i.e.* the theoretical maximum) and feed-limited production of beef cattle. The difference between potential or feed-limited production and actual production on farms is defined as the yield gap. LiGAPS-Beef allows to quantify yield gaps for different beef production systems across the globe, and identifies biophysical constraints for beef cattle under potential and feed-limited production. Yield gap analysis, including identification of constraints, can provide insights in options to increase beef production and resource use efficiency in a sustainable way.

3.1 Introduction

Global demand for agricultural products is expected to increase by 60% between 2007 and 2050. In the same period, this expected increase is even larger for the animal-source foods meat (+76%), milk (+62%), and eggs (+65%), whereas the projected expansion of global arable land is only 7% (Alexandratos and Bruinsma, 2012). Meeting future demand for food, therefore, requires an increase in agricultural production per unit of land (Van Ittersum *et al.*, 2013), even if food waste is reduced and more plant-based diets are consumed in developed countries. Potential production of both crops and livestock is obtained under ideal management, and is determined by climate and by crop or livestock genotype only. Production is referred to as limited production if water or nutrient availability affects crop growth, and if drinking water, feed quality, or quantity affect livestock growth (Van de Ven *et al.*, 2003, Van Ittersum *et al.*, 2013, Van der Linden *et al.*, 2015). Actual crop and livestock production is the production realised in practice. Next to the limiting factors for growth, actual crop production can be affected by pests, diseases, and weeds, while actual livestock production can be affected by diseases and stress (Van Ittersum and Rabbinge, 1997, Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015). Differences between potential or limited production, and actual production are defined as yield gaps. Quantification of yield gaps enables to assess how much agricultural production can be increased from a bio-physical perspective. Identifying regions with a large exploitable yield gap is crucial to increase future food production (Van Ittersum *et al.*, 2013).

Potential production can be estimated by means of experiments and by assessing maximum farmer's yields. This, however, requires ideal management conditions, which is hard to realise in practice. Potential production, therefore, may be underestimated under experimental and farm conditions (Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013). In addition, experiments have to be replicated in time and space for a solid estimation of potential and limited production (Cassman *et al.*, 2003), which is costly and laborious. Mechanistic models simulating crop growth provide an alternative means to estimate potential and limited production under different environmental conditions (Lobell *et al.*, 2009). Such models simulate interactions among crop genotype, climate, water, and nutrients (Bouman *et al.*, 1996, Jones *et al.*, 2003, Keating *et al.*, 2003). Crop growth models have contributed to identify causes of yield gaps, to increase crop production in various regions, and to synthesize theoretical and experimental knowledge.

Mechanistic models simulating livestock production are available for cattle (Hoch and Agabriel, 2004, Tedeschi *et al.*, 2004, Bryant *et al.*, 2008, Rufino *et al.*, 2009), for pigs (Whittemore and Fawcett, 1976, Van Milgen *et al.*, 2008) and for chicken (King, 2001). In order to simulate potential and limited livestock production, these mechanistic models should integrate interactions among animal genotype, climate, feed quality and available feed quantity in sufficient detail to ensure applicability under a wide range of agro-ecological conditions. They must then also simulate full life spans of animals.

Few of the livestock models currently available allow the user to specify different genotypes or breeds (Whittemore and Fawcett, 1976, King, 2001, Hoch and Agabriel, 2004). Some models do not include the effect of climate on growth (Hoch and Agabriel, 2004, Van Milgen *et al.*, 2008, Rufino *et al.*, 2009), or climate is included empirically through a lower critical temperature (Whittemore and Fawcett, 1976), a temperature humidity index (Bryant *et al.*, 2008), or an effective temperature index (Tedeschi *et al.*, 2004). A model with empirical components can be applied only to conditions that resemble the experimental conditions the model was calibrated for (Birkett and de Lange, 2001), which limits its applicability. The model of Hoch and Agabriel (2004) uses metabolisable energy (ME) as an input, which does not allow to distinguish between ME deficiencies caused by feed quality and quantity limitation. The model of Bryant *et al.* (2008) applies to dairy cattle, and does not simulate the young stock phase. To our knowledge, therefore, mechanistic livestock models that integrate effects of genotype, climate, feed quality, and feed quantity in sufficient detail are lacking.

Our objective is to present a mechanistic, dynamic model that allows to simulate potential and limited livestock production, analogous to mechanistic models that simulate potential and limited crop production. This livestock simulation model is named LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle). It integrates thermoregulation, feed digestion, and energy and protein utilisation in a novel way, and simulates beef production at animal and herd level. We illustrated our model by simulating potential and feed-limited production of Charolais and Brahman × Shorthorn cattle in France and Australia.

3.2 Model description

3.2.1 Approach, inputs and outputs

LiGAPS-Beef consists of three sub-models, that jointly simulate a bovine animal: a thermoregulation model, a feed digestion model, and an energy and protein utilisation model. The thermoregulation sub-model simulates the heat balance of a bovine animal. The feed digestion sub-model simulates feed intake and feed digestion in the rumen and intestines. The energy and protein utilisation sub-model simulates the partitioning of energy and protein over metabolic processes, such as maintenance, growth, lactation, and gestation. The sub-models on thermoregulation, feed digestion, and energy and protein utilisation are interconnected by flows of energy and protein within an animal (Fig. 3.1). Energy flows distinguished are gross energy (GE), digestible energy (DE), ME, net energy (NE), and heat.

The thermoregulation sub-model requires daily weather data (Supplementary Table S1) and parameters for specific genotypes, or breeds (Supplementary Table S2) and generic parameters (Supplementary Tables S5 and S6) as input. Climate conditions

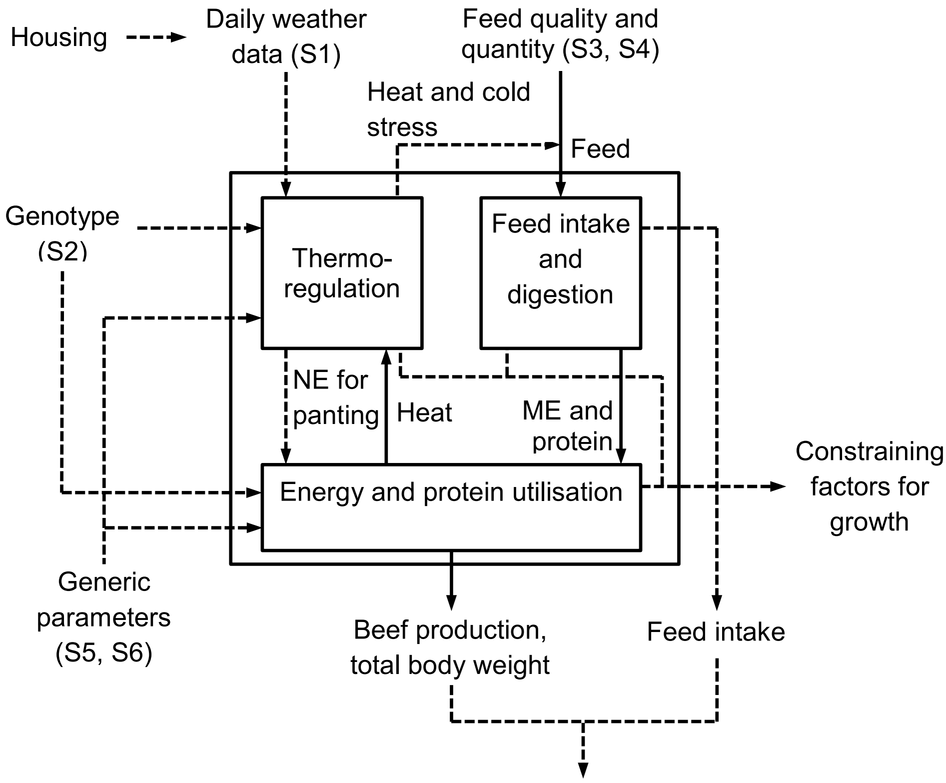

Figure 3.1 Representation of LiGAPS-Beef (Livestock Simulator for Generic analysis of Animal Production Systems – Beef cattle) simulating beef production of a bovine animal, with its three sub-models. Solid arrows indicate flows of material or energy. Dashed arrows indicate a flow of information. Beef production and cumulative feed intake allow to assess feed efficiency. The S followed by a number refers to the table numbers in the Supplementary Information. ME = metabolisable energy; NE = net energy.

around the animal can deviate from outdoor climate conditions if cattle are housed (Fig. 3.1). Output of the thermoregulation sub-model is a heat balance, which affects feed intake and digestion negatively under hot climate conditions, and positively under cold climate conditions (Fig. 3.1). The feed intake and digestion sub-model has feed composition and available feed quantities (Supplementary Tables S3 and S4) as input, and ME and digested protein as outputs. The latter are both inputs for the energy and protein utilisation sub-model, together with breed-specific parameters. The energy and protein utilisation sub-model simulates heat production from metabolic processes, which is an input for the thermoregulation sub-model. The thermoregulation sub-model also simulates energy requirements for panting and shivering, which affect the energy and protein utilisation sub-model (Fig. 3.1). LiGAPS-Beef also uses generic parameters (Supplementary Tables S5 and S6). Main outputs of the full model are feed intake, total body weight (TBW), beef production, feed efficiency (FE), and the most constraining bio-physical factors for growth, which can be related to the genotype, heat stress, cold stress, digestive capacity, energy requirements, and protein requirements. Model outputs are given for each simulated day, and allow to calculate average daily gain, average feed intake, and feed efficiency for a given period of time.

Breed-specific parameters and daily weather data allow to simulate potential production. Addition of feed composition and availability to the breed-specific parameters and weather data allows to simulate feed-limited production. For potential production, the minimum inputs required are (intrapolated) daily weather data, fifteen breed-specific parameters (Table 3.1), a description of the housing system, and the periods animals are housed. Additional data required for feed-limited production are the ME and crude protein (CP) content of feeds and feed quantities available. LiGAPS-Beef is written in the programming language R, version 2.15.3 (RCoreTeam, 2013), and the time step of the model is one day. Animals can be simulated over their whole life span, which can be more than ten years for beef cows.

3.2.2 Thermoregulation sub-model

The thermoregulation sub-model assesses the amount of heat that can be released under warm and cold conditions. Estimates of heat release from the animal are based on thermoregulation models of McGovern and Bruce (2000) and Turnpenny *et al.* (2000a). Inputs are breed-specific parameters, heat production, and daily weather data. Heat production is a result of various metabolic processes calculated in the energy and protein utilisation sub-model. Daily weather data required are average temperature, solar radiation, vapour pressure, wind speed, cloudiness, and rainfall (Supplementary Table S1). Weather data from meteorological stations are assumed to represent outdoor grazing conditions, and indoor climate data are applicable if animals are housed. The output of this sub-model is the heat balance, eventually the

Table 3.1. Minimum breed-specific parameters required for LiGAPS-Beef. Crosses indicate whether parameters are sex-specific.

Parameter	Unit(s)	Male	Female
Fraction *Bos taurus* and *B. indicus* genes		x[a]	x[a]
Coat colour[b]		x[a]	x[a]
Birth weight[c]	kg TBW	x	x
Maximum adult weight[c]	kg TBW	x	x
Gompertz integration constant[c]		x	x
Gompertz rate constant[c]	kg d^{-1}	x	x
Gompertz reduction[c]	kg TBW	x	x
Maximum carcass %		x	x
Minimum % of maximum adult weight for gestation			x

[a] Parameters for male and female animals are the same
[b] Coat colour enables to calculate reflectance of solar radiation
[c] Gompertz curves: $TBW = (A + (B – A + E) \times e^{(-C \times e^{(-D \times t)})}) – E$, where A = birth weight; B = maximum adult weight; C = integration constant; D = rate constant; t is time in days, and E is a reduction factor.
TBW = total body weight

requirements for additional energy under cold conditions to maintain body temperature, and the required reduction in heat production under warm conditions.

The thermoregulation model represents an animal as a cylinder consisting of three layers: body core, skin, and coat (Fig. 3.2 A). Cattle are isothermal animals with a body temperature of approximately 39°C. Heat produced in the body core is released through respiration, or passed on to the skin. Heat from the skin is released through sweating, or passed on to the coat. Heat from the coat is released through long wave radiation and convection, and solar radiation is partly reflected (Fig. 3.2 A). To maintain body temperature, the sum of heat production and heat load via solar radiation is equal to the sum of heat release through respiration, sweating, reflection of solar radiation, long wave radiation, and convection, both under hot and cold conditions (McGovern and Bruce, 2000, Turnpenny *et al.*, 2000a) (Fig. 3.2 A).

Cattle can regulate heat release by three mechanisms: adjustment of the respiration rate; vasoconstriction and vasodilatation; and adjustment of the sweating rate. Minimum heat release refers to a minimum respiration rate, maximum vasoconstriction, and minimum sweating, whereas maximum heat release refers to the opposites. Heat production is a balancing variable in the thermoregulation sub-model to maintain body temperature. If heat production is lower than the minimum heat release, additional energy is required. If the genotype, feed quality, and feed quantity allow heat production from metabolic processes to be higher than the maximum heat release under the prevailing weather conditions, animals must reduce feed intake to decrease heat production, and to equal heat production and release (Fig. 3.1). If heat production is between minimum and maximum heat release, the animal is in its thermoneutral zone.

3.2.3 Feed intake and digestion sub-model

The feed intake and digestion sub-model simulates feed intake, digestion of the ingested feed, and the energy and protein supply from digestion. The feed intake and digestion model is based on a rumen model of Chilibroste *et al.* (1997) and the fill unit system developed by the Institut National de la Recherche Agronomique (INRA) (Jarrige *et al.*, 1986). Input for the feed intake and digestion sub-model are feed types, feed composition, fill units, available feed quantities, and energy and protein requirements as calculated by the energy and protein utilisation sub-model. Both ME and digestible CP are outputs of the feed intake and digestion sub-model (Fig. 3.1). Feed intake cannot exceed maximum digestion capacity of an animal, which is proportional to its metabolic body weight. The fill unit system developed by INRA is used to calculate maximum rumen digestion capacity and rumen fill, which is feed intake expressed in fill units (FU) divided by the maximum FU intake, which is approximately 0.100 FU $kg^{-0.75}$ total body weight (TBW) for pregnant beef cows kept in stables. One kg dry matter (DM) of a reference pasture grass has a FU of one, whereas other feed types have a FU relative to this reference pasture (Jarrige *et al.*, 1986). To compensate for grazing, maximum feed intake was increased from 0.100 to 0.123 FU $kg^{-0.75}$ TBW. Feed intake is the minimum of feed intake to meet energy and protein requirements, feed intake corresponding to the maximum rumen digestion capacity, and feed availability.

Following the rumen model of Chilibroste *et al.* (1997), feed is divided in seven constituents (Fig 3.2 B). Feed digestion occurs in the rumen, and in the small and large intestines. Feed digestion and passage to the small intestines are described by first-order reactions. All feed constituents are digested in the rumen, except for undegradable neutral detergent fiber (UNDF) and undegradable crude protein (UCP), which fully end up in the faeces (Fig. 3.2 B). Soluble, non-structural carbohydrates (SNSC) and soluble crude protein (SCP) are fully digested in the rumen. Insoluble non-structural carbohydrates (INSC), degradable neutral detergent fibre (DNDF), and degradable crude protein (DCP) are partly digested in the rumen, and partly pass to the intestines for further digestion. Digestion rates are different among feed constituents, whereas passage rates are the same for all seven feed constituents in a feed type (Chilibroste *et al.*, 1997). Passage rates are increasing with increasing rumen fill. Feed DM digested corresponds to DE, while feed DM not digested ends up in the faeces (Fig. 3.2 B). Digested carbohydrates have a GE content of 17.4 MJ per kg DM, and CP a GE content of 23.8 MJ per kg DM. Total DE equals DE in digested carbohydrates and DE in CP. We assumed that ME is 0.82 times DE for cattle (NRC, 2000).

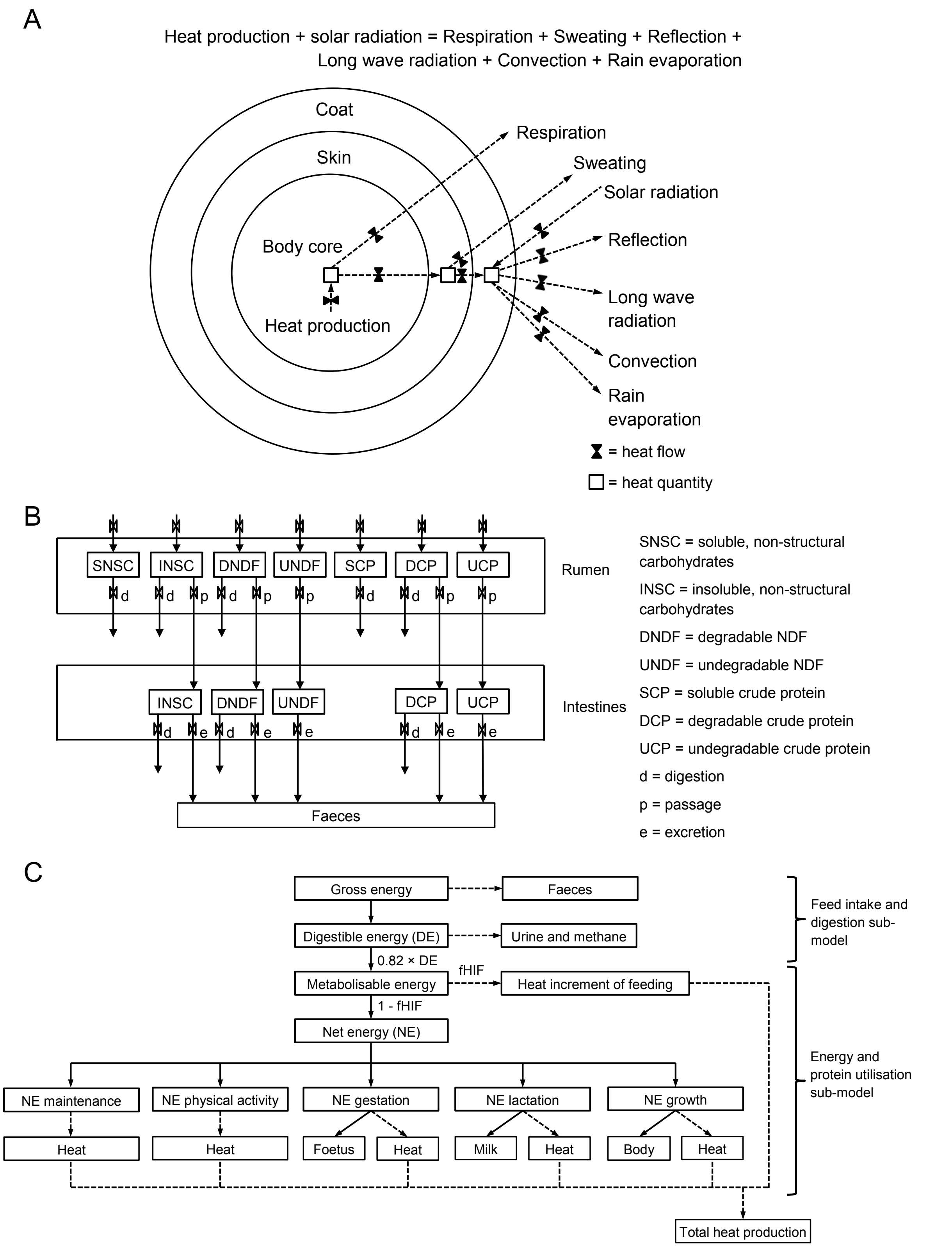

Figure 3.2 (A) Schematic overview of heat flows in the thermoregulation sub-model. (B) Digestion of feed constituents in the rumen and intestines in the feed intake and digestion sub-model, partly adapted from Chilibroste *et al.* (1997). (C) Schematic overview of energy flows in the energy and protein utilisation sub-model. fHIF = fraction heat increment of feeding. Adapted from NRC (1981).

3.2.4 Energy and protein utilisation sub-model

The amount of NE available to the animal equals ME minus heat increment of feeding (Supplementary Figure S1). The latter includes heat production from chewing, rumination, digestion, and absorption of feed, as well as heat production from rumen fermentation. The total digestibility of the five digestible feed components determines the heat increment of feeding. Heat increment of feeding is assumed to be a fraction of ME (Baldwin *et al.*, 1980). This fraction depends on the feed type (Chandler, 1994). Protein requirements for chewing, rumination, digestion, and absorption of feed are assumed to be proportional to the heat increment of feeding. Both NE and protein are partitioned over various metabolic processes, including maintenance, physical activity, gestation, milk production, and growth (Fig. 3.2 C, Supplementary Figure S2, S4, and S5). The NE for maintenance and physical activity is fully converted into heat, while NE for growth, gestation, and lactation is assumed to be converted partly into heat and partly into animal tissue or milk. The sum of heat increment of feeding and heat production from NE equals the total heat production (Fig. 3.2 C).

Net energy for maintenance is equal to heat production during fasting. Net energy for physical activity (*i.e.* grazing and walking) is required for cattle under outdoor conditions, whereas it is assumed to be negligible for cattle in feedlots and stables. Net energy and protein requirements for maintenance are a function of metabolic body weight. Requirements for physical activity can be a function of metabolic body weight ($kg^{0.75}$) or TBW in LiGAPS-Beef. Partitioning of protein is simulated similarly to NE partitioning. Protein requirement was assumed to be 0.48 g per MJ NE (CSIRO, 2007) for maintenance, physical activity, and also per MJ heat increment of feeding. Net energy (Fox *et al.*, 1988) and protein requirements for gestation (CSIRO, 2007) and for lactation (Jenkins and Ferrell, 1992) are breed and sex specific. The genetic potential for animal weights over time is described by breed and sex specific Gompertz curves, if other factors than the genotype are not affecting growth (*i.e.* if sufficient NE and protein are available for growth). NE requirement for growth is calculated from weight increase of body tissues. Body tissues are split up, as lack of feed influences the growth of tissues differently, in non-carcass tissue, and carcass tissues, which consist of bone, muscle, and fat (intramuscular fat, intermuscular fat and subcutaneous fat). Beef is defined as deboned carcass. Each body tissue consists of protein, lipid, ash, and water, from which only protein (44 kJ g^{-1}) and lipid (54 kJ g^{-1}) accretion require NE. Daily NE requirement for growth is subsequently calculated from daily protein and lipid accretion in all body tissues multiplied with the energy efficiency for protein and lipid accretion. Daily protein requirement for growth is the sum of protein accreted daily in each of the body tissues, multiplied with the efficiency for protein accretion. Rumen contents are a fixed fraction of the TBW, and do not require NE and protein for growth.

Net energy and protein for growth are balancing variables, while other metabolic processes are maintained. If heat production from metabolic processes and heat load from solar radiation is below the minimum heat release, additional NE is required (Fig. 3.1), which can reduce NE and protein availability for growth. If heat production is above the maximum heat release, feed intake is reduced, and hence NE and protein availability for growth. The same holds for conditions where the maximum digestion capacity is reached, or where the available feed quantity is not sufficient to meet NE and CP requirements. Body tissues are not affected equally by sub-optimal NE supply (Hornick *et al.*, 2000). Smallest reductions in growth occur in the non-carcass tissue, while the fat tissue in the carcass is affected most. Compensatory growth can occur after a period of growth retardation (Hornick *et al.*, 2000) under favourable climatic conditions and adequate NE and protein availability.

3.2.5 Upscaling from animal to herd level

The combined sub-models described in the previous three sections simulate the growth of one animal. Upscaling from the animal level allows to simulate beef production for full beef production systems, with a herd that consists of multiple individuals. A herd can be subdivided in a productive herd (calves raised for beef) and a reproductive herd. The reproductive herd generally accounts for approximately 70% of the feed intake, but its contribution to beef production is much lower (De Vries *et al.*, 2015). Hence, simulating potential and feed-limited production for beef production systems, and assessing their yield gaps, requires to account for both the productive and reproductive herd. Heifers replace cows at the end of their lifetime in the reproductive herd. The number of replacement heifers equals the number of culled cows in a reproductive herd with a fixed number of heads. The smallest possible herd includes one reproductive cow. Reproductive bulls are assumed to be a negligible fraction of the smallest possible herd, as the ratio cows to bulls is generally high. Replacement offspring required in the smallest possible herd equals consecutively one heifer that can generate offspring after the cow is slaughtered at the end of her lifetime. Hence, the smallest possible herd consists of one cow and its offspring, minus a replacement heifer. This smallest possible herd is defined as a herd unit. A herd in a beef production system consists of multiple herd units (Van der Linden *et al.*, 2015). LiGAPS-Beef sums inputs and outputs for all animals in a herd unit to assess potential and limited production at herd level. Culling rates of reproductive cows and slaughter weights of calves not used for replacement can be specified by the model user.

Potential production at herd level is achieved if the genotype and climate affect growth of beef cattle only (Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015). Feed is provided *ad libitum* under potential production, and feed quality is sufficient to meet NE and protein requirements. In addition, the diet should contain sufficient fibrous material. Feed quality is determined also by its heat increment of feeding. A low heat increment of feeding is advantageous under warm and hot conditions to prevent heat stress, whereas a high heat increment of feeding is advantageous under cold conditions. Finding the ideal feed composition for each animal and each day, however, is complicated. We propose the diet under potential production is the same for all animals and time periods, contains sufficient fibre, and consists of high-quality feeds. A diet for potential production that is fed *ad libitum* and consists of 65% wheat and 35% high quality hay closely meets these requirements for all beef cattle and situations. The ME content of this diet (11.3 MJ ME kg^{-1} DM) is relatively high and the FU value (0.76 kg^{-1} DM) low. The diet contains sufficient fibre, and is available in many countries worldwide. Such a fixed diet also allows comparison of feed efficiency (FE, beef produced per unit of DM feed intake) among different beef production systems. It should be noted that beef production and FE can be increased further by adapting diets daily to the most constraining factors for growth. Potential production is achieved under management practices (*e.g.* culling) that maximize FE at herd level (Van der Linden *et al.*, 2015). Best management practices are also applied under feed-limited production, which is analogous to limited crop production. Contrary to the diet under potential production, the diet under feed-limited production can differ in feed quality and available feed quantity over time and between locations.

3.3 Evaluation of sub-models

We evaluated the thermoregulation sub-model, and the feed intake and digestion sub-model, independently from other sub-models, by model comparison against experimental data and sensitivity analysis. The experimental data were not used for model calibration (*i.e.* independent data), which is also referred to as model validation. Independent evaluation of the energy and protein utilisation sub-model was not performed in this paper, as it requires a significant amount of detailed inputs of the thermoregulation and feed intake and digestion sub-model. Next, the energy and protein utilisation sub-model is the largest and central one. Evaluation of this sub-model, therefore, is inherently included in an evaluation of the full model reported in the companion paper (Van der Linden *et al.*, 2017b).

3.3.1 Comparison of sub-models against independent data

Thermoregulation sub-model

The thermoregulation model was calibrated by adjusting parameters for respiration and sweating rates to fit to temperature-humidity indices (Supplementary Figure S7). After calibration, simulated heat release was compared with measured heat release from experiments. In experiments, heat release of Aberdeen Angus × Shorthorn steers (323-361 kg TBW) was measured at low temperatures (-1.1-3.1°C), with low (<7 mm) and high coat lengths (>24 mm) (Blaxter and Wainman, 1964). Heat release of Friesian (initial TBW 34.6 kg) and Jersey calves (initial TBW 27.8 kg) was measured at a range of temperatures (3-20°C) and two wind speeds (0.22 and 1.56

ms^{-1}) (Holmes and McLean, 1975). Coat length of the calves was not measured, but assumed to be fixed at 25 mm in model simulations. Steers and calves were expected to be below the thermo-neutral zone (TNZ) in most of these experimental treatments, and hence their measured heat release should correspond to minimum heat release simulated with the thermoregulation model.

Measured heat release and minimum heat release simulated with the thermoregulation sub-model were in agreement for steers with high coat lengths, whereas measured heat release was underestimated for steers with low coat lengths fed at sub-maintenance level (Fig. 3.3). A reduction in coat length by shaving might have resulted in a higher conductivity of the remaining coat structure. Skin temperatures of the steers were assessed reasonably by the thermoregulation sub-model (Supplementary Figure S8). Measured heat release and minimum heat release of Friesian and Jersey calves corresponded to each other, except for treatments at 20°C and at 12°C with a wind speed of 0.22 ms^{-1}. An explanation for these deviations is that calves might have been in the TNZ instead of below. The milk-fed calves had a ME intake equivalent to 125 Wm^{-2}, and a heat production of

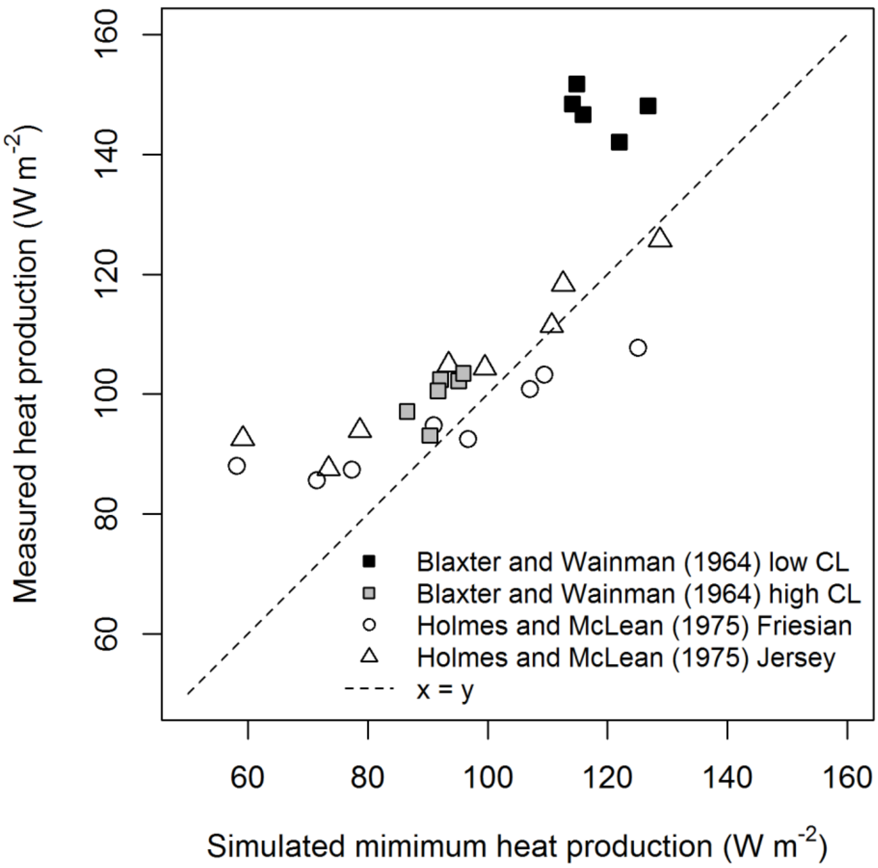

Figure 3.3 Simulated heat production and measured heat production for experiments with steers of Blaxter and Wainman (1964) and with Friesian and Jersey calves of Holmes and McLean (1975). CL = coat length

approximately 95 Wm^{-2}, based on their growth rates and an assumed energy retention of 16 MJ kg^{-1} TBW. As heat production equals heat release, a measured heat release below 95 Wm^{-2} is not possible. Hence, the expected heat release in the TNZ is 95 Wm^{-2}, which is higher than the minimum heat release simulated with the thermoregulation sub-model. Overall, the thermoregulation sub-model estimates minimum heat release reasonably.

Feed intake and digestion sub-model

We used the seven feed constituents and their digestion and passage rates (Supplementary Table S3) to calibrate the feed intake and digestion sub-model. Feed intake (kg DM day^{-1}) was not compared with independent measured data, as feed intake is affected by the energy and protein requirements simulated in the energy and protein sub-model. After calibration, simulated ME contents were compared with measured ME contents from MAFF (1986) and Kolver (2000). Goodness-of-fit of the regression line is reflected by the mean absolute error (MAE, Eq. 1) and the RMSE (Root Mean Square Error, Eq. 2) (Bennett *et al.*, 2013).

Eq. 1 $$MAE = \frac{\Sigma \mid O - S \mid}{n}$$

Eq. 2 $$RMSE = \frac{\sqrt{(O - S)^2}}{n}$$

Where O is the observed value, S is the simulated value, and n is the number of observations. In case simulated data resemble measured data perfectly, the regression line passes through the origin and has a slope equal to one (Bellocchi *et al.*, 2010).

Simulated and measured ME contents were in agreement with MAFF (1986) (R^2 adj. = 0.86; RMSE = 1.28 MJ ME kg^{-1} DM). The MAE was 1.06 MJ ME kg^{-1} DM, or 9.4% of the measured ME content. The intercept of the regression line was not significantly different from zero (P = 0.35) and its slope was not significantly different from one (P = 0.11). Simulated and measured ME contents were also in agreement with Kolver (2000) (R^2 adj. = 0.91; RMSE = 0.87 MJ ME kg^{-1} DM). The MAE was 0.69 MJ ME kg^{-1} DM, or 6.4% of the measured ME content. The intercept of the regression line was not significantly different from zero (P = 0.38) and its slope is not significantly different from one (P = 0.25) (Fig. 3.4, Supplementary Figure S6 and Table S9). Hence, simulated ME contents resembled measured ones well enough.

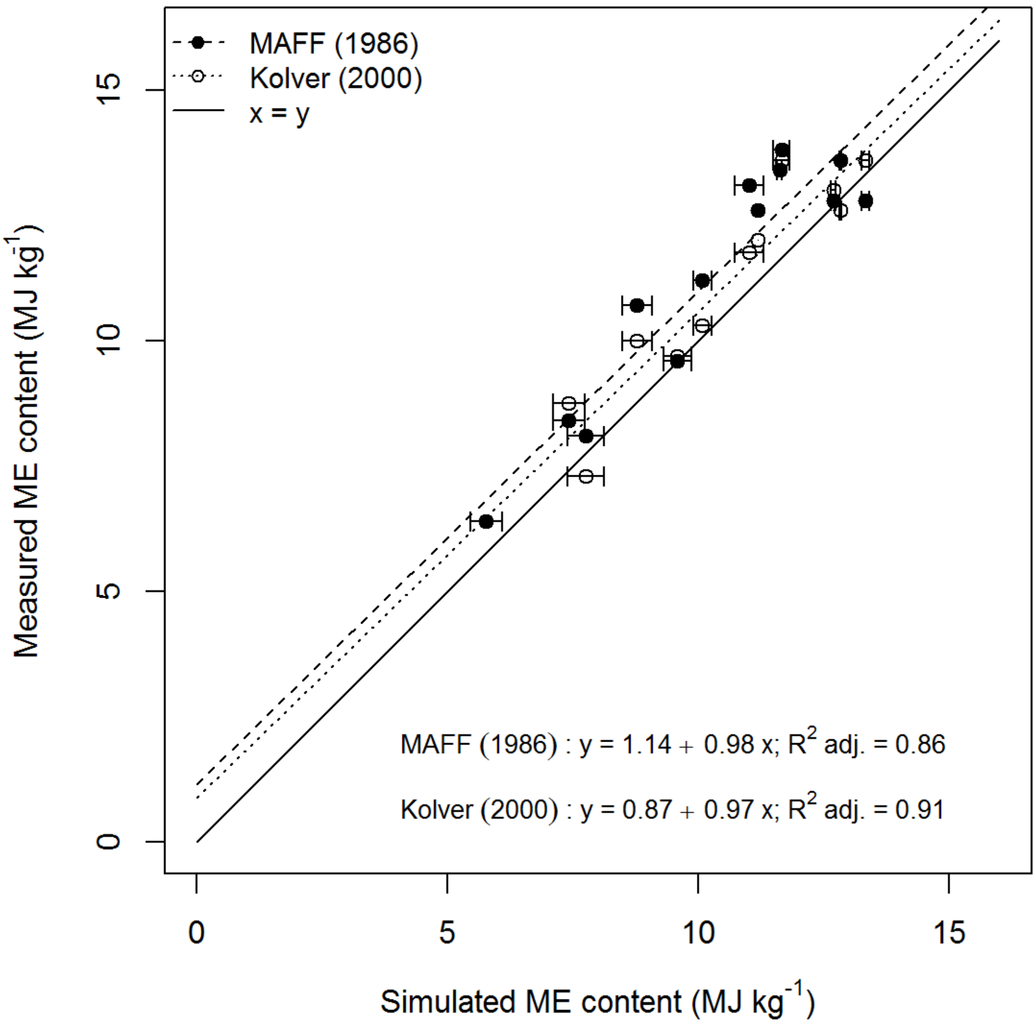

Figure 3.4 Simulated versus measured metabolisable energy (ME) content of 13 feed types given by MAFF (1986) and Kolver (2000). Error bars indicate maximum and minimum simulated ME contents.

3.3.2 Sensitivity analysis

Thermoregulation sub-model

Sensitivity analysis was conducted for the thermoregulation and feed intake and digestion sub-model. For the thermoregulation model, 23 cattle-specific parameters were investigated, together with eight breed-specific parameters, weather data, and heat production (Supplementary Tables S2, S6, and S8). Each of the 31 parameters in total was decreased and increased by 10%, while all other parameters were kept at their original values (*i.e.* one at a time approach). We furthermore assessed lower and upper critical temperature (LCT, UCT) for a wide range of temperatures, combined with feasible ranges of other climate factors, TBWs, and heat production levels.

Breed-specific parameters affecting the LCT and UCT most were: the sweating rate, minimum and maximum conductance between body core and skin, body temperature, and conductivity of the coat during rainfall (Supplementary Figures S9 and S10). A 10% decrease or increase in body core temperature is not likely to happen, but the actual variation of other sensitive parameters is often unknown. The LCTs and UCTs calculated from minimum and maximum values of the feasible ranges for climate factors differed considerably for temperature, relative humidity, wind speed, TBW, and heat production (Supplementary Figure S11). These differences were generally larger than differences in LCT and UCT induced by a 10% decrease or increase in the most sensitive parameters.

Feed intake and digestion sub-model

For the feed intake and digestion model, parameters of 13 feed types (Supplementary Table S3) were decreased by 10% to investigate the effect on ME and digestible CP content, while all other parameters were kept at their original values. Parameters included for each of the 13 feed types are: digestion rates, DNDF passage rate, protein uptake, five out of the seven feed components (excluding UNDF and UCP), and the slope and intercept of the Lucas equation reflecting protein uptake (Lucas *et al.*, 1961).

The ME contents of molasses (10.6%), wheat (5.3%), barley (4.4%), and concentrates (3.2%) were affected most by SNSC content, while ME contents of cereal straw (6.9%), hay (up to 5.9%), and grass (up to 5.5%) were most affected by DNDF and total CP content. Digestible protein content of all feeds was positively affected by a decrease in the intercept of the Lucas equation, and negatively by a decrease in its slope. Intercept and slope were affecting feeds with low CP contents (+80% and -90% for cereal straw) more than feeds with high CP contents (+1% and -11% for soybean meal). Digestible protein content was also affected negatively by a decrease in CP, DCP, and SCP content (Supplementary Tables S10-S12). The analysis suggested that ME content is less sensitive to changes of input parameters than digested protein content.

3.4 Model illustration

Model behaviour at animal and herd level was illustrated with simulations for ten beef production systems in France and Australia, which differed in terms of genotype, climate, housing system, and feeding strategy (Table 3.2). Breeds selected were Charolais and crossbred ¾ Brahman × ¼ Shorthorn (B×S) cattle. Weather data for France were from Charolles (46.4°N, 4.3°E), and for Australia from Kununurra (15.7°S, 128.7°E). Cattle in France were kept indoors from April to November, and outdoors from May to October, whereas cattle in Australia were outdoors year-round. Weaning time was 210 days in both countries. The diet to simulate potential production consisted of 65% wheat and 35% good quality hay, and was fed *ad* *libitum*. A low fraction of the diet consisted of barley under feed quality limitation, and the largest part was grass-based. Cattle were grazing on pasture when kept outdoors, but were fed hay when kept indoors in France (Table 3.2). The diet to simulate feed quality limited production consisted of *ad libitum* pasture, when cattle were outdoors, and *ad libitum* hay when cattle were indoors in France. For simplicity, the quality of grass and hay was fixed over time. Energy requirements for physical activity were based on metabolic body weights (70 kJ $kg^{-0.75}$) (CSIRO, 2007).

Charolais and B×S cattle were simulated at animal and herd level. At animal level, bull calves were simulated, with a slaughter weight of 460 kg for the Charolais breed, and 360 kg for the B×S breed. At herd level, the maximum age of conception for Charolais and B×S cows was set at 10 years, and calving occurred year-round. The FE of a herd unit was maximized by adjusting two parameters. First, the culling rate of cows was set at 50% per year after birth of the first calf, for each age cohort that spans one year. Cows generally give birth for the first time in their third year, and can thus produce up to eight calves with a maximum conception age of 10 years. Accounting for a culling rate of 50% per year per age cohort, cows give birth to one calf in their third year, on average 0.5 (0.5^1) calves in their fourth year, 0.25 (0.5^2) calves in their fifth year, and so on, up to 0.008 (0.5^7) calves in their tenth year (Supplementary Table S7). Adding up the number of calves born on average ($1 + 0.5^1 + 0.5^2 + \ldots + 0.5^7$), approximately two calves are obtained per cow and per herd unit, one male calf and one female calf for replacement, assuming a male to female ratio of one (Van der Linden *et al.*, 2015). The herd unit consists of one reproductive cow, and one male calf under a culling rate of 50% per year for each age cohort. This culling rate is the theoretical maximum culling rate, and increasing the culling rate further (>50%) would result in a lower number of replacement heifers than one, which implies that the herd size is not fixed, but decreases. Second, the slaughter weight of the male calves was optimized to maximize FE at herd level.

The most constraining factors for growth are an output of LiGAPS-beef. These factors can be the genotype or breed, climate (heat and cold stress), feed quality, and available feed quantity (Supplementary Figure S3). Feed quality limitation occurs if the feed digestion capacity is fully utilised, and animal requirements for energy or protein are still not met. Feed digestion capacity is fully utilised if feed intake equals the maximum feed intake, expressed in fill units (Jarrige *et al.*, 1986). Although feed quality limitation can result in energy or protein deficiency, feed digestion capacity is considered its primary cause. Feed quantity limitation occurs if the available feed quantity is not sufficient to meet the feed requirements of an animal with a diet other than 65% wheat and 35% hay, and if digestion capacity is not fully utilised. Feed quantity limitation can result in either energy or protein deficiency.

At animal level, Charolais bulls with similar slaughter weights had a higher FE in France than in Australia, under potential and feed-limited production (Table 3.3),

Table 3.2 Cases with potential and feed-limited production levels to illustrate the model at animal and herd level.

		Growth factors				
		Genotype	Climate		Feed composition	Feed quantity
Abbreviation	Production level		Country	Housing		
Pot Ch Fr	Potential	Charolais	France	indoors / outdoors[a]	Wheat (65%) + Hay (35%)	*ad libitum*
Pot Ch Au	Potential	Charolais	Australia	outdoors	Wheat (65%) + Hay (35%)	*ad libitum*
Pot B×S Fr	Potential	B×S	France	indoors / outdoors[a]	Wheat (65%) + Hay (35%)	*ad libitum*
Pot B×S Au	Potential	B×S	Australia	outdoors	Wheat (65%) + Hay (35%)	*ad libitum*
FQlty Ch Fr	Feed quality lim.	Charolais	France	indoors / outdoors[a]	Barley (5%) + Hay / Grass (95%)[b]	*ad libitum*
FQlty Ch Au	Feed quality lim.	Charolais	Australia	outdoors	Barley (5%) + Grass (95%)	*ad libitum*
FQlty B×S Fr	Feed quality lim.	B×S	France	indoors / outdoors[a]	Barley (5%) + Hay / Grass (95%)[b]	*ad libitum*
FQlty B×S Au	Feed quality lim.	B×S	Australia	outdoors	Barley (5%) + Grass (95%)	*ad libitum*
FQlty Ch Fr 1 kg	Feed quality lim.	Charolais	France	indoors / outdoors[a]	Barley (1 kg DM day^{-1}) + Hay / Grass[c]	*ad libitum*
FQlty Ch Fr 2%	Feed limited	Charolais	France	indoors / outdoors[a]	Barley (5%) + Hay / Grass (95%)[c]	Max. 2% TBW[d]

Au = Australia; B×S = ¾ Brahman × ¼ Shorthorn crossbred cattle; Ch = Charolais; FQlty = feed quality limited; Fr = France; lim. = limited; Pot = potential; TBW = total body weight

[a] Housed indoors from April to November

[b] Hay fed indoors (December-March), grazing outdoors (April-November)

[c] Barley is max. 65% of the diet, or 1 kg DM day^{-1}. The remaining part of the diet is from hay (December-March) and grass (April-November)

[d] Feed quantity available is 2% of the total body weight of the animal.

Table 3.3 Beef production, feed intake, feed efficiency, and beef characteristics in the ten cases at animal level and herd level.

		Cases[a]									
Level	Production characteristics	Pot Ch Fr	Pot Ch Au	Pot B×S Fr	Pot B×S Au	FQlty Ch Fr	FQlty Ch Au	FQlty B×S Fr	FQlty B×S Au	FQlty Ch Fr 1 kg	FQlty Ch Fr 2%
Animal	Beef production (kg)	206	192	156	154	192	213	156	158	195	196
	Feed intake (kg DM)	1126	1978	1008	992	2000	5084	1800	2285	1764	2423
	Feed efficiency (g beef kg^{-1} DM)	183	97	154	155	96	42	87	69	110	81
	Beef percentage	45	42	43	43	42	46	43	44	42	43
	Fat content beef	28	29	27	27	24	41	31	32	24	28
	Slaughter age (days)	258	497	268	279	335	910	392	464	299	477
Herd	Beef production repr. cow (kg)	507	371	259	295	488	-[b]	285	269	500	473
	Slaughter weight bull calf (kg)	936	717	580	560	878	-	575	638	717	992
	Beef production bull calf (kg)	490	342	291	275	442	-	287	339	346	519
	Beef production herd unit (kg)	998	713	550	570	930	-	572	608	847	991
	Feed efficiency repr. cow (g beef kg^{-1} DM)	55	40	44	49	35	-	32	27	37	33
	Feed efficiency bull calf (g beef kg^{-1} DM)	117	82	113	114	95	-	92	54	114	79
	Feed efficiency herd unit (g beef kg^{-1} DM)	74	52	64	67	49	-	46	38	51	47
	Feed fraction repr. cow	69	69	69	72	73	-	73	61	82	68

[a] See Table 3.2 for explanation of the cases. Au = Australia; B×S = Brahman × Shorthorn cattle; Ch = Charolais cattle; FQlty = feed quality limited production; Fr = France; Pot = potential production.

[b] No results due to inability of reproductive cows to cope with heat stress.

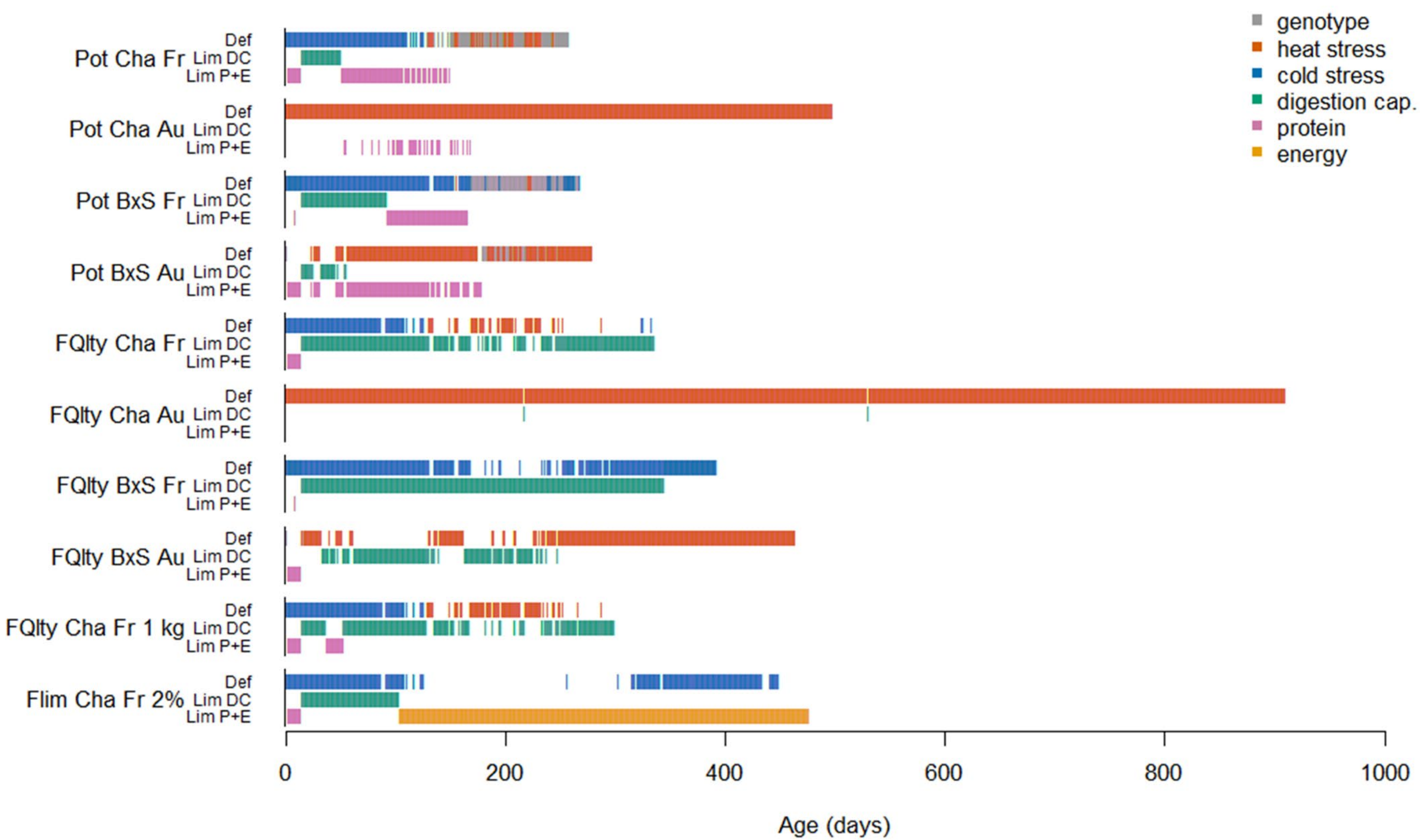

Figure 3.5 Constraining factors for growth of bulls in the ten cases at animal level. For explanation on the treatments, see Table 3.2. Defining factors (Def) for growth are genotype and climate (causing heat and cold stress). Digestion capacity is the primary cause of feed quality limitation (Lim DC). Protein and energy deficiency (Lim P + E) due to feed quantity limitation are indicated separately. Pot = potential production; Au = Australia; B×S = Brahman × Shorthorn cattle; Ch = Charolais cattle; FQlty = feed quality limited production; Fr = France.

which can be explained by heat stress (Fig. 3.5). The FE of B×S bulls was similar between France and Australia under potential production (Table 3.3). The major constraints were cold stress in France and heat stress in Australia. Under potential production, we also observed protein deficiencies and constraints for feed digestion capacity (Fig. 3.5, Supplementary Figures S12-S21). This implies that the diet consisting of 65% wheat and 35% hay was not fully adequate to achieve potential production. Feeding other diets with high protein contents did not result in complete elimination of feed quality limitation under potential production either. This implies that feed limitations still occurred with both the 65% wheat and 35% hay diet and a diet adapted for each animal and each day. Feed quality limitations occurred in the first half year of an animal (Fig. 3.5). This is also the period of rumen development, which is, amongst others, determined by genetics. Hence, the simulated feed quality limitations may have had a genetic cause, which would justify the use of the term potential production with a 65% wheat and 35% hay diet. The shift from a fully milk-based diet right after birth towards a diet consisting fully of solid feed at weaning is known to involve several critical processes, such as the development of anaerobic microbes and papillae in the rumen, and expansion of rumen volume (Khan *et al.*, 2016). The increase in digestion capacity over time in LiGAPS-Beef (up to 152 days after birth) may reflect these processes broadly, but a decisive confirmation of this explanation is not possible due to a lack of experimental data.

Feed quality limited production was higher in France than in Australia, for both Charolais and B×S bulls. The average diet quality, however, was higher in France than in Australia, due the high quality hay during winter. Charolais bulls on a grass-based diet with a feed quantity up to 2% of the TBW had a 16% reduction in FE compared to *ad libitum* supply of the same diet (Table 3.3), caused by feed quantity limitation from an age of approximately 100 days up to slaughter (Fig. 3.5).

At herd level, FE of Charolais cattle was highest in France, and lowest in Australia under potential and feed quality limited production (Table 3.3). This corresponds to literature indicating that *B. taurus* cattle have higher growth rates in temperate than in tropical climates (Burrow *et al.*, 2001). Under potential production, B×S cattle had similar FEs in both countries. Under feed quality limited production, FE was higher in France than in Australia for these cattle (Table 3.3). If cattle would not be kept in stables during winter in France, and are fed a similar diet, FEs in France and Australia (40.9 vs 41.0 g beef kg^{-1} DM) would be similar. Literature indicates, however, that growth rates of *B. indicus* cattle are higher in tropical climates than in temperate climates (Burrow *et al.*, 2001). Although B×S cattle have predominantly a *B. indicus* genotype, and are considered to be adapted to tropical climates, heat stress in Australia (average daily temperature 29.1°C) may have exceeded cold stress in France.

At herd level, FE under potential production was higher for Charolais cattle than for B×S cattle in France, but the reverse was true for Australia (Table 3.3). Under feed quality limited production, FE was highest for Charolais cattle in France, followed by B×S cattle, and Charolais cattle in Australia. For Charolais cattle, heat stress in Australia was simulated to result in mortality of reproductive cows, and as a consequence no beef was produced (Table 3.3). This result is explained by a higher heat increment of feeding under feed quality limited production than under potential production. To our knowledge, no literature is available on mortality of Charolais or other large-sized *B. taurus* cattle due to heat stress in northern Australia, as the breeds used in this regions are generally crossbreds between *B. indicus* and *B. taurus* cattle. All in all, the simulation results show that breeds adapted to a location and its prevailing climate conditions have a higher FE in this location than less-adapted breeds, both under potential and feed quality limited production (Supplementary Figures S22-S31).

The percentage feed consumed by the reproductive cow in a herd was approximately 70% for most cases (Table 3.3). This is in agreement with De Vries *et al.* (2015), who stated that maintaining reproductive cows requires the majority of resources in a herd. Reproductive cows accounted for 82% of feed intake when fed wheat at 1 kg per head per day (Table 3.3). Fixing the quantity of wheat at 1 kg per head per day decreases its proportion in the diet over the lifetime of an animal. Diets of calves are expected, therefore, to have higher wheat contents than diets of reproductive cows. Due to the high ME content of wheat, bull calves could suffice with lower amounts of feed than reproductive cows, which results in a higher percentage of feed consumed by reproductive cattle.

Feed efficiency was expressed per kg DM feed intake (Table 3.3), but it can be expressed also per MJ ME, or per kg CP. The decrease in feed efficiency between potential and feed quality limited production is caused partly by a lower ME content of the diet under feed quality limitation (8.8 MJ ME kg^{-1} DM for pasture, and 9.6 MJ ME kg^{-1} DM for hay) than under potential production (11.6 MJ ME kg^{-1} DM for 65% wheat and 35% hay). Expressing beef production per MJ ME instead of per kg DM changes the relative differences between potential and feed quality limited production.

In line with its objective, LiGAPS-Beef enables to simulate potential and feed-limited production in different beef production systems (Table 3.3). The thermoregulation sub-model can deal with a wide range of climate conditions, and the feed intake and digestion sub-model can deal with a wide range of feed types (Fig. 3.4, Supplementary Information, Chapter 3). The model illustration and the evaluation of the thermoregulation sub-model and the feed intake and digestion sub-model suggest that the outcomes of LiGAPS-Beef and its sub-models gave reasonable results under a wide range of conditions. The model can be assumed to be applicable to a wide range of beef production systems as well. The companion paper

(Van der Linden *et al.*, 2017b) goes beyond illustration and focusses on further model evaluation. LiGAPS-Beef reveals bio-physical factors that constrain growth also (Fig. 3.5). Identification of these constraining factors is a crucial step in yield gap analysis, and a starting point to list improvement options to mitigate yield gaps (Van Ittersum *et al.*, 2013). The model also allows exploration of the potential of specific improvement options to decrease the yield gap. The bio-physically oriented yield gap analysis can subsequently be joined with socio-economic analyses to explore feasible, and location-specific improvement options, that are required to meet the increasing demand for livestock products.

3.5 Conclusions

This paper presents the mechanistic model LiGAPS-Beef, which simulates growth of cattle in different beef production systems, based on concepts of production ecology. The model integrates thermoregulation, feed intake and digestion, and energy and protein utilisation in a novel way. LiGAPS-Beef aims to simulate potential and feed-limited growth, and to identify the most constraining factors for growth. The thermoregulation and feed intake and digestion sub-models resembled measured data from experiments. Illustration of the model for Charolais (*B. taurus*) cattle herds showed that potential and feed-limited production (*ad libitum* grass-based diet with 5% wheat) were higher in France (74 and 49 g beef kg^{-1} DM) than in Australia (52 and 0 g beef kg^{-1} DM), due to heat stress. Brahman (*B. indicus*) × Shorthorn (*B. taurus*) cattle had similar production levels in France and Australia, both under potential (64 and 67 g beef kg^{-1} DM) and feed-limited production (46 and 41 g beef kg^{-1} DM). Breeds adapted to a region and its climate conditions achieve a higher FE in such a region than less-adapted breeds. In line with its aim, LiGAPS-Beef has simulated potential and feed-limited production and has identified constraining factors for cattle. The model provides scope, therefore, to explore improvement options that mitigate yield gaps in beef production systems.

Additional information

Supplementary Information accompanying this Chapter is available at http://dx.doi.org/10.18174/406579. The source code of LiGAPS-Beef is freely accessible at http://dx.doi.org/10.18174/386763. Updates and model applications will be published on the model portal of the Plant Production Systems group of Wageningen University, the Netherlands (http://models.pps.wur.nl/content/ligaps-beef).

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Chapter 4

LiGAPS-Beef, a mechanistic model to explore potential and feed-limited beef production 2. Model evaluation

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This chapter is under review

Abstract

LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle) is a mechanistic model designed to simulate potential and feed-limited beef production across the globe and to identify constraining factors for growth. The model integrates effects of cattle breed, climate, housing, feed quality and feed quantity. LiGAPS-Beef allows quantification of yield gaps, and identification of strategies for sustainable intensification. A full description of LiGAPS-Beef, as well as an evaluation of two underlying sub-models, is presented in a companion paper (Van der Linden *et al.*, 2017a). The aim of this paper is to evaluate LiGAPS-Beef by comparison of model simulations against independent experimental data and sensitivity analysis. Independent datasets were from three different beef production systems: ¾ Brahman × ¼ Shorthorn cattle in Australia, grazing on pastures with *Leucaena leucocephala* and *Digitaria eriantha*; Hereford cattle in Uruguay, grazing on pastures with *Festuca arundinacea* and *Trifolium* species; and Meuse-Rhine-Yssel cattle, grazing in nature areas in the Netherlands. Simulated average daily gains (ADGs, in kg day^{-1}) for cattle in Australia, Uruguay, and the Netherlands resembled measured ADGs reasonably well to good (mean absolute error = 0.13 kg day^{-1}, equal to 15.4% of mean measured ADG). This indicates that the constraining factors affecting ADG are, most likely, estimated fairly well too. Sensitivity analysis showed that model output was most sensitive to energy requirements for maintenance, and conversion of digestible energy (DE) to metabolisable energy (ME), especially under feed quality limited production. Model output was affected most after changing parameters from the energy and protein utilisation sub-model under potential production. Model output under feed-limited production was most affected after changing parameters from both the energy and protein utilisation sub-model and the thermoregulation sub-model.

Implications

The livestock model LiGAPS-Beef is designed to estimate potential (*i.e.* theoretical maximum) production and feed-limited beef production, and to identify constraining factors for cattle growth in different beef production systems across the globe. This paper evaluates LiGAPS-Beef and shows that its estimates for growth of cattle are reasonably accurate for beef production systems in Australia, Uruguay, and the Netherlands. LiGAPS-Beef allows to identify the most constraining bio-physical factors for growth (genotype, climate, feed quality, feed quantity), which provides insight in options how to increase beef production in a sustainable way.

4.1 Introduction

Population growth and increasing wealth will impel future demand for food products in general, and for animal source food in particular. This confronts future agriculture with an increasing competition for land, water, and energy. Moreover, use of land and resources for agriculture also results in negative impacts on the environment (Godfray *et al.*, 2010). Sustainable food production requires, therefore, enhanced resource use efficiency and mitigation of environmental impacts (Herrero and Thornton, 2013). Sustainable intensification (*i.e.* reducing environmental impacts and increasing food production per unit of land simultaneously) is proposed as a pathway to achieve such sustainable food production (Godfray *et al.*, 2010). Regions with high scope for sustainable intensification are those displaying a large yield gap. The latter is defined as the difference between potential (*i.e.* theoretical maximum) or limited production and actual production (Van Ittersum *et al.*, 2013).

Quantification of potential and limited production in crops is conducted with mechanistic crop growth models (Van Ittersum *et al.*, 2013). These models are based on concepts of production ecology, and their use is well-established in crop science (Van Ittersum and Rabbinge, 1997, Jones *et al.*, 2003, Keating *et al.*, 2003). Such models also identify constraining factors for crop growth, and facilitate, thereby, the design of options to mitigate yield gaps and to improve production or resource use efficiency (Van Ittersum *et al.*, 2013). Models based on concepts of production ecology have not been applied, however, in livestock production. Although many livestock growth models include some notions of production ecological concepts, quantification of potential and limited production in livestock systems requires substantial extension and integration of existing models (Van der Linden *et al.*, 2015).

For this reason, we developed a mechanistic livestock model for beef cattle, which was presented in a companion paper (Van der Linden *et al.*, 2017a). This model is named LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle). LiGAPS-Beef aims to simulate potential and feed-limited production in different beef production systems across the world, and to identify constraining factors for growth. LiGAPS-Beef allows the user to specify different cattle breeds, climates, housing types, and feeding strategies. These inputs allow the model to simulate potential and feed-limited beef production for an individual animal (*i.e.* animal level), and for a group of animals differing in sex and age (*i.e.* herd level) (Van der Linden *et al.*, 2017a). Beef production at animal level is simulated by inter-connected sub-models dealing with thermoregulation, feed intake and digestion, and energy and protein utilisation. Beef production at herd level is assessed by upscaling from animal level and accounting for herd population dynamics. LiGAPS-Beef was illustrated at animal and herd level, and its thermoregulation sub-model and feed digestion sub-model were evaluated separately (Van der Linden *et al.*, 2017a).

Evaluation of LiGAPS-Beef is needed before use in practical applications, to assess its usefulness and accuracy to simulate cattle growth in different beef production systems. Preceded by model calibration, model evaluation can be done through model comparison against independent experimental data and through sensitivity analysis. Comparison of model simulations against independent experimental data not used for calibration is also referred to as validation, but we will use the term model comparison throughout this paper. Such comparison allows to quantify the accuracy of model estimates, and is essential for credibility and confidence that a model is appropriate for the aim it was designed for (Bellocchi *et al.*, 2010). Sensitivity analysis is important if models are applied outside conditions they were calibrated for (Prisley and Mortimer, 2004). In the companion paper, model comparison and sensitivity analysis were performed for the thermoregulation and the feed digestion sub-model separately (Van der Linden *et al.*, 2017a). The energy and protein utilisation sub-model was not evaluated separately, since it is the largest and central component in LiGAPS-Beef requiring detailed input from the thermoregulation and feed intake and digestion sub-models.

Our aim in this paper is to evaluate the full model LiGAPS-Beef by means of model comparison and sensitivity analysis to investigate whether the model is able to simulate beef production in different systems accurately, and to identify constraining factors for growth. A beef production system generally includes a herd that consist of a productive herd (calves for slaughter) and a reproductive herd (cows). As the productive herd is dependent on the reproductive herd, both are essential components of the beef production system. Furthermore, the reproductive herd requires approximately 70% of the feed intake, but contributes to a minority of the beef production (De Vries *et al.*, 2015). Including the reproductive herd is required, therefore, to assess beef production per unit feed intake and per hectare in a full beef production system (Van der Linden *et al.*, 2015). Although LiGAPS-Beef, in line with its intended use, is to be evaluated preferably at herd level, we used data of beef production at animal level for model comparison, because data at herd level were too scarce. Model comparison was conducted for beef cattle in Australia, Uruguay, and the Netherlands. We performed sensitivity analysis to assess the sensitivity of model output after changing input parameters of the model.

4.2 Materials and methods

The cattle growth model LiGAPS-Beef consists of a thermoregulation sub-model; a feed intake and digestion sub-model; and an energy and protein utilisation sub-model (Van der Linden *et al.*, 2017a) (Fig. 4.1). The thermoregulation sub-model simulates heat release and the heat balance of beef cattle, based on existing thermoregulation models. This sub-model requires daily weather data (either outdoors or housed), heat production from metabolic processes, and genetic parameters as input, and gives minimum and maximum heat release as output. Cold conditions can increase feed intake, whereas warm conditions can decrease feed intake. The feed intake and digestion sub-model needs the energy requirements of cattle, and the daily quality and quantity of the available feed as input. Feed intake is calculated from energy requirements and the available feed. Feed digestion gives ME and protein as major outputs, which are used as input for the energy and protein utilisation sub-model, as well as genetic parameters. Energy and protein are distributed over metabolic processes such as maintenance, growth, gestation, and lactation. Energy and protein for growth are allocated to different tissues (non-carcass tissue, and bone, muscle and fat tissue in the carcass). Beef is defined as deboned carcass. Metabolic processes generate heat, which is an input for the thermoregulation sub-model. The thermoregulation sub-model, at its turn, increases energy requirements under warm conditions due to panting (Fig. 4.1).

4.2.1 Model calibration and comparison against independent experimental data

Model calibration preceded model comparison at animal level. Data used for model calibration were not used for model comparison. Both data for calibration and comparison were obtained from experiments conducted in beef production systems in Australia, Uruguay, and the Netherlands. Model comparison occurred between simulated and measured average daily gains (ADGs). A collective of constraining bio-physical factors affects and determines the simulated ADGs in LiGAPS-Beef. Hence, these constraining factors allow to explain ADGs and beef production levels. Identification of constraining factors is key to reveal options to mitigate yield gaps (Van Ittersum *et al.*, 2013). Factors defining growth are cattle genotype, or breed, and climate (Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015). The climate can cause heat and cold stress. Feed quality and quantity are factors that can limit growth in LiGAPS-Beef due to energy or protein deficiency (Van der Linden *et al.*, 2017a). We did not compare simulated constraining factors with measured ones from experiments, because data are scarce and often qualitative. The constraining factors determining ADGs in Australia, Uruguay, and the Netherlands are expected to be different for beef production. We assume, therefore, that if ADGs are simulated accurately with LiGAPS-Beef for three different beef production systems, the constraining factors determining ADGs are captured accurately too, and compensation between errors in constraining factors are unlikely to occur. The

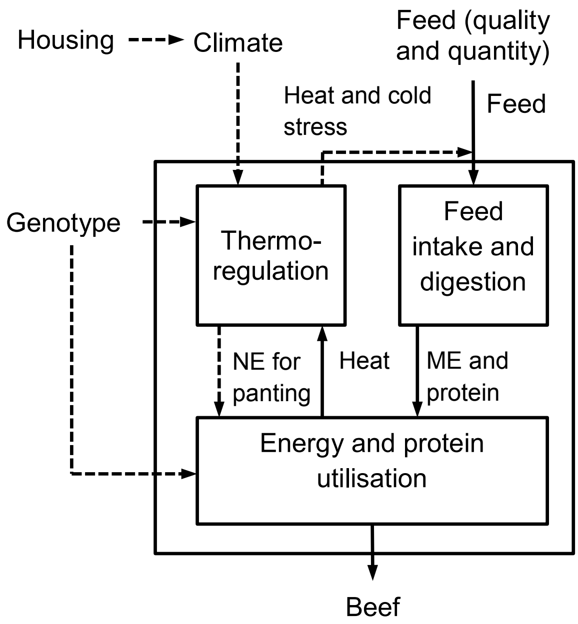

Figure 4.1 Representation of LiGAPS-Beef (Livestock Simulator for Generic analysis of Animal Production Systems – Beef cattle) simulating beef production of a bovine animal, with its three sub-models. Solid arrows indicate flows of material or energy. Dashed arrows indicate a flow of information. ME = metabolisable energy; NE = net energy.

likelihood of compensation between errors in constraining factors is reduced by model comparison against independent data. Comparison of results from the thermoregulation sub-model and the feed intake and digestion sub-model indicated that the sub-models performed well enough to simulate heat release and feed digestion (Van der Linden *et al.*, 2017a).

Beef production in Australia

Three experiments were conducted in Australia at the Frank Wise Institute of Tropical Agricultural Research, located in the Ord river irrigation area in north western Australia (15.65° S, 128.72°E). The cattle breed used in this system was crossbred ¾ Brahman × ¼ Shorthorn (B×S). Cattle grazed irrigated pastures with *Leucaena leucocephala* (a legume tree) and *Digitaria eriantha* (a tropical grass). The climate was characterized by a dry and wet season, with average temperatures of 26.2 °C and 31.7 °C, respectively (Petty *et al.*, 1998). One experiment included the defining factor climate by measuring growth of cattle during the dry and wet season (Petty *et al.*, 1998). The experiment of Petty and Poppi (2008) was conducted in the dry season, but muddy soils were created artificially in one treatment to mimic soil conditions of the wet season. This particular treatment was excluded, as these muddy soils may have reduced feed intake despite abundance of feed. Two experiments investigated effects of feed quality through supplementation of cracked maize (Petty *et al.*, 1998, Petty and Poppi, 2012), and one experiment through supplementation of molasses (Petty and Poppi, 2012). Steers were implanted with the hormonal growth promotant Compudose 200 in Petty and Poppi (2008), which is known to increase growth by 25% (Frisch and Hunter, 1990a). Heifers were implanted with the hormonal growth promotant Synovex-H in Petty and Poppi (2012), which is known to increase growth by 26% (Frisch and Hunter, 1990b). Cattle were weighted every two weeks, without prior fasting. Their average daily gain (ADG) was calculated as the slope of the regression line for body weight over time.

Weather data used for model simulations were obtained from the nearby Kimberley research station (15.65° S, 128.71°E). Feed was amply available and, therefore, feed quantity was not expected to be limiting during these experiments (Petty *et al.*, 1998). Drinking water was assumed to be available *ad libitum*. Micronutrient deficiencies were assumed to be absent, as cattle were supplied with vitamins and minerals (Petty *et al.*, 1998, Petty and Poppi, 2008), or mineral blocks (Petty and Poppi, 2012). Cattle were treated against internal and external parasites to prevent diseases (Petty *et al.*, 1998, Petty and Poppi, 2008). Main input parameters for model comparison and calibration were obtained from literature (Table 4.1). LiGAPS-Beef was calibrated by using all measured data for ADG from Petty *et al.* (1998). Calibration was done by adjustment of the following feed parameters of the pasture to minimize the root mean square error (RMSE): heat increment of feeding, fill units, soluble non-structural carbohydrates, and the digestible neutral detergent fibre content. Maize was assumed to have a dry matter (DM) concentration of 85%. To account for the effect of hormonal growth promotants, the increase in energy for growth in LiGAPS-Beef was set equal to the measured increase in growth from literature (Frisch and Hunter, 1990a and 1990b). After calibration, data from Petty and Poppi (2008 and 2012) were used as independent datasets for model comparison.

Beef production in Uruguay

Experiments in Uruguay were conducted at the experimental station of the Agronomy Faculty of the University of Uruguay, which is located in Paysandú, in the west of Uruguay (32.33°S, 58.03°W). Hereford steers grazed on improved pastures with fescue (*Festuca arundinacea*) and clover (*Trifolium repens* and *T. pratense*). The experiments were conducted in summer, when ADG is reported to be lower than in winter. Feed quality for half of the cattle was improved by supplementing cracked maize at 1% of the total body weight (TBW) per day, whereas the other half did not receive maize. Feed quantity available was set at 3, 6, and 9 kg DM pasture per 100 kg TBW, which resulted in a 2 × 3 factorial design (Beretta *et al.*, 2006). Cattle were withdrawn from feed and drinking water fourteen hours before weighing, which occurred every two weeks.

Weather data used for model simulations were recorded at the experimental station. Like the experiments in Australia, drinking water, micronutrients, diseases, and stress were assumed not to affect growth. Data used for model calibration and comparison comprised the experiment conducted in the summer of 2002. The model was

Table 4.1 Model input used for calibration and comparison of the model.

	Australia			Uruguay	The Netherlands
Paper	Petty *et al.* (1998)	Petty and Poppi (2008)	Petty and Poppi (2012)	Beretta *et al.* (2006)	Wallis de Vries (1996)[a]
Timeline					
Age at start of experiment (days)	305[b]	305[b]	366	488	367 (356)[b]
Duration adaptation phase (days)	44[b]	30	58	NA	NA
Duration experiment (days)	168[c]	81	92	71	784 (795)
Age at end of experiment (days)	517	416	515	559	1151
Genotype and climate					
Genotype	B×S	B×S	B×S	Hereford	Meuse-Rhine-Yssel
Animal	Steer	Steer	Heifer	Steer	Steer
Estimated maximum adult weight (kg TBW)	775	775	675	850	1050
Initial weight (kg TBW)	213	179	252	282	315
Season(s)	Dry and wet	Dry	Dry	Summer	Year-round
Period	August 1992-January 1993	August-October 1995	August-November 1994	January-March 2002	May 1989-July 1991
Average daily temperature (°C)[d]	30.6	28.3	28.7	23.7	10.2 (10.0)
Average max. daily temperature (°C)[d]	38.0	37.2	37.5	29.4	14.6 (14.4)
Average rainfall (mm day^{-1})[d]	1.49	0.23	0.15	5.35	1.98 (1.80)
Feed types and quantity					
Pasture quantity (kg DM 100 kg^{-1} TBW)	*Ad libitum*	*Ad libitum*	*Ad libitum*	1.6 – 4.3	Variable
Maize quantity (kg FW)	0.5, 1.0, 1.5, 2.0	NA	0.75 or 1.50	1% of TBW	NA
Molasses quantity (kg FW)	NA	NA	1.25, 2.50, 3.75, 5.00	NA	NA

B×S = ¾ Brahman × ¼ Shorthorn; FW = fresh weight; NA = not applicable; TBW = total body weight

[a] Value between brackets indicate data for the Karshoek, a mixed heathland-riverine nature area, if deviating from the other areas.

[b] Estimated from data in the papers.

[c] Duration of the experiment includes a dry season (70 days) and a consecutive wet season (98 days).

[d] Only for the experimental period; the adaptation period is not included.

calibrated with data of the treatment with a pasture availability of 3 kg DM per 100 kg live weight per day without maize supplementation. Calibration was done in such a way that the simulated ADG equalled the measured ADG. Parameters calibrated were heat increment of feeding, fill units, soluble non-structural carbohydrates, and the digestible neutral detergent fibre content of pasture. The fill unit was multiplied with a factor accounting for the available biomass (Jouven *et al.*, 2008), and the energy requirement for grazing was calculated from the available biomass too (Freer *et al.*, 1997). Estimated pasture intake by Beretta *et al.* (2006) was adopted as maximum feed intake. Main input parameters for genotype, climate, feed types, and feed quantities were obtained from literature (Table 4.1). The other five treatments in

Beretta *et al.* (2006) were used as independent datasets for model comparison. We assumed that the loss of TBW during the fasting period prior to weighing was 10%, which is equal to the full rumen content in LiGAPS-Beef. The ADGs were calculated as the slopes of the regression lines for body weights over time.

Beef production in the Netherlands

An experiment with beef cattle was conducted in the Netherlands in the Renkumse Benedenwaarden, a riverine nature area (51.97°N, 5.72°E), the Doorwerthse Heide, a heathland area (52.00°N, 5.78°E), and Karshoek, a mixed heathland-riverine nature area (52.53°N, 6.53°E). Steers of the Meuse-Rhine-Yssel breed were used in this experiment that lasted for more than two years (Table 4.1). The riverine, heathland, and mixed heathland-riverine areas were each grazed by a group of steers. In addition, another group of steers was kept in the riverine area during summer, and in the heathland area during winter (Wallis de Vries, 1996). The riverine area had a heavy clay soil and pastures with *Lolium perenne*, *Agrostis stolonifera*, and *Elymus repens*. The heathland area had a sandy soil, and its vegetation was dominated by heather (*Calluna vulgaris*) and the grass *Deschampsia flexuosa*. Mineral deficiencies were limiting growth of cattle in the heathland area, and no supplements were given. Weight of cattle, pasture intake, and pasture quality were measured every two months during the experiment (Wallis de Vries, 1996).

Weather data used for model simulations were taken from nearby stations in Wageningen (51.97°N, 5.67°E) and Enschede (52.27°N, 6.90°E). Measured pasture quality and intake were used as model inputs. Cattle had ample access to drinking water, and they were treated against internal and external parasites annually (Wallis de Vries, 1996). We assumed, therefore, that a lack of drinking water and occurrence of diseases did not affect cattle growth. Although mineral deficiencies limited growth in the heathland area, LiGAPS-Beef was not adjusted for that, as it does not include flows of minerals. The model was calibrated for ADG in the first four months for cattle in the riverine area, by adjusting the parameter for net energy (NE) requirements for physical activity, which includes grazing. The ADG in the rest of the experiment in the riverine area was used for model comparison, as well as the ADGs of steers in the heathland, the mixed heathland-riverine area, and the ADG of steers grazing in the riverine area during summer and in the heathland during winter.

Statistical analysis

Model performance is reflected in the mean absolute error (MAE, Eq. 1) and the RMSE (Eq. 2) (Bennett *et al.*, 2013). Linear regression between simulated and measured ADGs from independent datasets was used to assess the goodness-of-fit for calibration in Australia and for model comparison in all three countries.

Eq. 1 $$MAE = \frac{\Sigma \mid O - S \mid}{n}$$

Eq. 2 $$\text{RMSE} = \frac{\sqrt{(O - S)^2}}{n}$$

Where O is the observed value, S is the simulated value, and n is the number of observations.

4.2.2 Sensitivity analysis

Sensitivity analysis was performed at herd level to identify changes in feed efficiency (FE) upon changes in parameters. This insight can be used to prioritize which parameters need to be estimated more precisely (Zuidema *et al.*, 2005). Sensitivity analysis for FE (g beef kg^{-1} DM feed) was done for 117 parameters. The parameters were each decreased and increased by 10%, with all other parameters kept constant (*i.e.* one-at-a-time approach). A few parameters were changed by less than 10%, since biological limits did not allow a change of 10%. Body core temperature was increased by 1 °C (*i.e.* 2.6%) and the reference skin temperature used to calculate maximum sweating capacity was changed by 1%. The parameters of the Gompertz curve were changed all together because they are interrelated, except for the rate constant, which is not interrelated. The change in FE caused by a parameter was calculated as the average of the absolute change in FE for a 10% decrease and a 10% increase of the parameter.

Sensitivity analysis was executed at herd level for B×S cattle, which are adapted to a tropical climate, and for Hereford cattle, which are adapted to a temperate climate. Four baseline scenarios were used for the sensitivity analysis: B×S cattle in Australia under potential production; B×S cattle in Australia, grazing *ad libitum* on pasture; Hereford cattle in Uruguay under potential production; and Hereford cattle in Uruguay, grazing *ad libitum* on pasture. Beef production with Meuse-Rhine-Yssel cattle in the Netherlands was not included in the sensitivity analysis due to a lack of data to assess growth curves of female animals. Under potential production, cattle were permanently housed, and the diet consisted of wheat (65%) and good quality hay (35%). Under feed quality limitation, pasture quality in Australia and Uruguay was the same as for model calibration. Within the herd, slaughter weights of male B×S and Hereford calves were set at 390 kg TBW, which corresponds to the highest TBWs observed at the end of the experiments of Petty *et al.* (1998). Weather data used were from the year 1992 in Australia and 2002 in Uruguay. Weaning age was set at 210 days in both countries. The culling rate for a cohort of cows after birth of the first calf was set at 50% per year. As cows were assumed to conceive up to an age of ten years, each cow gives, on average, birth to two calves. The female calf is used as a replacement for the reproductive cow and is not part of the herd unit, but gives rise to the next one (Van der Linden *et al.*, 2015, Van der Linden *et al.*, 2017a). Hence, one herd unit consists of a reproductive cow and one male calf.

4.3 Results

4.3.1 Model calibration

Calibration resulted in a MAE of 0.085 kg TBW day^{-1}, or 11.3% of measured ADGs in Australia in the dry and wet season (R^2-adj. = 0.62). The RMSE was 0.109 kg TBW day^{-1}, or 14.4% of measured ADGs. The intercept of the regression line, however, was significantly different from zero ($P < 0.001$) and the slope was significantly different from one ($P < 0.001$). The model underestimated ADG for two treatments with maize supplementation (1.0 and 1.5 kg FM maize head^{-1} day^{-1}) in the dry season, but overestimated ADG for the highest level of maize supplementation (2.0 kg FM maize head^{-1} day^{-1}) (Fig. 4.2). Simulated and measured ADGs were equal for both Uruguay and the Netherlands, as calibrations were based on single treatments.

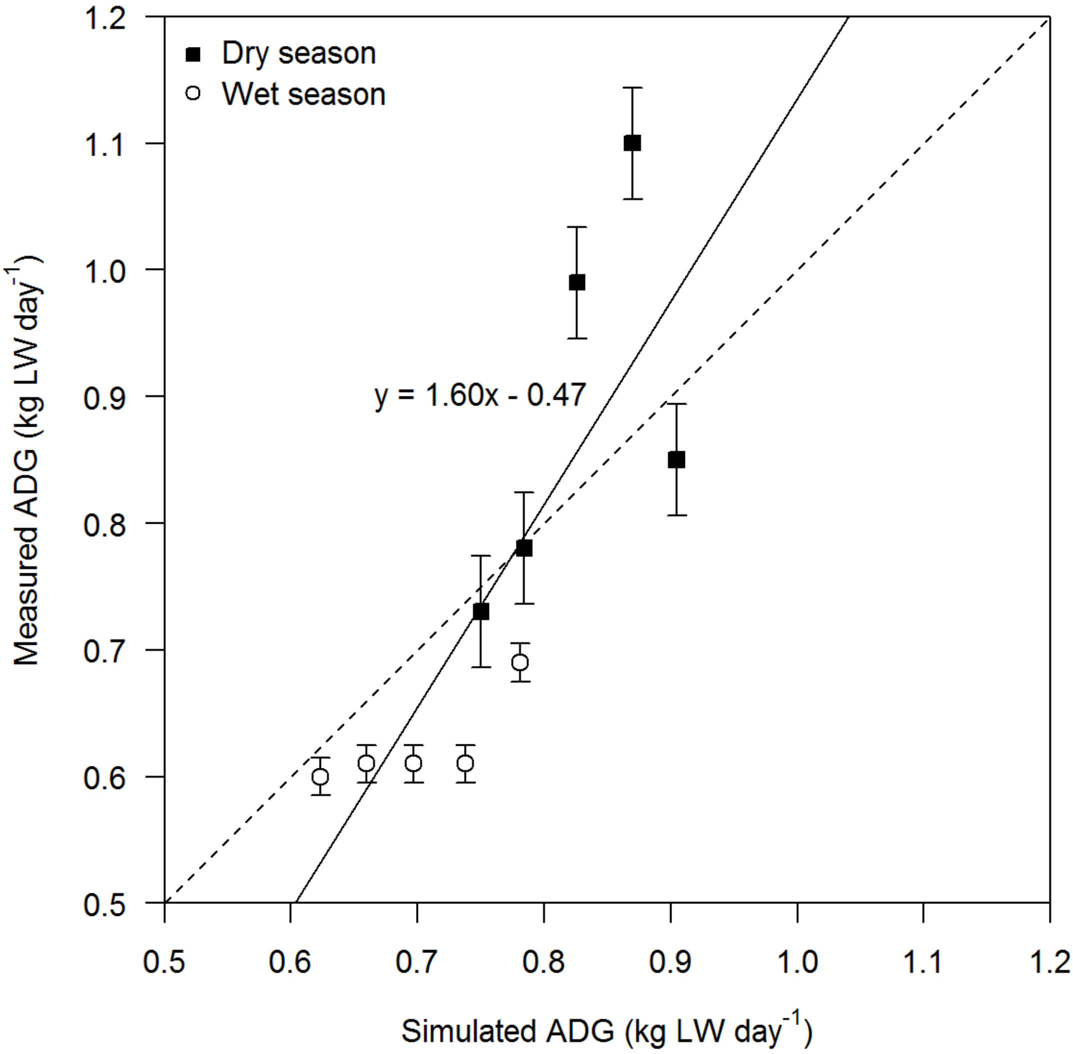

Figure 4.2 Comparison between simulated and measured average daily gain (ADG) for the calibration dataset in Australia. Measured data are from Petty *et al.* (1998). Bars indicate standard errors. LW = live weight.

4.3.2 General model comparison

Comparison of simulated and measured ADGs of the independent datasets from Australia, Uruguay, and the Netherlands, resulted in a MAE of 0.147 kg TBW day^{-1}, or 18.3% of mean measured ADG. The RMSE was 0.183 kg TBW day^{-1}, or 22.9% of measured ADGs. The regression line (R^2-adj. = 0.43) had an intercept significantly different from zero (*P* = 0.009), and a slope significantly different from one (*P* = 0.003). The largest difference between simulated and measured ADGs was observed for cattle in the heathland area in the Netherlands (Fig. 4.3). Chemical analysis of bones indicated that cattle in the heathland area had mineral deficiencies (Wallis de Vries, 1996). Without the heathland dataset, the MAE was 0.128 kg TBW day^{-1}, or 15.4% of mean measured ADG. The RMSE was 0.152 kg TBW day^{-1}, or 18.3% of

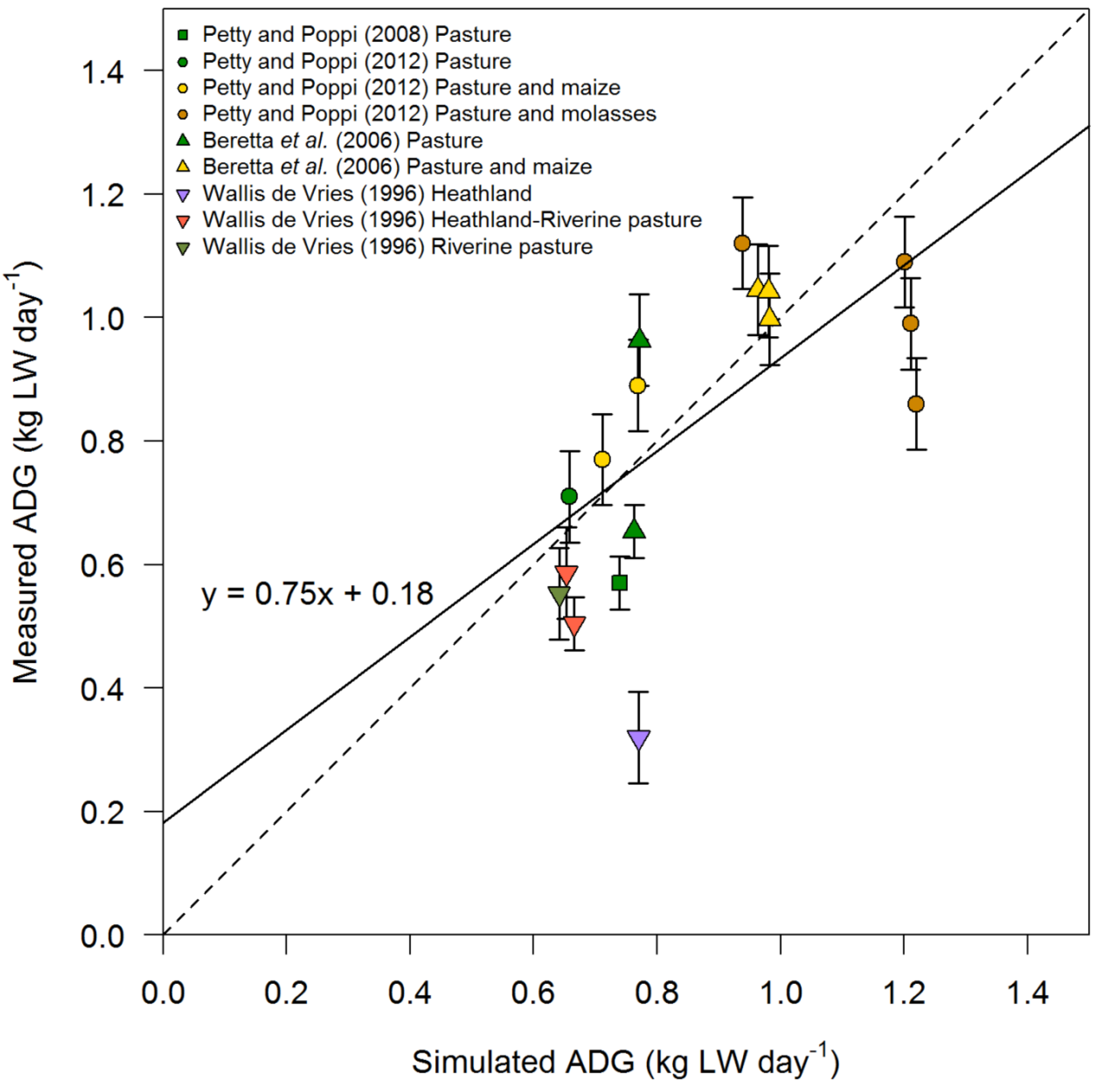

Figure 4.3 Comparison between simulated and measured average daily gain (ADG) for the independent datasets. Bars indicate standard errors. Data of Petty and Poppi are from Australia, data of Beretta *et al.* (2006) from Uruguay, and data of Wallis de Vries (1996) from the Netherlands. The heathland area of Wallis de Vries is excluded in the solid regression line. LW = live weight.

measured ADG. The regression line (R^2-adj. = 0.50) had an intercept not significantly different from zero (P = 0.097), and a slope (0.75 kg kg^{-1}) significantly different from one (P = 0.001).

So far, model comparison was only conducted for ADGs, but it can be extended to feed intake, if measured in experiments. Comparison of *ad libitum* simulated and measured pasture intake for the dry and wet season in Australia from Petty *et al.* (1998) indicated that LiGAPS-Beef overestimated measured pasture intake, especially at low pasture intake (MAE = 1.05 kg DM day^{-1}, or 21.0% of mean measured intake, R^2-adj. = 0.55) (Supplementary Figure S7). The intercept and slope of this regression line were significantly different from zero (P = 0.002) and one (P = 0.007).

4.3.3 Specific model comparison and constraining factors in Australia, Uruguay and the Netherlands

Australia

The MAE of simulated ADGs for B×S cattle in Australia was 18.1% of the mean measured ADG. Simulated ADGs were lowest if cattle had access to pasture only, without supplementation of maize or molasses. Increasing maize availability in Petty *et al.* (1998) and Petty and Poppi (2012) resulted in increasing ADGs (Supplementary Table S1, Supplementary Figures S1-S5, S8-S9, S14-S15). Supplementation with 1.25 and 2.50 kg molasses in Petty and Poppi (2012) increased ADG compared to no supplementation, but more molasses did not further increase ADGs (Supplementary Table S1, Supplementary Figures S9-S13). For the experiment of Petty *et al.* (1998), simulated ADGs were higher in the dry season compared to the wet season. The climate was the most constraining factor according to the model, causing heat stress during most of the experimental periods, except if molasses was fed at 2.50 kg $head^{-1}$ day^{-1} or more (Supplementary Table S1). For these amounts of molasses, the genotype was most constraining for growth, especially at supplementation of 3.75 or kg molasses $head^{-1}$ day^{-1} or higher. Using a temperature humidity index (THI) (Mader *et al.*, 2006), the average THI values were 70 in the dry season and 81 in the wet season in the experiment of Petty *et al.* (1998). Feed quality was constraining ADG for 20% of the experimental period in Petty and Poppi (2008). Protein deficiency only occurred in the experiment of Petty and Poppi (2012) with 5.00 kg molasses (Supplementary Table S1).

Uruguay

The MAE of simulated ADGs for Hereford cattle in Uruguay was 9.8% of the mean measured ADG. Simulated ADG was lowest with a pasture availability of 3% of the TBW without maize supplementation. The ADG increased with a pasture availability of 6% of the TBW, but did not further increase with an availability of 9% of the TBW. The ADGs were increased by maize supplementation to similar levels, irrespective of

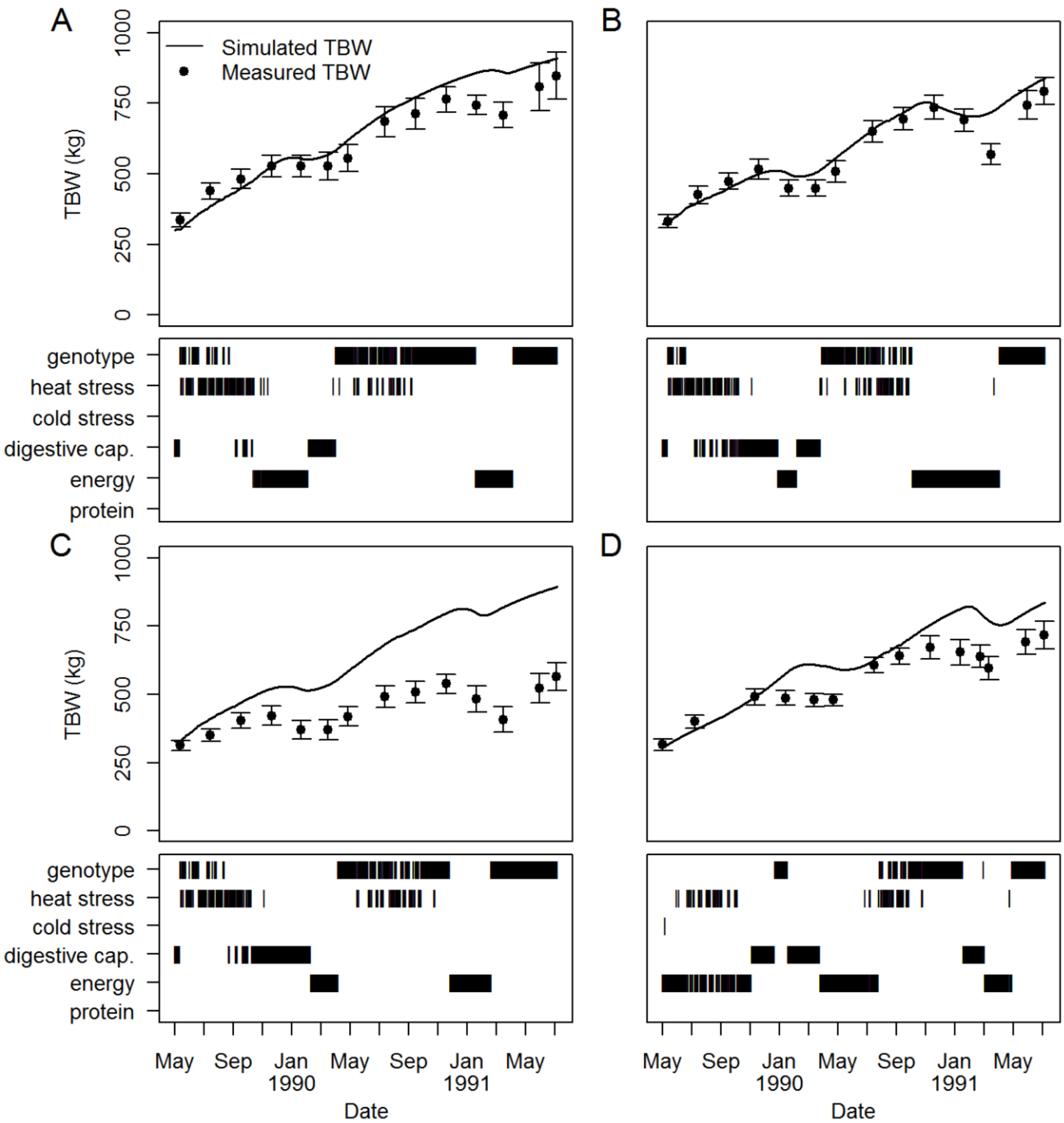

Figure 4.4 Simulated and measured total body weight (TBW) and constraining factors for Meuse-Rhine-Yssel cattle grazing in a riverine area (A), a riverine area during summer and a heathland area during winter (B), a heathland area (C), and a connected riverine / heathland area (D). Bars indicate confidence intervals. The most constraining factors are indicated for each day. Measured data are from Wallis de Vries (1996).

the amount of pasture available. Genotype and heat stress were the constraining factors with maize supplementation, whereas feed quality and quantity (energy deficiency) were also constraining growth without supplementation (Supplementary Table S2, Supplementary Figures S16-21). Calculated THI values (Mader *et al.*, 2006) in the experiment were above 74 for four days.

Table 4.2 Parameters in the model affecting feed efficiency most at herd level after a -10% and +10% change in their parameter values (table continued on next page).

	B×S cattle, Australia, potential			B×S cattle, Australia, feed-limited		
Rank	Parameter	Change	Sub-model	Parameter	Change	Sub-model
1	Gestation period	10.4%	E	NE for maintenance	14.0%	E
2	DE to ME conversion	8.2%	F	Maintenance multiplier	14.0%	E
3	NE for maintenance	5.7%	E	DE to ME conversion	11.0%	F
4	Maintenance multiplier	5.7%	E	Body area multiplier	10.3%	T
5	Slope Lucas equation	4.4%	E	Body area	10.3%	T
6	Protein accretion efficiency	3.2%	E	Gestation period	10.1%	E
7	N recycling	3.1%	E	Body temperature[a]	8.5%	T
8	Carcass fraction	2.8%	E	Sweating capacity[b]	7.2%	T
9	Carcass growth	2.6%	E	Conductivity body core-skin	6.8%	T
10	Weaning age	2.3%	E	Temperature exhaled air	6.3%	T

DE = digestible energy; ME = metabolisable energy; NE = net energy, E = energy and protein utilisation sub-model; F = feed digestion sub-model; T = thermoregulation sub-model

[a] Body temperature was increased by 1 °C.

[b] Sweating capacity was increased by 1%.

The Netherlands

Simulated ADGs for Meuse-Rhine-Yssel cattle in the Netherlands were, on average, between 0.64 and 0.77 kg day^{-1} (Supplementary Table S3, Supplementary Figures S22-S25). Both simulated and measured ADGs were low or negative during winter, and high during spring and summer. The simulated ADG in the heathland area (0.77 kg ADG day^{-1}) was more than twice as high as the measured ADG (0.32 kg ADG day^{-1}) (Figs 4.3 and 4.4C). Excluding the heathland area, the MAE of simulated ADG was 19.3% of the mean measured ADG. The maximum measured ADG was 2.30 kg per head per day for cattle grazing in the riverine area during summer and in the heathland area in winter. Simulations indicated that the genotype was generally a constraining factor from late spring until late summer or early autumn. Heath stress occurred in summer periods. THI values (Mader *et al.*, 2006) in the experiment were below 74 (normal) in the experiment. Digestive capacity and energy deficiency were generally constraining growth in the winter period, and they were more frequent in the winter of 1989/1990 than in the winter of 1990/1991 (Fig. 4.4).

4.3.4 Sensitivity analysis

At herd level, change in FE as a result of change in individual biological parameters was generally lower under potential production than under feed quality limited production (Table 4.2, Supplementary Figure S26). Under potential production in Australia and Uruguay, none of the ten most sensitive parameters was from the thermoregulation sub-model. Under feed quality limitation, however, six out of these ten parameters were from the thermoregulation model in Australia, and five out of these ten parameters in Uruguay. Conversion of digestible energy (DE) to metabolisable energy (ME), NE requirements for maintenance, a multiplier of NE

Table 4.2 Continued.

	Hereford cattle, Uruguay, potential			Hereford cattle, Uruguay, feed-limited		
Rank	Parameter	Change	Sub-model	Parameter	Change	Sub-model
1	Gestation period	9.9%	E	Maintenance multiplier	12.4%	E
2	DE to ME conversion	9.2%	F	NE for maintenance	12.4%	E
3	NE for maintenance	5.9%	E	DE to ME conversion	12.2%	F
4	Maintenance multiplier	5.9%	E	Gestation period	11.7%	E
5	Slope Lucas equation	3.2%	E	Body area multiplier	6.9%	T
6	Carcass fraction	3.0%	E	Body area	6.9%	T
7	Min. weight for gestation	2.6%	E	Body temperature[a]	6.6%	T
8	Initial carcass weight	2.5%	E	Min. weight for gestation	4.1%	E
9	Rate constant Gompertz curve	2.4%	E	Temperature exhaled air	4.0%	T
10	Weaning age	2.2%	E	Conductivity body core-skin	3.9%	T

DE = digestible energy; ME = metabolisable energy; NE = net energy, E = energy and protein utilisation sub-model; F = feed digestion sub-model; T = thermoregulation sub-model

[a] Body temperature was increased by 1 °C.

requirements for maintenance, and the gestation period were among the ten most sensitive parameters under potential and feed quality limited production at herd level in Australia and Uruguay (Table 4.2). Besides these four parameters, three out of the six remaining parameters were the same under potential production, and five out of the six parameters were the same under feed-limited production. After a 10% change in parameters, the change in FE exceeded 10% with one parameter under potential production in Australia, and with six parameters under feed quality limited production. Change in FE exceeded 10% upon changing four parameters under feed quality limited production in Uruguay (Table 4.2).

4.4 Discussion

4.4.1 General model comparison

A key assumption for model comparison was that ADG in experiments was not affected by growth limiting factors such as vitamins and minerals, and by growth reducing factors (diseases and stress). Chemical analysis of bones, however, provided evidence that sodium, phosphorus, and calcium deficiencies limited growth of cattle in the heathland area in the Netherlands (Wallis de Vries, 1996). These minerals are not included in LiGAPS-Beef. Given the strong evidence for mineral deficiencies, and the large discrepancy between simulated and measured ADG in the heathland area (Figs 4.3 and 4.4C), it seems justified to exclude the data of cattle kept in the heathland area from the independent dataset. Mineral deficiencies might also have played a role in the other experiments, but to a lesser extent. The same holds for vitamins, drinking water, diseases, and stress, but the extent to which they might have affected ADG seems fairly limited, given the fit between simulated and measured ADGs (Fig. 4.3).

Model calibration resulted in a relative MAE of 11.3% of the mean average ADG, whereas the MAE was 15.4% for the ADGs under model comparison. This indicates that the largest part of the MAE is not captured with LiGAPS-Beef, even under calibration. One explanation for this could be unexpected results in experiments. For example, feeding cattle 2.0 kg FM maize head^{-1} day^{-1} in the experiment of Petty *et al.* (1998) resulted in lower ADG than feeding 1.0 or 1.5 kg FM maize head^{-1} day^{-1} (Supplementary Table S1), which seems to be conflicting with our knowledge of animal nutrition. The regression line between simulated and measured ADGs had an intercept not significantly different from zero, but a slope significantly different from one, which indicates that simulated ADGs did deviate significantly from measured ADGs. As a comparison, the grass growth model LINGRA (Light INterception and utilisation – GRAss) had a relative MAE between 13-21% for different locations across Europe, which is considered a good performance for a crop growth model (Bouman *et al.*, 1996). Hence, the MAEs of LiGAPS-Beef and LINGRA are in the same range, although both MAEs cannot be compared directly due to differences in the precision of experimental measurements.

Whether this model performance is sufficient depends on the research aim and context. LiGAPS-Beef aims to simulate potential and limited beef production in different systems across the globe, and to identify constraining factors for cattle growth. We deem the current performance of LiGAPS-Beef as reasonable to good. The constraining factors for growth affect the simulated ADGs. Because ADGs are estimated fairly well with LiGAPS-Beef in different beef production systems, it seems plausible that the constraining factors for growth are estimated reasonably well too. This holds promise for LiGAPS-Beef as a tool to identify constraining factors in a generic way. Such factors form key information in yield gap analyses. Based on the constraining factors identified, one can next identify promising options to narrow yield gaps.

LiGAPS-Beef was calibrated for ADGs in the experiment of Petty *et al.* (1998), and not for feed intake. The relative MAE of feed intake was 21%, which may be high for a dataset that is calibrated for ADG. Feed intake from this experiment was overestimated with LiGAPS-Beef at low feed intake. Petty and Poppi (1998) used pasture cages to calculate feed intake. Using different measurement techniques can result in different estimates of pasture intake, even in the same experiment (Undi *et al.*, 2008). The discrepancy between simulated and measured feed intake may be caused, next to inaccurate model assumptions, by unexpected and inexplicable results.

4.4.2 Specific model comparison and constraining factors in Australia, Uruguay, and the Netherlands

Australia

The ADG was overestimated for the experiment of Petty and Poppi (2008). Pasture quality was stable in 1992/1993 over the wet and dry season, and it was therefore assumed, that pasture quality was similar for the experiments conducted in other years (Petty and Poppi, 2008). Hence, overestimation of feed quality seems no likely explanation for the overestimation of ADG, and its cause remains unknown. Although LiGAPS-Beef estimated trends in ADGs reasonably well in general, cattle fed with higher levels of molasses showed larger deviations. Increasing supplementation of molasses resulted in a quadratic decrease in measured ADGs (1.12 kg to 0.86 kg head^{-1} day^{-1}) (Petty and Poppi, 2012), but simulated ADGs showed an inverse trend (0.94 kg to 1.22 kg head^{-1} day^{-1}). Acidosis might not explain the negative quadratic relation between molasses supply and ADG, as Brahman crossbred steers fed with high proportions of molasses (50 and 75%) showed no severe decrease in rumen pH. Increasing molasses supplementation decreases fibre digestibility of the whole diet significantly, but total digestibility increases significantly (Tuyen *et al.*, 2015). Causes for decreasing ADGs under high molasses supply are not fully clarified yet, and consequently cannot be included in the model. Model users should be careful when simulating high molasses supplementation with LiGAPS-Beef.

Model simulations indicated that heat stress was the most constraining factor for growth in Australia, except at high molasses supplementation in the experiment of Petty and Poppi (2012) (Supplementary Table S1). The average THI value of 70 in the dry season indicates that heat stress can exist, and the average THI value of 81 in the wet season indicates emergency (Mader *et al.*, 2006). Hence, THI values are in agreement with model simulations and notions of Petty *et al.* (1998) that heat dissipation might have limited feed intake and ADG. Feed quality limitation was identified as a constraining factor in the experiment of Petty and Poppi (2008), but hardly in the other two experiments (Supplementary Table S1). Cattle in the experiment of Petty and Poppi (2008) had lower body weights at the start of this experiment than in the other two experiments, and consequently their maximum intake expressed in fill units was lower. Because urea was added to molasses, protein limitations were not expected in the experiment of Petty and Poppi (2012), but simulations with 5.0 kg molasses per head per day identified protein deficiency as a constraint (Supplementary Table S1). Even if urea (30 g kg^{-1} molasses) would be fully converted in protein, this would yield 86 g protein per kg molasses, which is relatively low compared to grasses. Hence, protein deficiencies might have affected ADG at very high molasses supplementation.

Uruguay

Simulated ADGs were 0.76 and 0.77 kg per head per day for cattle without maize supplementation and a pasture availability of both 6 and 9% of TBW (Supplementary Table S2). Measured ADGs (0.65 and 0.96 kg per head per day) differed considerably, as well as pasture intake (2.6% and 4.3% of the TBW per day). An explanation for these differences is that the quality of pasture actually consumed increases with increasing pasture availability, as this offers more opportunities for diet selection (Zemmelink, 1980, Beretta *et al.*, 2006). Data on pasture quality for the different treatments were, however, not collected in the experiment. Simulated and measured ADGs were similar with maize supplementation, irrespective of pasture availability (Fig. 4.3). This result is in line with the expectation that maize supplementation reduces dependency of cattle on pasture. Genotype and heat stress were the constraining factors with maize supplementation in Uruguay (Supplementary Table S2). THI values indicated an alert for heat stress for four days in the experiment, which corresponds to the simulations identifying heat stress as a constraining factor.

The Netherlands

Body weight dynamics were generally within the confidence intervals in the riverine area and with grazing in the riverine area during summer and in the heathland during winter (Fig. 4.4). For the latter area, the ADG between the third and second last measurement was 2.3 kg per head per day, which seems exceptionally high. To our knowledge, such ADGs are not likely, and they may be explained by varying rumen contents of cattle during TBW measurements. Model simulations did not identify cold stress as a major constraint for growth (Supplementary Table S3), which may be explained by the relatively high weights of cattle in the experiments. Digestive capacity and energy deficiency were limiting cattle growth in winter (Fig. 4.4). This result is not surprising, as feed quality and available feed quantity are expected to be low in nature areas during winter (Supplementary Table S3).

4.4.3 Validity domain and future applications of LiGAPS-Beef

Overall model performance was reasonable to good, but performance in the three countries resulted in mixed outcomes. In line with its aim, LiGAPS-Beef is assumed to be generically applicable to beef production systems across the world with different breeds, climates, and feeding strategies. The global validity domain assumed for LiGAPS-Beef can be backed up by model comparison against independent experimental data in Australia, Uruguay, and the Netherlands. Hereford and Meuse-Rhine-Yssel cattle belong both to *B. taurus* breeds, but the MAE in Uruguay was smaller than in the Netherlands (Table 4.3). Although the MAE differs between Uruguay and the Netherlands, both countries have a temperate climate. The MAE in Uruguay was smaller than in Australia and the Netherlands (Table 4.3). Still, model simulations that did not capture the variation in ADG very well for nonsupplemented cattle grazing on pasture in Uruguay (Fig. 4.3). Diet quality constrained cattle growth in the Netherlands, but was hardly constraining growth in Australia. Nevertheless, the MAE of these two countries were similar (Table 4.3). Model comparison for B×S cattle in Australia showed that ADGs for cattle supplemented with high levels of molasses (3.75 and 5.0 kg per head per day) were overestimated, but ADGs for cattle in Australia supplemented with maize (0.75 and 1.5 kg per head per day) resembled measured ADGs reasonably well.

Due to these mixed results on model performance with different breeds, climates and feeding strategies, the model validity domain cannot be delineated in much detail. Further model evaluation is required to assess the validity domain of LiGAPS-Beef. Given that LiGAPS-Beef estimated ADGs reasonably well to good, future applications of LiGAPS-Beef may focus on assessing yield gaps in specific beef production systems. The constraining factors for growth simulated by the model can subsequently be used in yield gap analysis to identify which factors constrain cattle production most. The next step would be to explore bio-physical improvement options to mitigate some of the most constraining factors. Taking into account economics (*e.g.* input and output prices), social considerations (*e.g.* labour requirements, education), and animal welfare, the most promising and feasible improvement options could be implemented.

The conversion from DE to ME, NE requirements for fasting maintenance, the multiplier of NE requirements for fasting maintenance, and the gestation period were among the parameters affecting model output most in each of the scenarios (Table 4.2). Increasing the efficiency of the DE to ME conversion increases also the NE available for metabolic processes, such as growth, which explains why this parameter affects FE to a large extent. Decreasing the NE requirements for maintenance, or the maintenance multiplier (similar effect) increases the NE available for growth. Increasing the gestation period results in a higher feed intake by the cow per calf produced, and consequently, the feed efficiency decreases. Besides these four parameters that are consistently in the top ten of the most sensitive

Table 4.3 Mean average error (MAE), expressed as a percentage of the mean measured average daily gain (ADG), in Australia, Uruguay, and the Netherlands, under calibration, comparison with independent datasets.

		Countries		
	Overall MAE	Australia	Uruguay	The Netherlands[a]
Calibration ADG	-	11.3%	-[b]	-[b]
Comparison ADG[c]	15.4%	18.1%	9.8%	19.3%

[a] The ADG from the heathland area is not included due to mineral deficiencies.

[b] Calibration was done for one treatment in Uruguay and the Netherlands, resulting in the same measured and simulated ADGs.

[c] Comparison of simulated ADGs from LiGAPS-Beef with measured ADGs from independent datasets.

parameters, there were another three common parameters under potential production in Australia and Uruguay, which were all from the energy and protein utilisation sub-model. These parameters are the slope of the Lucas equation to assess protein digestibility, the carcass fraction, and weaning age (Table 4.2). Increasing the slope of the Lucas equation increases the protein digestibility of feeds, and also their energy digestibility, as protein also contains GE. As expected, increasing the carcass fraction increases the feed efficiency. Increasing the weaning age increased the feed conversion efficiency of calves (more milk intake per calf) and cows (less calves and associated milk production per cow at similar culling rates).

There were another five common parameters under feed-limited production in Australia and Uruguay. These parameters were the body area, the body area multiplier, body temperature, conductivity between body core and skin, and temperature of the exhaled air, which were all from the thermoregulation sub-model (Table 4.2). Increasing the body area (or its multiplier), the conductivity between body core and skin, and the temperature of exhaled air allows an animal to release more heat. Decreasing body temperature decreases the temperature difference between the body core and the outside environment, which decreases heat release. Apart from the four parameters common to all scenarios, other common parameters under potential production were from the energy and protein partitioning sub-model, and from the thermoregulation sub-model under feed-limited production. This could be explained by the higher heat increment of feeding and consequently a higher heat production under feed-limited production, which makes thermoregulation and heat release more urgent compared to potential production.

Most parameters were changed by 10% in the sensitivity analysis, but their variance is often unknown. A parameter for calculation of the body area appeared in the top ten most sensitive parameters under feed quality limited production (Table 4.2). The body area of a 400 kg animal decreases by 41% upon a 10% decrease in this particular parameter, according to the formula used to calculate body area from body weight (Thompson, 2011). In comparison, the body area of *B. indicus* cattle is only 12% larger than for *B. taurus* cattle at the same weight (Johnston *et al.*, 1958). A 10% change in this particular parameter is, therefore, not very likely. The same holds for more parameters, such as the gestation period, which was among the most sensitive parameters in each of the scenarios (Table 4.2). Values of 0.81 or 0.82 are generally accepted for DE to ME conversion, and a value of 0.85 may be appropriate for diets containing high percentages of cereal grains (CSIRO, 2007). Even with grain-based diets, a change of 10% in this conversion is not expected. Fasting maintenance requirements are known to vary between breeds and sex (NRC, 2000). As its variance often is not fully known, NE requirements for fasting maintenance should be prioritized to be measured more precisely. A limitation of this sensitivity analysis is that one parameter was increased at a time while the others were kept constant. We did not investigate effects of changing combinations of parameters, except for the parameters of the Gompertz curves.

4.5 Conclusions

LiGAPS-Beef has been designed to be applicable to different beef production systems across the world. This paper evaluates model performance for beef production systems in Australia, Uruguay, and the Netherlands strongly differing in cattle breeds, climates, and feeding strategies. Model estimates for ADGs resembled measured ones from independent datasets at animal level reasonably well to good (MAE = 0.128 kg TBW day^{-1}, or 15.4% of mean measured ADG). The model accuracy in estimating ADGs suggests that the underlying constraining factors for growth are also likely to be estimated reasonably well. This opens opportunities to use LiGAPS-Beef as a tool for yield gap analysis and simulation of improved practices to mitigate the yield gap. Sensitivity analysis showed that model output is less sensitive to a 10% change in parameters under potential production than under feed quality limited production. Model output was affected most by parameters from the energy and protein utilization sub-model under potential production, and by parameters from the thermoregulation sub-model and energy and protein utilisation sub-model under feed quality limited production.

Additional information

Supplementary Information accompanying this Chapter is available at http://dx.doi.org/10.18174/406580. The source code of LiGAPS-Beef is freely accessible at http://dx.doi.org/10.18174/386763. Updates and model applications will be published on the model portal of the Plant Production Systems group of Wageningen University, the Netherlands (http://models.pps.wur.nl/content/ligaps-beef).

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Chapter 5

Yield gap analysis of feed-crop livestock systems: the case of grass-based beef production in France

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This Chapter is under review

Abstract

Sustainable intensification is a strategy contributing to global food security. The scope for intensification in crop sciences is assessed through yield gap analysis using crop growth models based on concepts of production ecology. In earlier publications, concepts of production ecology were applied to livestock production, which resulted in a model for beef cattle named LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle). This paper aims to assess yield gaps of feed-crop livestock systems, to analyse the underlying causes of the yield gaps, and to identify feasible improvement options, for the case of grass-based beef production systems with Charolais cattle in the Charolais area of France. We combined LiGAPS-Beef with a grass growth model to simulate cattle grazing pasture. A wheat growth model simulated the growth of wheat for concentrate production, and a grass growth model simulated the grass growth for the production of hay and grass silage. Cattle and feed crop production were integrated to simulate potential and resource-limited live weight (LW) production per hectare. Potential production with an *ad libitum* grass silage diet was 2.38 t LW ha^{-1} $year^{-1}$. Actual LW production is 15% of this potential, in other words, the relative yield gap is 85%. This yield gap is explained by feeding diets other than the *ad libitum* grass silage diet (41% of potential production), water-limitation in feed crops (31%), culling rates, sale or slaughter weights, calving dates, age at first calving, and stocking densities (9%), and calving interval and calf mortality (2%). Beef production under feed-limited cattle growth and water-limited grass growth was 0.66 t LW ha^{-1} $year^{-1}$, resulting in a relative yield gap of 47%. Yield gap mitigation decreased the operational profit per kg LW under the regulations for bovine and grassland subsidies operational in 2014, showing that policies were not conducive to narrow yield gaps. The method applied in this study is generic, and we argue, therefore, that yield gap analysis based on concepts of production ecology can be applied to other feed-crop livestock systems in the world also.

5.1 Introduction

Sustainable intensification is proposed as a possible strategy to increase food production on existing farmland, while reducing negative impacts of agriculture on the environment (Garnett *et al.*, 2013). The scope for intensification in agriculture can be assessed by mechanistic models based on concepts of production ecology (Van Ittersum and Rabbinge, 1997, Evans and Fischer, 1999, Van der Linden *et al.*, 2015). These bio-physical models simulate potential (*i.e.* theoretical maximum) and resource-limited production, and can be used to identify the major bio-physical constraints for production. The difference between potential or resource-limited production, and actual production achieved on farms, is defined as the so-called yield gap, which indicates the bio-physical scope to intensify production on a given area (Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013).

Mechanistic models can be used also to identify constraining bio-physical factors for crop growth, which is a crucial step in yield gap analysis. Insights from yield gap analyses contribute to the exploration of improvement options that increase production and mitigate yield gaps. Yield gap analysis has been applied numerous times in crop production systems with local to more global approaches (Van Ittersum *et al.*, 2013). Assessing yield gaps of crops with mechanistic models is widely established in crop sciences (Bouman *et al.*, 1996, Jones *et al.*, 2003, Keating *et al.*, 2003).

Although concepts of production ecology were initially applied in crop sciences only, they have been extended to the livestock sciences (Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015). This led to the development of LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle), a mechanistic model simulating potential and feed-limited growth of beef cattle. This model simulates cattle growth, and can be used to identify constraining factors for beef and live weight (LW) production (Van der Linden *et al.*, 2017a). Model evaluation showed that LW gain was simulated reasonably to good (Van der Linden *et al.*, 2017b).

LiGAPS-Beef seems an adequate tool to analyse yield gaps in beef production systems, and yield gap analysis based on concepts of production ecology has not been applied to livestock systems yet. Livestock production is dependent on feed production, and feed production has to be taken into account to when assessing the scope to increase livestock production per hectare of farmland. The aim of this paper is, therefore, to quantify yield gaps of feed-crop livestock systems, to analyse the yield gaps, and to explore improvement options, for the case of grass-based beef production systems with Charolais cattle in the Charolais area of France.

The Charolais area is the northern part of the Massif Central, which is a major region for beef production in France where 35% of the national suckler-cow herd is kept

(Veysset *et al.*, 2014a). The main breed used in France is the Charolais breed, which accounts for 1.5 million suckler cows out of the 4.1 million. In the Charolais area, 41% of the French Charolais cows are kept (Veysset *et al.*, 2015). The Charolais area was selected as a case for yield gap analysis because of its important contribution to beef production in France, good data availability, and scope to increase farm profitability via yield gap mitigation. Beef production systems in the Charolais area are dependent on coupled and decoupled premiums (*i.e.* respectively premiums linked to and independent of cattle production) from the European Union's common agricultural policy (CAP), and the value of premiums received by farmers is larger than their net income (Veysset *et al.*, 2005, Veysset *et al.*, 2014b).

5.2 Materials and Methods

5.2.1 General approach

Yield gaps for beef production systems in the Charolais area were quantified from the perspective of a feed-crop livestock system. The feed-crop livestock system includes beef cattle and the land area to produce all the feed consumed by these cattle, irrespective whether it was produced on-farm or off-farm. Cattle production was expressed as feed efficiency (FE), in kg LW per ton dry matter (DM), whereas crop production was expressed as annual yield, in ton DM per hectare per year. Multiplication of cattle and crop production results in kg LW production per hectare per year (Van der Linden *et al.*, 2015).

All feed was assumed to be produced in the Charolais area of France. Concentrates fed to cattle were represented by wheat. Grasslands were assumed to consist of perennial ryegrass (*Lolium perenne* L.) only. Yield gaps in feed-crop livestock systems were defined as the difference between potential (or resource-limited) LW production and actual LW production per hectare (Van der Linden *et al.*, 2015). Potential crop production is determined by the genotype of the crop species, and the climate. Limited crop production is determined by water and nutrient supply, in addition to the genotype and climate (Van Ittersum and Rabbinge, 1997). Potential production is the most relevant benchmark for irrigated crop production, and water-limited production for rainfed crop production (Van Ittersum *et al.*, 2013). In analogy, potential livestock production is determined by the genotype of the livestock species, and the climate. Limited livestock production is determined by feed quality and the quantity of available feed (Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015).

Potential, resource-limited, and actual production were assessed for both feed crops and cattle. Actual production in the Charolais area was calculated from literature (Veysset *et al.*, 2005, Réseaux d'Élevage Charolais, 2014, Veysset *et al.*, 2014a). Potential and feed-limited production of beef cattle were simulated with the model LiGAPS-Beef (Van der Linden *et al.*, 2017a). Potential and water-limited production of fresh grass, hay, grass silage, and wheat were simulated with crop growth models, whereas potential and water-limited production of maize were adopted from literature. Grass production for hay and grazing was simulated with the model LINGRA (Light INterception and utilization – GRAss) (Schapendonk *et al.*, 1998). LiGAPS-Beef was combined with LINGRA, accounting for the mutual influence of cattle and grass. Next, yield gaps were quantified, their major causes were identified, and improvement options for yield gap mitigation were explored.

5.2.2 Actual production

Actual production was calculated for twelve farm types with Charolais cattle (Réseaux d'Élevage Charolais, 2014). A farm type represents a typical farming system among the diversity of systems found in the Charolais area, and it reflects the consistent functioning of this system. Data for the farm types are multiple-year averages, and were derived from observations (farm networks) and expert knowledge. Eight out of the twelve selected farm types were cow-calf systems, where calves are sold to fattener systems. Four farm types were cow-calf-fattener systems that produced heavy calves (678-715 kg LW) for slaughter (Table 5.1). The peak in calving ranged from late December to late March in the farm types. Cattle grazed from spring to autumn, and were housed during winter. Farm types specialised in beef production had actual wheat yields of 5.0 t DM ha^{-1} $year^{-1}$, and farm types focusing on beef *and* cereal crops had yields of 5.6 t DM ha^{-1} $year^{-1}$ (Veysset *et al.*, 2014a). Actual grass intake on permanent grassland was 4.8 t DM ha^{-1} $year^{-1}$, and grass intake from grazing after hay production was 1.9 t DM ha^{-1} $year^{-1}$ (Veysset *et al.*, 2005). Grass intake was assumed to be equal for all farm types, since it was not specified per farm type. Actual maize (10.0-10.5 t DM ha^{-1} $year^{-1}$) and hay production (3.2-5.7 t DM ha^{-1} $year^{-1}$) in the farm types were based on Réseaux d'Élevage Charolais (2014). Wheat, maize, hay, and grass production per hectare were multiplied with their respective area to calculate the total feed intake of the cattle herd per year. We assumed that feed stocks do not decrease or accumulate over the years. The percentage of wheat in the diets fed varied between farm types from 4.8% to 17.0%. Three farm types cultivated maize on-farm, which was fully used as a cattle feed. Supplementation of maize accounted for 8.3% to 10.4% of the diet in these farm types. Maize biomass (grain content 50% of the DM) was fully harvested at the end of September and ensilaged. The total percentage of cereals in the diet was calculated as the percentage of wheat plus 50% of the percentage of maize silage, where the latter represents the grain content of maize silage. Data of actual LW production were available at farm level (Réseaux d'Élevage Charolais, 2014) (Table 5.1). The actual FE was calculated as the total LW production (kg LW per year) divided by the total feed production (t DM per year) for each of the farm types. Production was expressed as LW in all farm systems, because carcass or edible beef weights were not available for the cow-calf systems due to off-farm fattening. The

Table 5.1 Farm characteristics of twelve farm types in the Charolais area of France (Réseaux d'Élevage Charolais, 2014).

Number farm type[a]	Calf fattening	Grassland area (ha)	Percentage grassland in total area (%)	Hay production (t DM $year^{-1}$)	Concentrate intake (t FM $year^{-1}$)	Number of cows	Selling weight male calves (kg LW)[b]	Selling weight female calves (kg LW)[b]	LW production (t $year^{-1}$)	Revenue beef production (k€ $year^{-1}$)	Number of workers[c]
11021	no	71	91.0	136	41.4	60	352	300	22.7	48.9	1.0
11031	no	117	90.7	183	68.9	90	420	423	39.6	87.1	1.5
11065	no	118	90.8	188	89.3	104	400	372	42.0	95.3	1.5
11105	no	120	100.0	203	48.6	98	470	390	39.6	93.7	1.5
11111	no	280	100.0	460	87.0	215	460	435	85.5	193.5	2.5
11131	yes	130	83.9	264	139.5	106	699[d]	713[d]	68.4	151.6	1.7
11140	yes	127	81.9	314	168.4	115	715[d]	678[d]	77.0	168.5	2.5
21010	no	82	65.6	163	48.7	76	330	300	28.6	63.3	-
21020	no	110	78.6	186	66.2	87	420	420	38.6	88.2	-
31020	no	67	38.3	145	56.3	65	395	350	27.7	61.3	-
31041	yes	130	46.4	283	190.2	92	699[d]	718[d]	61.1	134.5	-
31060	yes	168	60.0	349	195.0	168	707[d]	704[d]	96.2	210.1	-

DM = dry matter; FM = fresh matter; LW = live weight.

[a] Numbers of farm types as indicated in Réseaux d'Élevage Charolais (2014).

[b] If calves are slaughtered at different weights, the weighted average is calculated.

[c] The labour allocation between beef cattle and food crops is not given in Reseaux d'Elevage Charolais (2014). The number of workers is given only for farms specialised in beef production, since labour in other farms is used for production of food crops as well.

[d] Calves are fattened on-farm. LW is calculated as 0.615 / carcass weight for male calves, and 0.575 / carcass weight for female calves (Réseaux d'Élevage Charolais, 2014).

Eurostat method was used to calculate the stocking density in livestock units (LUs) for the farm types (Eurostat, 2013).

5.2.3 Potential and resource-limited production

The crop growth model LINGRA was used to simulate the production of hay and grass silage, and to simulate grass production under grazing. Potential and water-limited wheat production were simulated with the model LINTUL-2 (Light INTerception and UtiLization – 2) (Van Ittersum *et al.*, 2003). Both LINGRA and LINTUL-2 require genetic parameters, daily weather data, and information on irrigation and crop management (Fig. 5.1). The genetic parameters used were mainly default values for these models, and non-default parameters are listed in Appendix 5A. Daily weather data were obtained for Charolles, a city in the Charolais area (46.4 °N, 4.3 °E) for the years 1998-2012 (Agri4Cast, 2013). Average temperature (1998-2012) was 11.4 °C, and average precipitation was 790 mm per year. The water holding capacity of the soil in the Charolais area was set at 0.15 cm^3 cm^{-3}, which corresponds to a silty clay loam soil and a silt soil (Piedallu *et al.*, 2011). The total DM loss for production, conservation, and feeding was assumed to be 20% for hay (Van der Linden *et al.*, 2015), and 10% for grass silage and maize silage (Köhler *et al.*, 2013). Water-limited production of feed crops was assumed to occur under rainfed conditions, without additional irrigation. Grass for hay production was harvested each time the aboveground biomass exceeded 4.3 t DM ha^{-1} $year^{-1}$. Under potential or water-limited crop production, nutrient limitations were not taken into account, nor were the effects of pests, diseases, and weeds. Potential and water-limited maize production were not simulated, but based on literature, since it was only fed in three farm types, and no genetic parameters were available for simulation of green maize production. Potential green maize production for silage was assumed 25.2 t DM ha^{-1} $year^{-1}$, and water-limited production 19.6 t DM ha^{-1} $year^{-1}$ in the Charolais area (De Koning and van Diepen, 1992).

Grazing cattle affect pasture growth by defoliation and trampling. Pasture growth, in turn, affects grass intake and growth of beef cattle (Fig. 5.1). LiGAPS-Beef and LINGRA were combined to account for pasture quality, selective grazing, trampling, defoliation of grass by cattle, and effects of feed quality and feed availability on cattle growth. In this chapter, grass production under grazing is assumed equivalent to grass intake. More information on the adaptation and extension of models is provided in Appendix 5A. Yields of wheat, maize, hay, and grass silage were assumed to be independent of cattle production, as these feeds are harvested mechanically.

LiGAPS-Beef was used to simulate potential and feed-limited production of Charolais cattle for all farm types. Breed-specific parameters were the default parameters for

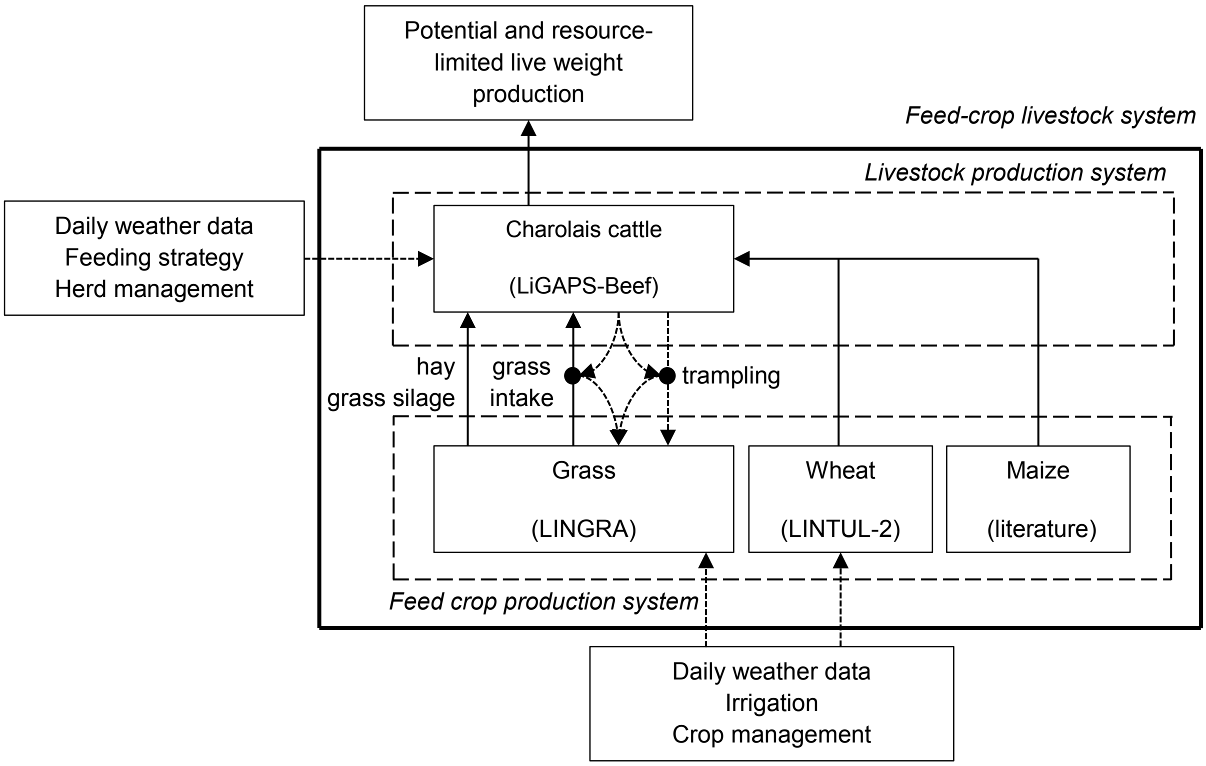

Figure 5.1 Schematic overview of the approach to assess potential and resource-limited live weight production with Charolais cattle in France in a feed-crop livestock system. Solid arrows indicate a flow of mass; dashed arrows information or inputs. LiGAPS-Beef = Livestock simulator for Generic analysis of Animal Production Systems; LINTUL = Light INTerception and UtiLisation; LINGRA = LINtul GRAss.

Charolais cattle listed in LiGAPS-Beef. Daily weather data for LiGAPS-Beef were the same as used for the crop growth models. Mortality of cows, and stress and diseases (unless diseases result in calf mortality) were not accounted for in the model simulations. Drinking water was assumed to be available *ad libitum*. Calves were weaned at 240 days after birth in all model simulations. The total milk production, equivalent to milk intake by the calf, was 1,600 l up to weaning, with a peak milk production of 9 l day^{-1}. The source codes of LINGRA and LINTUL-2 are freely accessible (http://models.pps.wur.nl/model). All models have a daily time step, and are available in the programming language R (R Core Team, 2013).

Three main production levels were defined for integrated feed-crop livestock systems with their (crop) plant and animal (cattle) components. Each production level is represented by a four-letter code: the first two letters indicate the growth conditions of plants (P_P = plants potential; P_L = plants water-limited) and the third and fourth letter indicate the growth conditions of animals (A_P = animals potential; A_L = animals feed-limited).

Table 5.2 Production conditions under the three main production levels for beef production systems in the Charolais area, and their variants. Production conditions can correspond to the actual conditions (x) or are optimized to maximize LW production per hectare (o).

	Production levels			Variants of production levels			
Production conditions	P_LA_L	P_PA_L	P_PA_P	P_LA_L – MMI	P_LA_L – M	P_PA_L – Hay	P_PA_L – Silage
Calf mortality[a]				x			
Calving interval[a]				x			
Culling rate	o	o	o	x	x	o	o
Selling weights calves[b]	o	o	o	x	x	o	o
Calving date	o	o	o	x	x	o	o
Age at first calving[c]	o	o	o	x	x	o	o
Stocking density	o	o	NA[d]	x	x	NA[d]	NA[d]
Diet composition[e]	x	x		x	x		
Housing conditions	x	x	x	x	x	x	x

P_LA_L = resource-limited production; P_PA_L = potential crop production with feed-limited cattle production; P_PA_P = potential cattle production with a 65% wheat and 35% hay diet fed *ad libitum*; P_LA_L – MMI = resource-limited production with actual cattle management, calf mortality, and calving intervals; P_LA_L – M = resource-limited production with actual cattle Management; P_PA_L – Hay = feed-limited cattle production with *ad libitum* hay; P_PA_L – Silage = feed-limited cattle production with *ad libitum* grass silage; NA = not applicable.

[a] Calf mortality is zero, and the minimum calving interval is one year, except for P_LA_L – MMI. Calf mortality and calving interval correspond the actual mortality and interval for P_LA_L – MMI.

[b] Selling weights equal slaughter weights for the cow-calf-fattener systems.

[c] The actual age at first calving is three years. Under optimum management, the age at first calving can be two years.

[d] Optimization of the stocking density is not applicable without grazing.

[e] Diets are specified for P_PA_P (65% wheat; 35% hay), P_PA_L – Hay, and P_PA_L – Silage.

- Production level P_LA_L: feed crop production is water-limited, and cattle production is feed-limited, so we refer to this production level as the resource-limited production for a feed-crop livestock system. Crop management is assumed to be ideal under water-limited conditions, except for the supplementation of water (Van Ittersum and Rabbinge, 1997). Likewise, livestock management is assumed to be ideal under feed-limited conditions, except for the supplementation of feed (Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015). Ideal implies that management decisions on culling rates, selling or slaughter weights, calving dates, age at first calving, and stocking densities are optimized for maximum LW production per hectare (Table 5.2). Culling rates of cows are set to 50% per year per age cohort after the birth of the first calf, which is the maximum culling rate provided mortality is absent. Cows produce, on average, two calves in their lifetime at this culling rate, one male and one female calf. The female calf is used as replacement for the cow (Van der Linden *et al.*, 2015, Van der Linden *et al.*, 2016b). The slaughter weight per calf was assessed in a stepwise procedure with an interval of 50 kg LW to maximize LW production per hectare. Since calves have higher FEs than reproductive cows, maximizing LW production per hectare results in higher selling weights than currently observed in cow-calf systems. Hence, cow-calf systems have to fatten their calves, just like the cow-calf-fattener systems. Farm types that are currently cow-calf systems are thus changed into cow-calf-fattener systems under resource-limited production. Heifers can conceive from 475 kg LW onwards, which is 50% of their maximum adult weight (950 kg LW). The age at first calving can be two years. Calving date (interval: 5 days) and stocking densities (interval: 0.1 cow plus offspring ha^{-1} grassland) were optimized also for maximum LW production per hectare.

- Production level P_PA_L: crop production is potential, and cattle production feed-limited. Cattle production is the same as for P_LA_L, but crop growth is now potential (= irrigated) instead of water-limited. Stocking densities are adapted to the potential grass production to maximize LW production per hectare.
- Production level P_PA_P: potential crop and cattle production. Cattle are fed a diet of 65% wheat and 35% hay *ad libitum*. This diet is assumed to sustain the potential growth of cattle (Van der Linden *et al.*, 2015, Van der Linden *et al.*, 2017a).

Besides these three main production levels, two variants of the resource-limited production (P_LA_L) were defined to disentangle the yield gap between resource-limited and actual production to a larger degree:

- Resource-limited production with actual cattle management, calf mortality, and calving intervals (P_LA_L – MMI (actual cattle Management, calf Mortality, and calving Intervals)): the farm management decisions on culling rates, selling or slaughter weights, calving dates, age at first calving, and stocking densities correspond to the actual decisions. In addition, actual calf mortality and calving intervals are adopted (Table 5.2). The age at first calving is set to three years, which corresponds with the actual age at first calving in the Charolais area.
- Resource-limited production with actual cattle management (P_LA_L – M (actual cattle Management)): the farm management decisions on culling rates, selling or slaughter weights, calving dates, age at first calving, and stocking densities correspond to the actual decisions.

Furthermore, two variants of the production level P_PA_L were defined to investigate the LW production per hectare with the provision of *ad libitum* diets:

- In the variant P_PA_L – Hay, the diet consists of good quality hay only, and is available *ad libitum*. This diet replaces the grass-based diet in P_PA_L.
- In the variant P_PA_L – Silage, the diet consists of grass silage only, and is available *ad libitum*.

More information on input parameters and model settings for each of these production levels and their variants is provided in Appendix 5A. The diet and management for the production levels P_PA_P, P_PA_L – Hay, and P_PA_L – Silage are the same for all farm types, which implies that these production levels are the same for all farm types.

Relations among farm characteristics and relative differences between production levels (P_LA_L – MMI, P_LA_L – M, P_LA_L, P_PA_L) and actual production were assessed with a correlation matrix. Pairs of variables were analysed using the Pearson product-moment correlation and the Spearman's rank correlation coefficient. The Benjamini & Hochberg method was applied to correct *P*-values in the correlation matrix for multiple testing. The correlation matrix was calculated and plotted with the R package 'corrplot' (Friendly, 2002).

5.2.4 Economic calculations

Next to bio-physical factors, yield gaps can be explained by economic factors, such as the dependence on agricultural premiums. We investigated, therefore, the relation between yield gap mitigation and farm profit. Economic data for the twelve farm types were available in Réseaux d'Élevage Charolais (2014). Revenue from beef cattle was defined as revenue from LW sold, which excluded premiums. Operational costs for cattle production covered costs for concentrates, veterinary services, straw, and fertilizers for forage crops. Operational profit from beef production was defined as the revenue from beef production minus the operational costs for beef production. Gross farm surplus was defined as total farm revenues from beef and crop production, including premiums, minus the operational and fixed costs (excluding depreciation and financial costs) for beef and crop production. Relations among farm size, economic performance, and the relative difference between resource-limited production with actual cattle management (P_LA_L – M) were assessed with a correlation matrix, as described in the previous section.

Farmers received premiums based on the CAP related to agricultural markets and rural development policy. Premiums included suckler cow premiums (coupled per cow), direct payments per ha of agricultural area (Veysset *et al.*, 2014c), the agri-environmental grassland premium (Prime Herbagère Agro-Environnementale, PHAE), and the compensatory allowance for permanent natural handicaps (Indemnité Compensatoire des Handicaps Naturels, ICHN) for farms in mountainous and less-favoured areas, which applies to most of the Charolais area (Réseaux d'Élevage Charolais, 2014, Veysset *et al.*, 2014c). To be eligible for the PHAE premium, grassland had to represent at least 75% of the total agricultural area, and the administrative stocking rate had to be kept below 1.4 LU per ha forage area (Veysset *et al.*, 2014c). The PHAE premium was € 76 ha^{-1} $year^{-1}$ for a maximum of 100 ha per farm (Réseaux d'Élevage Charolais, 2014).

5.3 Results

5.3.1 Potential, resource-limited, and actual production of feed crops and cattle

Potential grass production for hay making was 20.8 t DM ha^{-1} year^{-1}, which resulted in a hay production of 16.6 t DM ha^{-1} year^{-1} and a grass silage production of 18.7 t DM ha^{-1} year^{-1} (Table 5.3). Water-limited grass production for hay making was 9.4 t DM ha^{-1} year^{-1}, which resulted in a hay production of 7.5 t DM ha^{-1} year^{-1} (Table 5.3). Under potential production, hay produced on average 157 GJ metabolisable energy (ME) ha^{-1} year^{-1}, grass silage 208 GJ ME ha^{-1} year^{-1}. A hectare used to produce the 65% wheat and 35% hay diet produced 9.9 t DM ha^{-1} year^{-1} and 118 GJ ME ha^{-1} year^{-1} (on average 81% of the land used for wheat production, and 19% for hay production). The 65% wheat and 35% hay diet contained a higher ME content (11.8 MJ kg^{-1} DM) than hay and grass silage (9.5 and 11.1 MJ kg^{-1} DM). The actual FE for all farm types was 64.3 kg LW t^{-1} DM on average, and the actual, weighted production of the feed crops (grass, hay, maize, wheat) was 5.5 t DM ha^{-1} year^{-1}. The actual FE of cattle increased significantly with an increasing fraction of cereals in the diet (P < 0.001; R^2-adj. = 0.78) (Fig. 5.2). The actual stocking densities ranged from 1.21 to 1.81 LU ha^{-1} forage production.

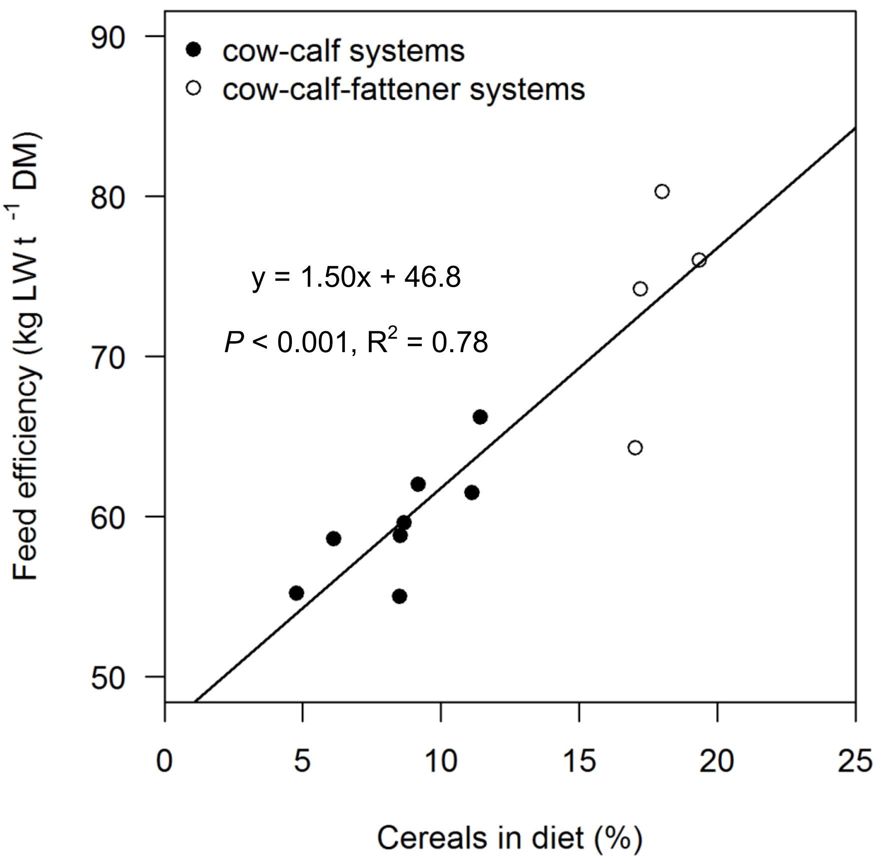

Figure 5.2 Actual feed efficiency of Charolais cattle versus the percentage of cereals in the diet. Each dot represents one farm type. LW = live weight; DM = dry matter.

Table 5.3 Potential, water-limited, and actual production of feed crops and their relative yield gaps. Values between parentheses indicate standard deviations. Potential and water-limited crop production are averages over the years 1998-2012, except for maize silage.

Production level or relative yield gap	Unit	Grass[a]	Hay	Grass silage[b]	Maize silage	Wheat
Potential production	kg DM ha^{-1} $year^{-1}$	14.4[c]	16.6 (1.6)	18.7 (1.9)	25.2[d]	8.3 (1.2)
Water-limited production	kg DM ha^{-1} $year^{-1}$	7.2[e]	7.5 (2.8)	-	19.6[d]	7.2 (2.1)
Actual production	kg DM ha^{-1} $year^{-1}$	4.8[f]	3.2-5.7[g]	-	10.0-10.5[g]	5.0-5.6[h]
Relative yield gap, (potential – actual) / potential		67%	66-81%	-	58-60%	33-40%
Relative yield gap, (limited – actual) / limited		33%	24-57%	-	46-49%	23-32%

[a] Grass intake by cattle under grazing.
[b] Potential production of grass silage is assessed only for beef cattle fed *ad libitum* grass silage (P_PA_L – Silage).
[c] Average for the twelve farm types under feed-limited cattle production with potential grass production (P_PA_L).
[d] De Koning and van Diepen (1992).
[e] Average for the twelve farm types under resouce-limited production (P_LA_L).
[f] Veysset *et al.* (2005), grass intake from permanent grassland.
[g] Réseaux d'Élevage Charolais (2014).
[h] Veysset *et al.* (2014a).

Table 5.4 Live weight (LW) production of twelve farm types with Charolais cattle.

Number farm type[a]	Production level (kg LW ha^{-1} $year^{-1}$) Actual	P_LA_L	P_PA_L
11021	291	645	1397
11031	307	633	1364
11065	315	638	1337
11105	308	582	1255
11111	290	592	1289
11131	422	760	1544
11140	464	756	1514
21010	320	614	1348
21020	322	646	1396
31020	367	663	1388
31041	384	669	1323
31060	463	765	1545
Average	354	664	1392

P_LA_L = resource-limited production; P_PA_L = potential crop production with feed-limited cattle production
[a] Numbers of farm types as indicated in Réseaux d'Élevage Charolais (2014).

Actual production of Charolais cattle in the twelve farm types ranged between 290 and 464 kg LW ha^{-1} $year^{-1}$ and averaged 354 kg LW ha^{-1} $year^{-1}$ (Table 5.4). Model simulations indicated that the average LW production per hectare per year was 664 kg for P_LA_L, and 1,392 kg for P_PA_L (Table 5.4). The optimum slaughter weight under these two production levels was 750 kg LW and the optimum calving date was at Julian day 60 (1^{st} of March). The LW production was 1,418 kg ha^{-1} $year^{-1}$ for P_PA_P, 1,748 kg ha^{-1} $year^{-1}$ for P_PA_L – Hay, and 2,377 kg LW ha^{-1} $year^{-1}$ for P_PA_L – Silage. Since the LW production per hectare was highest for P_PA_L – Silage, this production level was set as potential production for the integrated feed-crop livestock system.

5.3.2 Yield gaps

Relative yield gaps for feed crops were smallest for wheat (Table 5.3). The relative yield gap for the beef production systems, benchmarked against the potential LW production (P_PA_L – Silage) per hectare, was 85.1% on average, and 46.9% when benchmarked against resource-limited production (P_LA_L). The LW production with P_LA_L - MMI was 416 kg LW ha^{-1} $year^{-1}$, and with P_LA_L - M 457 kg LW ha^{-1} $year^{-1}$. Elimination of water-limitation in feed crops almost doubled the DM production between P_LA_L and P_PA_L (Fig. 5.3, Table 5.5). The FE for P_LA_L – MMI and actual production were the same, but the crop production for P_LA_L – MMI was higher than for actual production (Table 5.5). Across the twelve farm types, relative differences between P_LA_L – MMI, P_LA_L – M, P_LA_L, and P_PA_L on the one hand, and actual production on the other hand, were negatively correlated with the percentage of cereals in the diet; this was also true for the LW production per LU (Fig. 5.4).

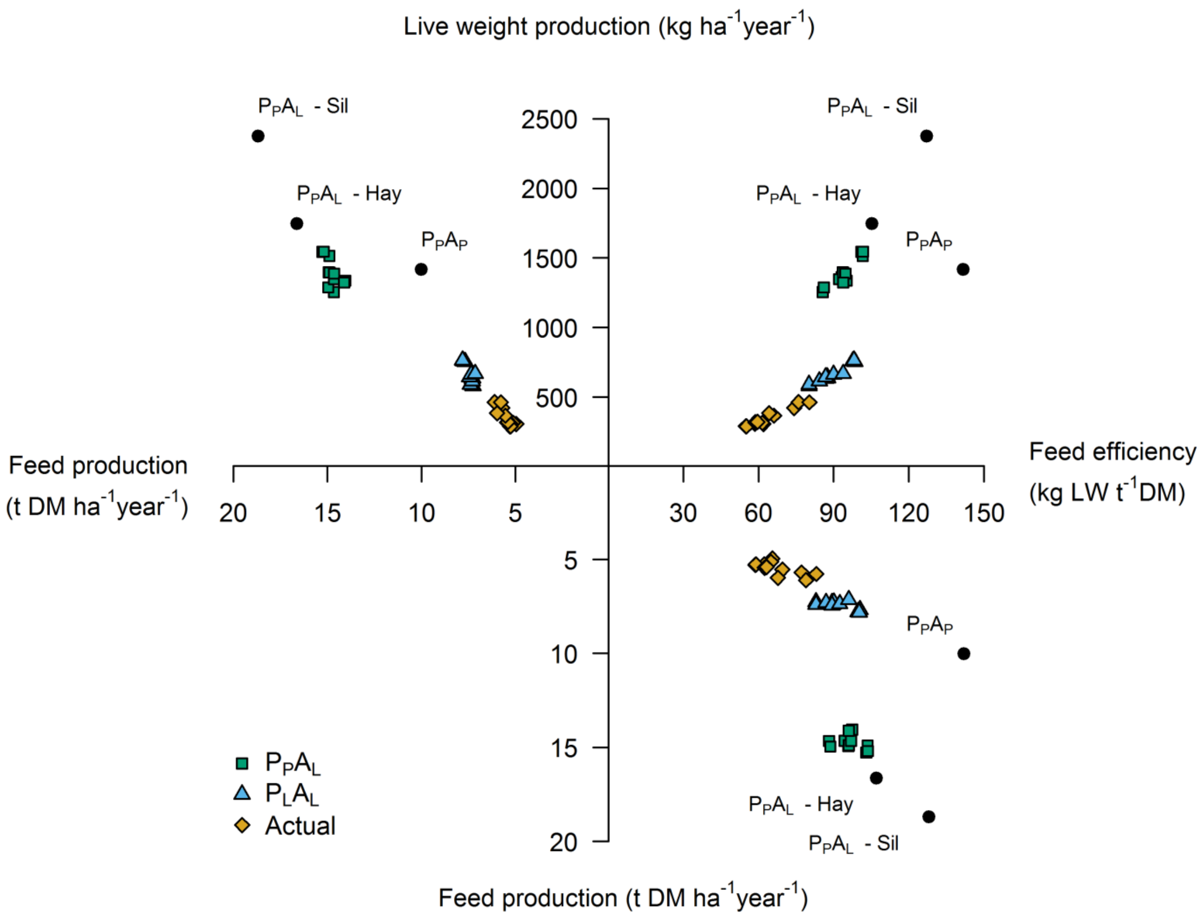

Figure 5.3 Feed production, feed efficiency, and live weight (LW) production of twelve farm types with Charolais beef cattle under actual production and the simulated production levels. DM = dry matter. For abbreviations of the production levels, see Table 5.2.

Table 5.5 Live weight (LW) production of the integrated feed-crop livestock system, feed efficiency of Charolais cattle, and production of feed crops for the different production levels as a percentage of the potential production of the integrated feed-crop livestock system (P_PA_L – Silage). LW production, feed efficiency, and crop production are averages over the twelve farm types.

Production level[a]	LW production	Feed efficiency	Crop production
Actual	15%	51%	29%
P_LA_L – MMI	18%	51%	38%
P_LA_L – M	19%	59%	33%
P_LA_L	28%	70%	40%
P_PA_L	59%	74%	79%
P_PA_P	60%	111%	54%
P_PA_L – Hay	74%	83%	89%
P_PA_L – Silage	100%	100%	100%

[a] For abbreviations of the production levels, see Table 5.2.

	$(P_LA_L$ - actual prod.) / P_LA_L	$(P_LA_L$ - M - actual prod.) / P_LA_L - M	$(P_LA_L$ - MMI - actual prod.) / P_LA_L - MMI	Land for feed production (ha per farm type)	Number of cows (per farm type)	Livestock units (per farm type)	Stocking density (LU per ha)	Live weight production (kg per LU)	Land used for forage production (% land for feed production)	Cereals in diet (%)
$(P_PA_L$ - actual prod.) / P_PA_L	**0.99**	**0.75**	**0.76**	NS	NS	NS	**-0.84**	**-0.83**	NS	**-0.89**
$(P_LA_L$ - actual prod.) / P_LA_L		**0.7**	**0.72**	NS	NS	NS	**-0.86**	**-0.75**	NS	**-0.82**
$(P_LA_L$ - M - actual prod.) / P_LA_L - M			**0.93**	NS	NS	NS	NS	**-0.87**	**0.72**	**-0.89**
$(P_LA_L$ - MMI - actual prod.) / P_LA_L - MMI				NS	NS	NS	NS	**-0.77**	**0.71**	**-0.84**
Land for feed production (ha per farm type)					**0.97**	**0.97**	NS	NS	NS	NS
Number of cows (per farm type)						**0.98**	NS	NS	NS	NS
Livestock units (per farm type)							NS	NS	NS	NS
Stocking density (LU per ha)								NS	NS	**0.77**
Live weight production (kg per LU)									NS	**0.93**
Land used for forage production (% land for feed production)										NS

Figure 5.4 Correlation matrix for the relative differences of production levels and several farm characteristics of the twelve selected farm types. A perfect positive correlation is indicated by 1, and a perfect negative correlation by -1. The Pearson product-moment correlation and the Spearman's rank correlation coefficient identified the same pairs of variables with significant correlations. LU = livestock unit; NS = Non-Significant ($P > 0.05$). For abbreviations of the production levels, see Table 5.2.

The yield gap between the silage diet and actual production per hectare was on average 2.02 t LW ha^{-1} $year^{-1}$, which was 85.1% of potential production. On average, 985 kg LW ha^{-1} $year^{-1}$, *i.e.* 41.5% out of 85.1%, was caused by the difference between the *ad libitum* diet with silage grass (P_PA_L – Silage) and the grass-based diets with potential feed crop production (P_PA_L) (*i.e.* a sub-optimal diet (Fig. 5.5 A)). Water-limitation in feed crops that are part of the grass-based diets (difference between P_PA_L and P_LA_L) accounted for 30.6% of the potential production (728 kg LW ha^{-1} $year^{-1}$) (Fig. 5.5 A). Differences in culling rates, selling or slaughter weights, calving dates, age at first calving, and stocking densities between P_LA_L and P_LA_L-M caused another 8.7% of potential production (207 kg LW ha^{-1} $year^{-1}$). Minor fractions of the relative yield gap were related to calf mortality and calving intervals (difference P_LA_L - M and P_LA_L – MMI; 40 kg LW ha^{-1} $year^{-1}$) and related to reducing factors, cow mortality, and nutrient limitations in feed crops (difference P_LA_L - MMI and actual production; 62 kg LW ha^{-1} $year^{-1}$) (Fig. 5.5 A). The relative yield gap under limited production (46.9%) is mainly caused by selling weights, culling rates, calving dates, and stocking densities (Fig. 5.5 B).

5.3.3 Farm economics

The gross farm surplus was 25-40% of the total farm revenues. Without premiums, the gross farm surplus was between -2 and 17% of the total farm revenues. Increasing the actual production to the production level P_LA_L - M does not result in a loss of the PHAE premium, as the eligibility criteria for the premium were still met. Across the twelve farm types, the relative difference between P_LA_L - M and actual production was positively correlated with the operational profit with bovine and PHAE premiums per kg LW (Fig. 5.6). The relative difference between P_LA_L - M and actual production was negatively correlated with the revenues from beef cattle per LU and per hectare of land used for feed; this was also true for the operational profit per LU (Fig. 5.6). For the seven farm types specialised in beef production (Table 5.1), the land area for feed production in a farm was positively correlated with the labour productivity and operational profit plus bovine premiums and PHAE per non-hired worker, but the land area was not correlated with operational profit per LU, per kg LW, and per ha feed crops (Fig. 5.6).

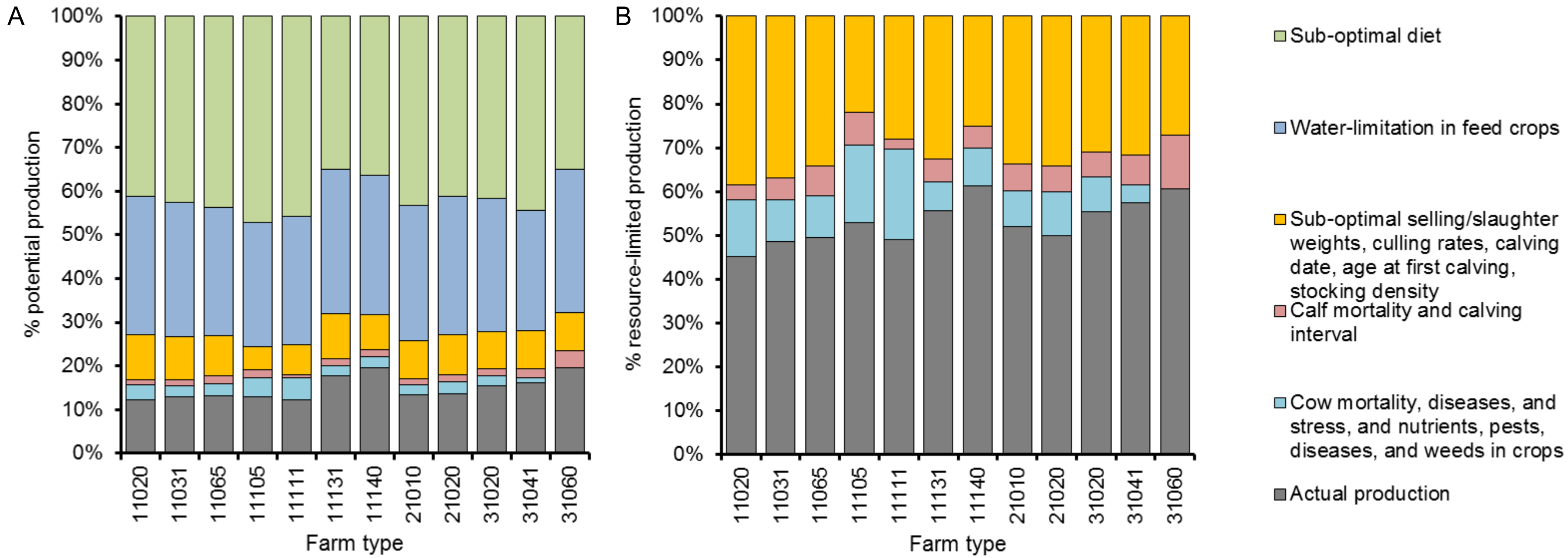

Figure 5.5 Yield gap analysis for farm types with Charolais cattle at crop-livestock systems level. Production is benchmarked against potential (A) and resource-limited (B) production. For potential production, 100% corresponds to 2,377 kg LW ha^{-1} $year^{-1}$, and for resource-limited production to 664 kg LW ha^{-1} $year^{-1}$ on average (Table 5.4). Numbers of farm types as indicated in Réseaux d'Élevage Charolais (2014).

	Revenue cattle (€ per LU)	Revenue cattle (€ per kg LW)	Revenue cattle (€ per ha feed crops)	Operational profit cattle (€ per LU)	Operational profit cattle (€ per kg LW)	Operational profit cattle (€ per ha feed crops)	Operational profit cattle + bovine and PHAE premiums (€ per LU)	Operational profit cattle + bovine and PHAE premiums (€ per kg LW)	Operational profit cattle + bovine and PHAE premiums (€ per ha feed crops)	Land for feed production (ha per farm type)	Labour productivity (kg LW per non-hired worker)	Operational profit cattle + bovine and PHAE premiums (€ per non-hired worker)
(P_LA_L - M - actual prod.) / P_LA_L - M	**-0.81**	NS	**-0.75**	**-0.82**	NS	NS	NS	**0.83**	NS	NS	NS	NS
Revenue cattle (€ per LU)		NS	**0.82**	**0.89**	NS	NS	NS	**-0.74**	NS	NS	NS	NS
Revenue cattle (€ per kg LW)			NS	NS	**0.73**	NS	NS	NS	NS	NS	NS	NS
Revenue cattle (€ per ha feed crops)				**0.77**	NS	**0.89**	NS	**-0.79**	NS	NS	NS	NS
Operational profit cattle (€ per LU)					**-0.8**	NS	NS	**-0.91**	NS	NS	NS	NS
Operational profit cattle (€ per kg LW)						NS	NS	**0.85**	NS	NS	NS	NS
Operational profit cattle (€ per ha feed crops)							NS	NS	**0.88**	NS	NS	NS
Operational profit cattle + bovine and PHAE premiums (€ per LU)								NS	NS	NS	NS	NS
Operational profit cattle + bovine and PHAE premiums (€ per kg LW)									NS	NS	NS	NS
Operational profit cattle + bovine and PHAE premiums (€ per ha feed crops)										NS	NS	NS
Land for feed production (ha per farm type)											**0.96**	**0.89**
Labour productivity (kg LW per non-hired worker)												**0.92**

Figure 5.6 Correlation matrix for the relative difference between resource-limited production with actual cattle management and actual production ((P_LA_L – M – actual prod.) / P_LA_L – M), and several economic parameters of the twelve selected farm types. A perfect positive correlation is indicated by 1, and a perfect negative correlation by -1. The Pearson product-moment correlation and the Spearman's rank correlation coefficient identified the same pairs of variables with significant correlations. Land for feed production, labour productivity, and operational profit from cattle per non-hired worker are assessed only for farm types specialised in beef production. LU = livestock unit; LW = live weight; NS = Non-Significant (*P* > 0.05); PHAE = Prime Herbagère Agro-Environnementale (grassland premium).

5.4 Discussion

5.4.1 Evaluation of results and methods

The potential and water-limited wheat yields that we simulated corresponded fairly well to literature (De Koning and van Diepen, 1992, Boogaard *et al.*, 2013). The simulated potential grass yield corresponded well with estimates of De Koning and Van Diepen (1992), and simulations and observations of potential yields reported by Schapendonk *et al.* (1998). Our estimate for the water-limited grass production was close to estimates of Smit *et al.* (2008) for the Charolais area, but much lower than reported by De Koning and Van Diepen (1992).

The calculated actual production from Réseaux d'Élevage Charolais (2014) was 290-464 kg LW ha^{-1} year^{-1} (Table 5.4). The actual production in the Charolais area with Charolais cattle was reported to be 368-373 kg LW ha^{-1} forage area year^{-1} for conventional farms in 2010 and 2011 (Veysset *et al.*, 2014a). Although the area to produce concentrates was not taken into account in Veysset *et al.* (2014b), their numbers are within the calculated range for the actual production. Comparing potential or resource-limited LW production from our research with LW production in literature was not straightforward, since LW production is generally not available at herd level, which includes the feed intake and LW production of cows. The LW production under potential growth of feed crops with feed-limited cattle growth (P_pA_l) was 1,392 kg LW ha^{-1} year^{-1} at herd level (Table 5.3). Although we are not aware of experiments with similar LW production levels in the Charolais area, we deem such production levels feasible from a bio-physical perspective. For example, the measured LW production on irrigated and fertilized pastures with pangola grass (*Digitaria decumbens* Stent) in Queensland, Australia, was 2,990 kg LW ha^{-1} year^{-1}, although cows were not included in the LW production (Skerman and Riveros, 1990). This reported LW production is expected to be lower at herd level, since cows have lower growth rates and FEs than the calves.

The models LINGRA and LiGAPS-Beef have each been evaluated by comparison of model results against independent experimental data (Schapendonk *et al.*, 1998, Van der Linden *et al.*, 2017b). The LW production and the grass intake simulated by the combined models are deemed possible, but an extensive evaluation has not been conducted yet. Future efforts may focus, therefore, on comparing model simulations with independent experimental data, for different grass-based systems with beef cattle. Important variables to be measured in such experiments are the grass biomass (green and dead biomass), grass quality (ME and crude protein content), grass intake, and LW gain.

The percentage of cereals in the diet was assumed to be the same for all cattle in a farm type and all for life phases, since detailed information on cereal supplementation was not available. In practice, cereals are expected to be supplied in periods when animals have the highest nutritional requirements. The FE under feed-limited production may be underestimated due to this assumption, and consequently the resource-limited LW production too.

Potential production of either crops or livestock is the theoretical maximum production of each system in the absence of growth limiting and reducing factors (Van Ittersum and Rabbinge, 1997, Van de Ven *et al.*, 2003). For integrated feed-crop livestock systems, we define potential production as the maximum LW production per hectare, irrespective of feed-limitation, to prevent negative yield gaps. In our case study in the Charolais area, the maximum LW production per hectare of the integrated feed-crop livestock system was achieved with a diet consisting of *ad libitum* grass silage (P_PA_L – Silage), while this diet resulted in feed-limited growth of cattle. Van der Linden *et al.* (2015) argued that the *ad libitum* diet with 65% wheat and 35% hay (P_PA_P) sustains potential cattle growth. This diet did not result in the highest LW production per hectare for the integrated feed-crop livestock system (Fig. 5.3), because one hectare of grass silage produced more biomass than one hectare with 65% wheat and 35% hay (18.7 vs 9.9 t DM ha^{-1} year^{-1}) and more ME (208 vs 118 GJ ha^{-1} year^{-1}).

5.4.2 Bio-physical factors explaining yield gaps

The yield gap between potential and actual production was 2.02 t LW ha^{-1} year^{-1}, and the relative yield gap was 85.1%. Replacing the grass-based diets with a diet consisting of *ad libitum* grass silage (difference between P_PA_L – Silage and P_PA_L) explains almost half of the yield gap (41.5% out of 85.1%). This difference is attributed to the elimination of feed quantity limitations with P_PA_L – Silage, and a higher average ME content of the diet, and a higher DM production per hectare. Elimination of water-limitation in feed crops (difference between P_PA_L and P_LA_L) explains approximately one-third of the yield gap (30.6% out of 85.1%) of the yield gap, which suggest that irrigation could increase LW production considerably.

Culling rates, slaughter weight of calves, calving dates, age at first calving, and stocking densities (difference between P_LA_L and P_LA_L - M) explain approximately one-tenth of the yield gap (8.7% out of 85.1%). Although this fraction may be perceived as relatively small, this fraction is still equivalent to 58% of the actual LW production. Weights of cows still increase during the first and second parity. Increasing the culling rate brings the advantage that more cows increase their LW while producing calves. Bull calves were sold in practice at 699-715 kg LW in the cow-calf-fattener systems (Table 5.1). Calves fattened in feedlots in the Charolais area were slaughtered at 730-750 kg LW (Morel *et al.*, 2016). In our simulations, the LW production per hectare was maximized with slaughter weights of 750 kg LW, which is in line with the slaughter weights in the Charolais area. The peak in calving date ranged from late December to the end of March in the twelve farm types. The optimum calving date simulated was at the 1st of March, which is within the range observed in practice.

Calf mortality and calving intervals (difference between P_LA_L - M and P_LA_L - MMI) explain a small percentage of the yield gap (1.7% out of 85.1%). Higher calf mortality and calving intervals require more cows to produce the same amount of LW, which increases feed intake and decrease FE. As expected, the difference between calf mortality and calving intervals is mainly attributed to an increase in FE (Fig. 5.3). Cow mortality, stress, and cattle diseases, as well as pests, diseases, weeds, and nutrient limitations in feed crops (difference between P_LA_L - MMI and actual production) explain a small percentage (2.6% out of 85.1%) of the yield gap (Fig. 5.5). This fraction of the yield gap is mainly explained by nutrient limitations and reducing factors in feed crops, because the difference is attributed to feed production per hectare, and not to a difference in FE of the Charolais cattle (Table 5.1). The similarity in FEs may imply that cow mortality, stress, and diseases are hardly affecting LW production. Under actual production, a higher percentage of cereals is likely to increase the average ME content of the grass-based diet fed in a farm type, which results in a higher LW production per LU, and smaller relative differences between production levels (P_LA_L – MMI, P_LA_L – M, P_LA_L, and P_PA_L) and actual production (Fig. 5.4).

5.4.3 Economic factors explaining yield gaps

The eligibility criteria for the PHAE premium, applicable in 2014, set limits to the stocking density, nitrogen fertilization, and the percentage land used for non-forage crops. Farms receiving the PHAE premium would still be eligible for this premium under resource-limited production with actual cattle management (P_LA_L – M). A shift from resource-limited production with actual cattle management to resource-limited production (P_LA_L), however, is likely to exceed the stocking density threshold, and consequently farms will not be eligible anymore for the PHAE premium. Application of irrigation is expected to result in a loss of the PHAE premium as well, as irrigation is expected to increase the carrying capacity of pasture. Other reasons why irrigation is not applied on pastures in the Charolais area are the high labour requirements, high operational costs, and high costs for the equipment. Land fragmentation contributes to the high investment and/or labour requirements. Even if economic constraints would not play a role, only a small fraction of the large pasture areas can possibly be irrigated, because of the limited water availability during summer. Building water storages is essential to irrigate larger areas.

Intensification might be economically attractive if the increased production would compensate for the loss of the PHAE premium and the marginal costs for inputs, including labour. Apparently intensification has not been economically attractive for farmers in the Charolais area, because yield gaps were considerable in all farm types, even in cow-calf-fattener systems that did not receive the PHAE premium (Fig.

5.5). Instead, our results indicated that the relative difference between P_LA_L - M and actual production was positively correlated with the operational profit plus the bovine and PHAE premiums (Fig. 5.6). This finding may suggest that mitigating yield gaps even decreases the operational profit plus the bovine and PHAE premiums per kg LW. Increasing the land area for feed production did not affect the operational profit plus bovine and PHAE premiums per LU, kg LW, and ha significantly (Fig. 5.6), which may suggest that any increases in operational profit plus bovine and PHAE premiums must be derived from farm expansion. A historical analysis of farm data in the Charolais area (Veysset *et al.*, 2015) showed indeed that the increase in LW production per hectare was only 5% for beef production systems in the Charolais area between 1990-2012, whereas their area increased by 62-68%. Farm expansion has been a more profitable strategy than intensification during these years, because expansion allowed to benefit from premiums (Veysset *et al.*, 2015). Hence, the CAP discouraged intensification of beef production systems in France (Veysset *et al.*, 2005). Furthermore, expansion may be stimulated by the relatively low prices of farmland (€ 2,800-4,000 ha^{-1}) in the Charolais area.

The seven farm types specialised in beef production (Table 5.1) were assumed to use their labour input for LW production only, because crop sales were a minor fraction of the farm revenues. The area of land used for feed production was positively correlated with labour productivity and operational profit plus bovine and PHAE premiums per non-hired worker (Fig. 5.6). These results may suggest that farm expansion led to an increase in the premiums received per farm, an increase in labour productivity, and a corresponding reduction in labour costs, which allows to increase the operational profit plus bovine and PHAE premiums per non-hired worker. In line with this suggestion, farm size was identified as a positive determinant of the income per worker (Veysset *et al.*, 2014c).

5.4.4 Future improvement options

Yield gaps in crop production can generally be mitigated up to 80% of the potential (or water-limited) production. The gap between 80% of potential (or limited) production and actual production is the exploitable yield gap (Cassman, 1999, Cassman *et al.*, 2003). Mitigating yield gaps further than the exploitable yield gap is considered to be economically unattractive, or not feasible from a practical perspective, or undesirable from an environmental perspective (Cassman *et al.*, 2003). Under the assumption that both crop and cattle production can be mitigated up to 80% of potential (or resource-limited) production, yield gaps in feed-crop livestock systems would be at least 36% ($1-0.8^2$). Deducting this percentage from the yield gaps, the exploitable yield gap at crop-livestock systems level was 49% of the potential production and 11% of the resource-limited production. These yield gaps suggest scope to intensify beef production.

After accounting for bio-physical, economic, and social factors, feasible improvement options can be identified for future mitigation of yield gaps (Van Ittersum *et al.*, 2013). The economic calculations were based on the CAP in force in 2014. In the new CAP for 2015-2020, the PHAE premium has been removed and cumulated with the compensatory allowance for permanent natural handicaps (ICHN). Farms located in mountainous and less-favoured areas receive a higher ICHN in 2015-2020 than in 2014, without any thresholds for stocking densities. The new CAP introduced a redistributive payment for the first 52 ha of agricultural area only, and a suckler cow premium decreasing gradually (decreasing premiums for 1-50, 51-99, and 100-139 cows), with an upper limit of 139 cows. These new measures could slow down farm expansion and give some importance to the search for intensification.

Given the new CAP, an improvement option is to increase stocking densities without loss of premiums. A higher stocking density requires a better grassland management through, for example, rotational grazing, and an early start of the grazing season. These measures, however, involve a higher workload. Another improvement option is to increase the culling rates to increase the LW production per hectare. Consequently, the share of LW production from cows will increase as well. As LW prices are higher for calves than for cows (Réseaux d'Élevage Charolais, 2014), this improvement option is probably not profitable. Application of irrigation as an improvement option is perhaps not profitable also, due to the high labour requirements and high costs.

The slaughter weight maximizing LW production per hectare was 750 kg under resource-limited production (P_LA_L). An improvement option could be to fatten calves in the actual cow-calf systems on grass-based diets, up to a weight of 750 kg LW instead of 330-460 kg LW. Charolais cattle are late maturing, however, and bred for more than 40 years to produce calves that can be fattened in Italian feedlots with a high fraction of cereals in the diet. Charolais calves cannot be finished on-farm with grass-based diets before 30 months of age. Animals slaughtered after 30 months have carcass weights over 450 kg, whereas the market requires animals with a maximum carcass weight of 400 kg. Fattening calves on-farm with grass-based diets requires a change in the whole value chain, redefinition of the breeding objectives, and development of new markets, otherwise this improvement option is unlikely to be adopted.

5.5 Conclusions

In this research, we conducted the first yield gap analysis with both livestock and crop growth models based on concepts of production ecology. This approach was applied to twelve beef production systems in the Charolais area. Relative yield gaps for LW production were on average 85% of the potential production per hectare, and 47% of the resource-limited production per hectare, which suggests scope for intensification. Applying yield gap analysis disentangled the major bio-physical causes of these yield gaps. Under the CAP in 2014, yield gap mitigation with preservation of decoupled premiums did not increase operational profit and premiums per kg LW and per hectare. The operational profit and premiums per kg LW even increased with an increasing difference between resource-limited production with actual cattle management (P_LA_L - M) and actual production. Hence, intensification of beef production was not economically attractive in the Charolais area before 2015. The current CAP 2015-2020 provides more scope for intensification. A feasible improvement option may be to increase stocking densities via better grassland management. The technical and economic relevance of all these options could be tested by coupling bio-physical and bio-economic models. Since yield gap analysis was applied successfully in the Charolais area, this generic method may be a useful tool to identify feasible improvement options for other feed-crop livestock systems across the world too.

Supplementary information

Supplementary information to this Chapter is provided in Appendix 5A. The source code of LiGAPS-Beef is freely accessible at http://dx.doi.org/10.18174/386763. The source code of LINGRA and LINTUL-2 is available on the model portal of the Plant Production Systems group of Wageningen University, The Netherlands (http://models.pps.wur.nl).

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Chapter 6

Exploring grass-based beef production under climate change by integration of grass and cattle growth models

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6.1 Introduction

Climate change affects livestock production on grasslands directly via an increased occurrence of heat stress, and indirectly via an effect on grass growth. Numerous models are used to simulate the effects of climate change on production of forages or feed crops. However, models simulating the direct effects of climate change on livestock production are scarce. Heat stress is studied with thermoregulation models simulating heat flows in animals. We incorporated a thermoregulation model in a cattle model to simulate growth and production of beef cattle, named LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems - Beef cattle) (Van der Linden *et al.*, 2016).

Grass sward and animals strongly interact in grazing systems. Animals defoliate grass and affect grass growth and quality, whereas grass growth and quality affect the feed intake and growth of animals. Projections for livestock production under climate change require, therefore, to account for the effects of climate change on grass growth and animal growth simultaneously. The aim of this research is to explore the direct and indirect effects of climate change on grass-based beef production with LiGAPS-Beef in combination with a grass growth model.

6.2 Materials and methods

Effects of climate change on beef production were investigated for grass-based farming systems in the Charolais Basin of France with weaned Charolais bull calves under continuous grazing. In this modelling study, grasslands were assumed to be represented by swards of perennial ryegrass (*Lolium perenne* L.), and the diet consisted of fresh ryegrass only. Weaned bulls (initial age 210 days; live weight 315 kg) were simulated during the grazing season, from March 25th to December 10th. The model LINGRA (Light INterception and utilisation – GRAss) was used to simulate the production of perennial ryegrass (Schapendonk *et al.*, 1998). This model was used to simulate water-limited grass production, and accounts for the crop genotype, climate, and water availability (soil water holding capacity 0.15 cm^3 cm^{-3}). The model LiGAPS-Beef was used to simulate feed-limited growth of beef cattle and beef production. The term beef is defined here as deboned carcass weight.

LiGAPS-Beef and LINGRA were connected by representing the following processes: heading and its effects on nutritional quality of the pasture (metabolisable energy and crude protein content), defoliation resulting from feed intake by cattle, trampling, selective grazing, and confined grass intake at low pasture biomass. Beef production was named limited under water-limited grass growth and feed-limited cattle growth. Beef production per hectare was simulated for stocking densities between 0.5 and 8.0 head ha^{-1}, with intermediate steps of 0.5 head ha^{-1}. Limited beef production per hectare was defined as the beef production under the optimal stocking density, which is a seven year average in this research. Actual beef production for grass-based beef production systems was estimated based on Réseaux d'Élevage Charolais (2012). Production per hectare and feed conversion efficiency (FCE) were calculated according to Van der Linden *et al.* (2015). The (relative) yield gap was calculated according to Van Ittersum *et al.* (2013).

Historic weather data were selected for Charolles (46.4°N, 4.3°E), France for 1999-2006 (reference climate). The representative concentration pathways (RCPs) 2.6 (smallest projected climate change) and 8.5 (largest climate change) were used to assess beef production in 2050. Temperature and CO_2 concentration increased 0.7°C and 71 ppm between the reference climate and 2050 under RCP 2.6, whereas rainfall decreased 4.5%. Temperature and CO_2 concentration increased 1.9°C and 168 ppm under RCP 8.5, and rainfall decreased 7.1%.

6.3 Results and discussion

Limited beef production was 452 kg ha^{-1} under the reference climate (1999-2006), and actual production was estimated at 265 kg ha^{-1}. This indicates a relative yield gap of 41%, which suggests considerable scope to increase beef production. The yield gap could only be calculated for the reference climate as actual production is unknown with future climate change. Relative yield gaps in crop-livestock systems are assumed to be at least 36% (100% × (1 - 0.8 × 0.8)), and mitigation of this gap is generally not economically attractive or practically feasible (Van der Linden *et al.*, 2015). As the relative yield gap of 41% is close to 36%, increasing beef production may not be an option for the present beef production system due to economic or practical constraints.

The yield gap might be explained by nutrient limitation in the grass (*e.g.* nitrogen, phosphorus, potassium), however this was not included in the version of LINGRA used. Furthermore, yield gaps might be explained by diseases and stress in cattle, by pests, diseases, and weeds in grassland, and by sub-optimal farm management. Predicted limited beef production per hectare had a larger standard error at near-optimal stocking densities (4-5 head ha^{-1}) than at sub-optimal stocking densities (*e.g.* 3 head ha^{-1}) (Figure 6.1 A). Farmers might opt, therefore, for sub-optimal stocking densities, reducing variation and associated risks in beef production. The average limited beef production per hectare and per head (Figure 6.1) resemble the outcomes of the Jones-Sandland equations (Jones and Sandland, 1974).

Limited beef production was 477 kg ha^{-1} under RCP 2.6 (+ 5.5% compared to the reference climate), and 514 kg ha^{-1} under RCP 8.5 (+ 13.8%) (Figure 6.1 A). Whether actual production can be increased by similar rates depends also on factors not included in the models. Average optimum stocking densities under feed-limited production were 4.3, 4.6, and 4.9 head ha^{-1} under the reference climate, RCP 2.6, and RCP 8.5, respectively. The average number of days with reductions in feed

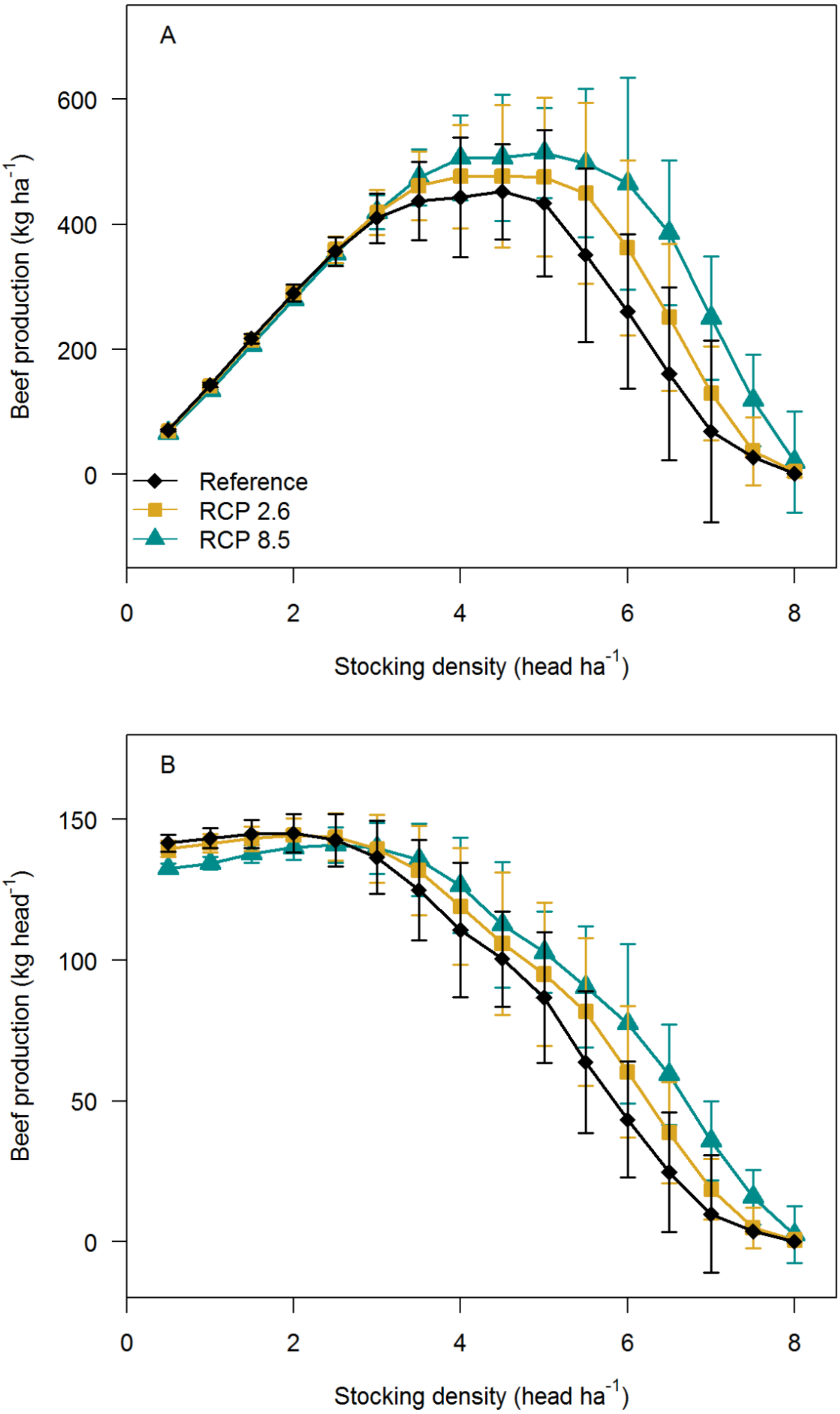

Figure 6.1 Limited beef production per hectare of grassland (A) and per head (B) for Charolais bull calves, under the reference climate (Reference, 1999-2006), and under Representative Concentration Pathway (RCP) 2.6 and RCP 8.5 in 2050. Bars indicate standard errors.

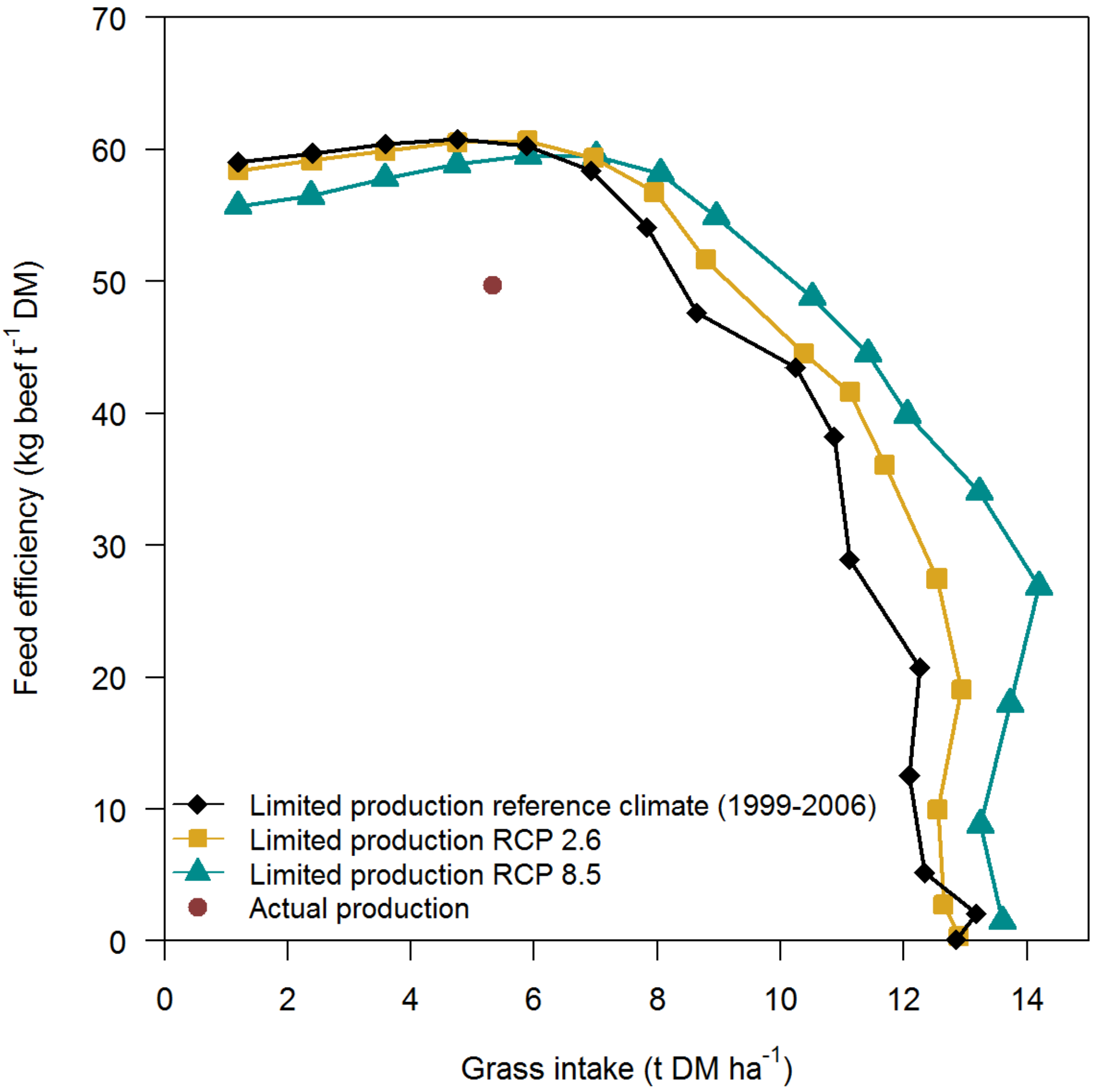

Figure 6.2 Feed intake and feed efficiency of bull calves under limited and actual beef production. DM = dry matter; RCP = representative concentration pathway in 2050.

intake due to heat stress was 15.8 days under the reference climate, 17.8 days under RCP 2.6, and 25.3 days under RCP 8.5. The average beef production per head increased with increasing stocking density, and reached an optimum before decreasing at further increase of stocking density (Figure 6.1 B). This is explained by a lower defoliation rate at lower stocking densities, which results in less regrowth of fresh biomass and more standing biomass. Higher temperatures under climate change increased the development rate of the standing biomass and decreased consecutively the metabolisable energy content and feed efficiency (FE).

Climate change decreased the FE at stocking densities below 2.5 head ha^{-1}. At higher stocking densities, average FE and feed intake were higher under climate change than under the reference climate, with the highest increases under RCP 8.5 (Figure 2). This is explained by a higher grass production under increased CO_2

concentrations. The performance of crop growth models needs to be evaluated further with data from experiments where projected climate conditions are mimicked. The integrated package with LiGAPS-Beef and LINGRA needs to be evaluated against data from grazing systems also.

6.4 Conclusions

Exploring the effects of climate change on beef production in grass-based systems by integrating a crop and a livestock model, indicated that climate change increased limited beef production of Charolais bull calves by 5.5%-13.8% in 2050 compared to the reference climate (1999-2006). These results do not indicate directly the increase of actual beef production that can be anticipated, because economic and practical constraints were not considered. However, the integrated models showed that there is scope to intensify grass-based beef production and mitigate the relative yield gap (41%) under the current climate from a bio-physical perspective.

Acknowledgements

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Chapter 7

General discussion

7.1 Introduction

The need for sustainable intensification in agriculture is widely acknowledged as a major pathway to meet the increasing global demand for food. So far, empirical methods have been used to assess the scope to increase livestock production, for example by comparing livestock production between the best farmers and average farmers. Results from empirical methods are location-specific, and their results apply only to similar farms under similar agro-ecological conditions. In addition, empirical methods account for all constraints to livestock production, whereas part or all of these constraints can soon be different due to economic and societal developments. Assessing the scope to increase production with empirical methods thus results in changing estimates over time. Empirical methods do not necessarily provide insight in the bio-physical scope to increase production too, as even the production of the best farmers may be below the theoretical maximum production. Empirical methods are thus not very suited to assess the scope to increase production in the context of sustainable intensification. Alternatively, mechanistic modelling could be a method to assess the bio-physical scope to increase livestock production. Nevertheless, the mechanistic livestock models currently available often do not include the main factors affecting livestock production (Appendix 1A), and are consequently not widely applicable in different farming systems under different agro-ecological conditions. Hence, a generic method to assess the scope to increase livestock production was not available at the start of this research.

The first two objectives of this thesis were to develop a generic framework to assess the scope to increase production of feed-crop livestock systems and to develop a generic livestock model that allows to estimate potential and feed-limited livestock production, both based on concepts of production ecology. The third objective was to apply the framework and model to feed-crop livestock systems, and conduct yield gap analyses. In accordance to the first objective, concepts of production ecology were defined in more detail for livestock systems to benchmark livestock production quantitatively (Chapter 2). Conform the second objective, the mechanistic model LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle) was developed to assess the scope to increase production of beef cattle under different agro-ecological conditions (Chapters 3-4). In accordance to the third objective, yield gap analysis was performed at feed-crop livestock system level, for different beef production systems in the Charolais region of France (Chapter 5). In addition, the beef production of grass-fed bull calves was simulated under two climate change scenarios (Chapter 6).

In line with the three research objectives, this general discussion reviews 1) the generic framework to benchmark production of feed-crop livestock systems, 2) the development and evaluation of LiGAPS-Beef, and 3) the quantification and analysis of yield gaps in feed-crop livestock systems. Thereafter, the discussion continues with 4) applications to benchmark production of feed-crop livestock systems, applications of the model LiGAPS-Beef, and 5) the main conclusions.

7.2 Developing a generic framework to benchmark production of feed-crop livestock systems quantitatively

7.2.1 Discussion of the main findings

A generic method to benchmark livestock production quantitatively was not available at the start of this PhD project. To provide such a generic method, concepts of production ecology for livestock were defined in more detail in Chapter 2, building on the work of Van de Ven *et al.* (2003). Two major additions to the work of Van de Ven *et al.* (2003) are the identification of the units and the proper system level suited to benchmark livestock production under different agro-ecological conditions. Feed efficiency (kg animal-source food (ASF) per kg feed intake) at herd level was used to benchmark livestock systems, whereas production of ASF per hectare per year was used to benchmark feed-crop livestock systems (Fig. 7.1). Expressing livestock production per unit area is essential in the context of sustainable intensification.

In literature, the production per animal (per year) is widely used as a benchmark for livestock production. This is useful to assess the scope to increase production of similar animals (*e.g.* kg milk per cow per year). The production per animal, however, does not account for the different life stages and purposes of animals in a herd. In addition, livestock production per farm can increase with an equal production per animal, but an increased feed efficiency, which indicates that feed efficiency at herd or flock level is a better benchmark to assess the scope to increase livestock production in relation to global food production (Gerssen-Gondelach *et al.*, 2015).

Benchmarking the scope to increase livestock production must account for feed production and feed intake of all animals in a herd, and not account for animals in specific life stages or animals with specific purposes only. Hence, the herd or flock level is most suited to investigate the scope to increase livestock production, as this level accounts for all animals within herds or flocks. The importance of accounting for feed intake fully has been emphasized in several descriptions of cattle models (Sanders and Cartwright, 1979, Naazie *et al.*, 1997, Pang *et al.*, 1999, Tess and Kolstad, 2000, Rufino *et al.*, 2009). The concept of the smallest 'herd unit' was used to scale up from individual animals to the herd level. In Chapter 2, a herd unit was defined as one reproductive animal and its offspring, minus the replacement offspring (*e.g.* a heifer replacing a cow).

After the conceptual framework to assess the bio-physical scope to increase livestock production per unit area was laid out in Chapter 2 (Fig. 7.1), it was subsequently applied to beef production systems in the Charolais region of France. The diet used to calculate potential beef production of feed-crop livestock systems was defined as

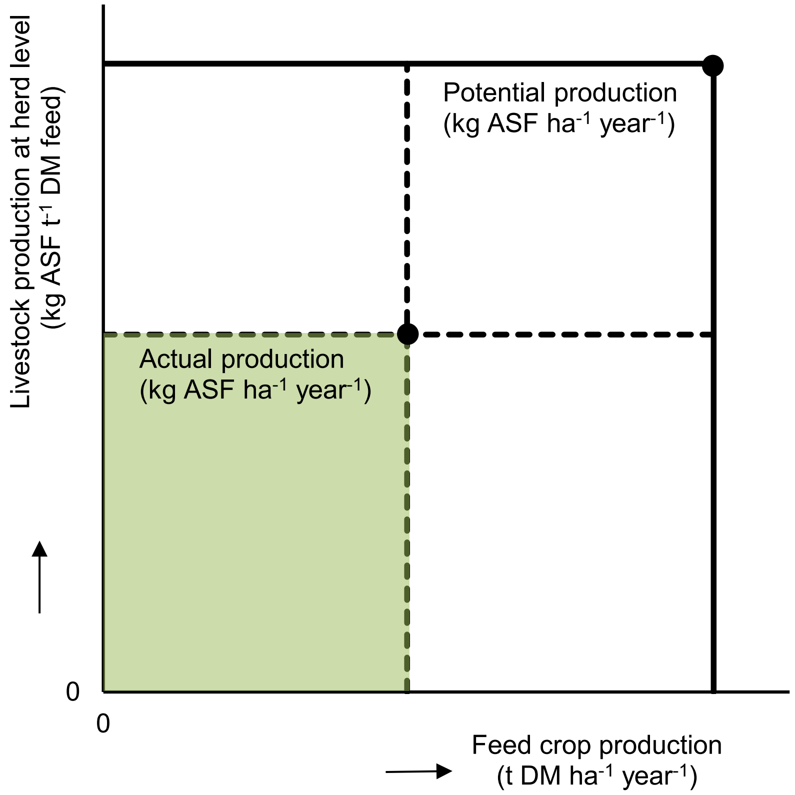

Figure 7.1 Conceptual framework to quantify yield gaps of feed-crop livestock systems, as defined in Chapter 2. Solid lines indicate the potential production of both feed crops and livestock production. Dashed lines indicate the actual production of feed crops and livestock. The green area indicates the actual production of animal-source food (ASF) per hectare. DM = dry matter.

an *ad libitum* diet consisting of 65% wheat and 35% hay. This diet was assumed to sustain potential growth of cattle. Potential production per hectare was calculated based on potential wheat and hay yields, and metabolisable energy requirements of cattle herds. The theoretical scope to increase beef production per unit area was defined as the difference between the potential and actual beef production per unit area in Chapter 2 (Fig. 7.1).

Applying concepts of production ecology to beef production in the Charolais region of France showed that yield gaps in feed-crop livestock systems were 79% of the potential beef production per hectare for an extensive cow-calf system, and 72% for a cow-calf-fattener system. These estimates were the first in literature for yield gaps of feed-crop livestock systems based on concepts of production ecology. Their magnitude implies that beef production could theoretically be increased approximately by a factor 5 and 4 respectively. These yield gaps thus suggest considerable scope to increase beef production in the Charolais region of France.

The simple calculations in Chapter 2 did not account for the climate, feed quality, and available feed quantity. Since these factors are essential in livestock production, livestock modelling is required to assess the scope to increase livestock production more generically.

7.2.2 Limitations of the generic framework

Production levels and yield gaps of feed-crop livestock systems were expressed quantitatively in Chapter 2, but product quality (beef quality) was neglected. Nevertheless, trade-offs between product quantity and product quality exist in beef production systems. For example, potential production was estimated with higher culling rates than under actual production in Chapter 2. These higher culling rates resulted in a larger beef production per hectare compared to lower culling rates. In addition, higher culling rates resulted in a higher proportion of live weight derived from cows compared to lower culling rates. Live weight prices of Charolais cows, which reflect beef quality, are lower than live weight prices of calves (Réseaux d'Élevage Charolais, 2014). Hence, increasing culling rates increases the beef production per hectare, but may not necessarily increase beef quality. Another example is beef production from Angus cattle, which are kept for their high quality beef rather than their high beef production (Casey and Holden, 2006). Accounting for the trade-offs between beef quantity and quality is not straightforward, as assessing beef quality remains a complicated issue, despite its many quantitative indicators.

Production levels and yield gaps were expressed as beef production per hectare per year, which accounts for beef production only. Beef farms in the Charolais region receive significant amounts of environmental subsidies for nature conservation and maintenance of landscapes (Veysset *et al.*, 2005, Réseaux d'Élevage Charolais, 2014, Veysset *et al.*, 2015). Landscape outputs, however, are not taken into account in the generic framework. In addition, cattle can have multiple outputs and functions, especially in tropical farming systems (Oosting *et al.*, 2014, Udo *et al.*, 2016). Examples of outputs are milk, beef, and manure, but also transport and traction. Livestock can even provide social status, and serve as an insurance or as a capital asset in regions where banks are inaccessible or unreliable (Udo *et al.*, 2016). A method to account for multiple outputs is presented, therefore, in Section 7.5.2 of this chapter.

7.3 Development and evaluation of LiGAPS-Beef

7.3.1 Discussion of the main findings

According to the framework presented in Chapter 2, assessing the scope to increase production of feed-crop livestock systems requires to benchmark both feed crop production and livestock production (Fig. 7.1). Crop growth models based on concepts of production ecology are widely used to assess the scope to increase crop production (Bouman *et al.*, 1996, Jones *et al.*, 2003, Keating *et al.*, 2003, Van Ittersum *et al.*, 2003), and can thus be readily applied to feed crops (x-axis Fig. 7.1). Literature review showed that the current livestock models were developed for other purposes than assessing the scope to increase production generically (Appendix 1A). Although many models contain aspects of concepts of production ecology, a generic model to assess the scope to increase livestock production (y-axis Fig. 7.1) was not available at the start of this research. Chapter 3, therefore, described the model LiGAPS-Beef, which aims to simulate potential and feed-limited production of beef cattle in different beef production systems under different agro-ecological conditions. This model combines existing models and concepts on thermoregulation (McGovern and Bruce, 2000, Turnpenny *et al.*, 2000a), feed intake and feed digestion (Chilibroste *et al.*, 1997), and energy and protein utilisation (NRC, 2000, CSIRO, 2007). The novelty of LiGAPS-Beef thus lies in the fact that it combines existing models which were never combined before. This combination provided new ways to visualise the most constraining factors for livestock production on a daily basis in Chapter 3 (Fig. 3.5, Supplementary Information Fig. S12-S31) and Chapter 4 (Fig. 4.4). Such graphs clearly illustrate which factor constrains livestock production at what moment, and provide opportunities to identify effective improvement options.

LiGAPS-Beef was developed with the purpose to estimate potential and feed-limited production of farming systems with beef cattle in different agro-ecological environments. In Chapter 4, the model was tested by simulating live weight gain in beef production systems in Australia, Uruguay, and the Netherlands. Evaluation of LiGAPS-Beef at animal level showed that live weight gain was predicted fairly well (mean absolute error = 15.4% of measured average daily gain). Together with the evaluation of sub-models in Chapter 3, the results of Chapter 4 provide confidence that LiGAPS-Beef is suited for its purpose.

7.3.2 Data availability and data accuracy for model evaluation

The performance of LiGAPS-Beef was evaluated for three different beef production systems (Chapter 4). Evaluating the model for more systems may further advance insight in its validity domain. Model evaluation is, however, hampered by a significant lack of experimental data. Firstly, experimental data are abundant for specific life phases of individual animals, but evaluation of LiGAPS-Beef requires preferably data over entire life spans of all animals within herds or flocks. Such data are scarce, since long-term experiments with multiple animals are costly and time-consuming. As a result, livestock production at herd and farm level is generally not measured in experiments (Morel *et al.*, 2016).

Secondly, many experiments report the live weight leaving the farm gate, whereas the amount of edible beef remaining after slaughter is a better indicator of the amount of food produced. Model evaluation in Chapter 4 was based on live weight production, as data about the production of edible beef were not available. Valuable additions to evaluate the predictions of LiGAPS-Beef with regard to edible beef production will be measuring the carcass percentage and the percentage of edible beef in carcasses.

Thirdly, LiGAPS-Beef is a dynamic model requiring daily inputs of weather, feed quality, and feed quantity. The accuracy of model output is expected to increase with an increasing accuracy of measured input data, and with smaller time steps. Measured weather data are freely accessible in on-line repositories for several regions in the world (AGBOM, 2016, NIWA, 2016). Generated or intrapolated weather data are available also for several regions (Agri4Cast, 2013), although these are inferior to measured weather data. Availability of weather data was generally not a bottleneck for model evaluation in this thesis, but it might be when simulating beef production systems in countries where weather data are hardly available or accessible. Experimental data about feed quality and the available feed quantity were much more scarce than weather data during model evaluation. The feed quality of feed types was often not measured in experiments. If absent, feed quality was assumed to correspond with the default values for feed quality given in feed tables (Jarrige, 1989, Chilibroste *et al.*, 1997, Kolver, 2000). The quality of some feed types, such as grasses, is known to vary significantly among grass species, grass cultivars, geographical locations, and seasons (Smith *et al.*, 1998). In addition, grass quality is affected by management and nitrogen fertilisation (Hoekstra *et al.*, 2007). The accuracy of the output of LiGAPS-Beef is likely to decrease if input data for forage quality are inaccurate.

Inaccurate data for crude protein content are not likely to affect beef production, as protein is not among the main constraining factors for growth in Chapters 3 and 4. Inaccurate data for the metabolisable energy content, however, do affect beef production. Sensitivity analysis in Chapter 4 showed that a 10% change in metabolisable energy content (conversion from digestible to metabolisable energy) resulted in a larger change of feed efficiency of ¾ Brahman × ¼ Shorthorn cattle in Australia (14%) and of Hereford cattle in Uruguay (12%) under feed quality limitation. These results suggest that some errors in feed quality result in even larger errors in the estimates of feed efficiency at herd level, and highlight the importance of accurate feed quality data.

Despite the difficulties in model evaluation, the silver lining is that simulations with LiGAPS-Beef allow more targeted measurements in livestock systems. The sensitivity analysis performed in Chapter 4 identified the most influential parameters. With regard to energy and protein utilisation, future experiments may measure and calculate energy requirements for maintenance, the conversion from digestible to metabolisable energy, protein absorption, and protein accretion efficiency. With regard to thermoregulation, the sweating capacity, body area, and heat transfer between the body core and skin may be determined more precisely. Measuring the genetic potential for growth and calculating parameters of the Gompertz curve is also key to ensure model accuracy. Using measurements this way, simulation and experimentation can reinforce each other.

7.4 Quantification and analysis of yield gaps of feed-crop livestock systems

7.4.1 Discussion of the main findings

Assessing the scope to increase livestock production from the perspective of feed-crop livestock systems is essential in the context of sustainable intensification (Fig. 7.1). Since crop growth models can assess the scope to increase crop production, the development of LiGAPS-Beef cleared the road to assess the scope to increase production of feed-crop livestock systems. Chapter 5 illustrated, therefore, the scope to increase beef production per unit area for twelve different beef production systems in the Charolais region of France. Yield gaps in the Charolais region were on average 85% (80-88%) of the potential live weight production per hectare, and 47% (39-55%) of the resource-limited production. These results indicate a large bio-physical scope to increase production. They also demonstrate that concepts of production ecology can be applied successfully to feed-crop livestock systems.

In this thesis, bio-physical benchmarks were used to assess the scope to increase livestock production. Using an empirical benchmark, the technical efficiency, in sub-Saharan Africa indicated that yield gaps in milk, egg, and chicken production were between 25% and 63% (Henderson *et al.*, 2016). Yield gaps based on concepts of production ecology include bio-physical constraints for production only, whereas empirical benchmarks include all constraints, including *e.g.* the socio-economic ones. Hence, comparing yield gaps obtained from bio-physical and empirical methods has its limitation. It merely reveals that both methods predict considerable scope to increase livestock production.

In Chapter 5, additional levels to benchmark production were introduced, next to the potential and resource-limited production. This allowed to break up yield gaps in components, and to investigate the contribution of specific factors to yield gaps. For example, the effect of sub-optimal cattle management (slaughter weights, culling rates, calving dates, age at first calving, and stocking densities) could be disentangled from the other factors causing the yield gap between resource-limited and actual production (Chapter 5, Fig. 5.5). Using more than two benchmarks for agricultural production is recommended in future research if yield gaps are analysed with the aim to identify detailed and location-specific improvement options.

Yield gaps of beef production systems in the Charolais region were on average 85% of the potential production and 47% of the resource-limited production (Fig. 7.2). Potential production was simulated with an *ad libitum* diet consisting of grass silage,

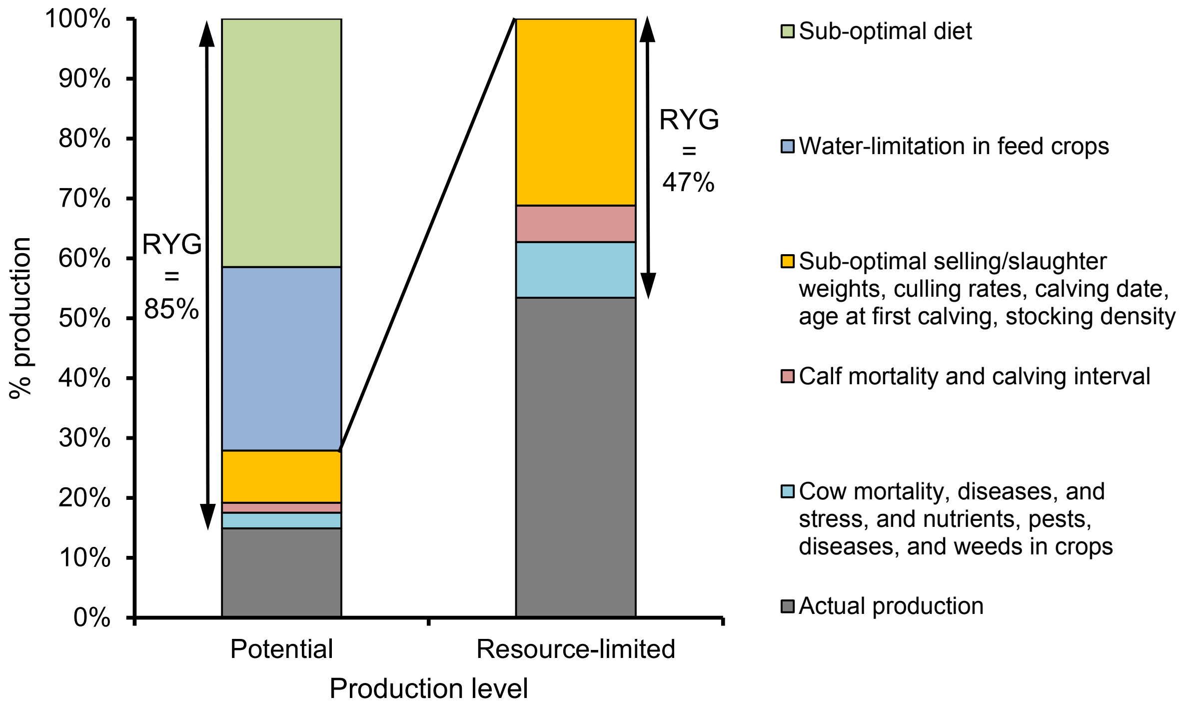

Figure 7.2 Average attribution of specific factors to the relative yield gap (RYG) of beef production systems in the Charolais region of France at feed-crop livestock system level. For potential production, 100% corresponds to 2,377 kg LW ha^{-1} $year^{-1}$, and for resource-limited production to 664 kg LW ha^{-1} $year^{-1}$ on average. Data for individual farm types are presented in Chapter 5.

whereas resource-limited production was simulated with the diet composition corresponding to practice. In practice, cattle grazed on pasture from spring to autumn, and were housed in winter, when diets consisted mainly of hay. Cereals accounted for 5-19% of the dry matter intake. Feeding the diet corresponding to practice instead of the *ad libitum* diet consisting of grass silage led to more feed quality limitation and to feed quantity limitation (*i.e.* a sub-optimal diet), and reduced potential production per hectare by 41% (Fig. 7.2). Water-limitation of feed crops further reduced potential production by 31%. Sub-optimal cattle management reduced potential production by 9%, and included management decisions on selling or slaughter weights, culling rates, calving dates, age at first calving, and stocking densities. Calf mortality and calving intervals longer than one year reduced potential production by 2%. Cow mortality, diseases and stress in cattle, and nutrient-limitation, and pest, diseases, and weeds in feed crops further reduced potential production by 3% (Fig. 7.2). These results demonstrate that the generic method laid out in this thesis allowed to analyse yield gaps in feed-crop livestock systems. Yield gap analysis contributes to the identification of improvement options. For example, besides improvements in cattle and grassland management, substituting hay by grass silage during the winter period may be a promising improvement option for intensification.

Chapter 6 investigated the beef production of Charolais bulls in grass-based systems in France under climate change. Due to the mechanistic nature of LiGAPS-Beef and the grass growth model LINGRA (Light INterception and utilisation – GRAss), the combined models allowed to account for the effects of increased temperatures and atmospheric CO_2-concentrations in grass-based beef farms. At the smallest projected climate change (representative concentration pathway (RCP) 2.6), the resource-limited beef production per hectare increased 5.5% between the start of the millennium (1999-2006) and 2050, and 13.8% at the largest projected climate change (RCP 8.5). This research is one of the first to simulate the effects of climate change on crops *and* livestock simultaneously. As noted in Chapter 6, the method can still be improved by adopting projected weather data that are not based on the weather variability at the start of the millennium, but account for the increased occurrence of extreme weather events, such as heavy rainfall.

7.4.2 Potential production of feed-crop livestock systems

The potential production of cropping systems is defined as the maximum theoretical production per unit area, where growth limiting and reducing factors are absent (Van Ittersum and Rabbinge, 1997, Evans and Fischer, 1999), and so is the potential production of livestock systems (Van de Ven *et al.*, 2003). Using these definitions, the potential production of feed-crop livestock systems could be defined as the maximum theoretical production of livestock per unit agricultural area used for feed crops, where growth limiting and reducing factors are absent.

Results of Chapter 5 clearly indicate that this definition cannot be met. The maximum theoretical production per hectare was obtained with a diet consisting of grass silage, which resulted in feed quality limitation. The *ad libitum* diet consisting of 65% wheat and 35% hay was assumed to eliminate growth limiting and reducing factors (Chapter 2), but did not result in the maximum theoretical production per hectare in Chapter 5. This was mainly explained by the higher potential production of grassland (20.8 t DM ha^{-1} year^{-1}) in the Charolais region compared to arable land used for wheat production (8.3 t DM ha^{-1} year^{-1}). The results of Chapter 5 reveal the dilemma whether to define potential production in feed-crop livestock systems as the theoretical maximum production per hectare, or as the production at which growth limiting (feed quality) and reducing factors are absent. In Chapter 2, the latter option was chosen, whereas the former option was chosen in Chapter 5. This dilemma will be discussed in the following paragraphs.

Like in Chapter 5, I propose to define potential production in feed-crop livestock systems as the maximum theoretical production per hectare, regardless of any feed quality limitation. This definition is chosen because it implies that live weight production cannot be higher than the maximum, and consequently yield gaps must be positive values. If the other definition would have been chosen, the actual production per hectare with grass-based diets may be higher per hectare than the potential production with a 65% wheat and 35% hay diet. This would result in a negative yield gap, which reflects a peculiar condition where farmers actually produce more than they theoretically could.

A diet consisting of *ad libitum* grass silage seems suited to assess potential production in feed-crop livestock systems, firstly because the yields of perennial grasses are generally higher than yields of wheat or annual crops used as concentrates. Secondly, grasses are used as feed for cattle all over the world. Thirdly, grass silages contain sufficient fibres to sustain rumen health. To assess potential production in feed-crop livestock systems, grass silage must be derived from a grass species adapted to the local conditions to ensure a high yield. So far, this section dealt with feed-crop livestock systems. For livestock systems, the diet under potential production (feed efficiency at herd level) is still the 65% wheat and 35% hay diet fed *ad libitum*, as defined in Chapter 2, and illustrated in Chapter 3.

7.4.3 Towards yield gap mitigation

Chapters 1, 2, 5, and 6 each contain notions that bio-physical improvement options alone are not sufficient to mitigate yield gaps: the bio-physical improvement options must comply with the economic, social, cultural, legislative, and ethical constraints set to livestock production by farmers and other stakeholders. Yield gap mitigation requires, therefore, a multi-disciplinary and/or participatory approach to assess all constraints for livestock production.

This critical notion does not undermine the relevance of the bio-physical research laid out in this thesis. Indeed, the bio-physical approach is very much compatible with a multi-disciplinary approach. Firstly, model simulations may identify a set of promising bio-physical improvement options, and subsequently knowledge of the constraints in their entirety can be used to eliminate the options that are not deemed feasible in practice. Alternatively, knowledge of the constraints in their entirety may identify a set of improvement options that are deemed feasible in practice, and subsequently model simulations may be used to select the most promising ones.

Secondly, the economic, social, cultural, legislative, and ethical constraints for agricultural production are variable in time, which implies that the actual production in agriculture will vary accordingly. Improvement options not deemed feasible today may be regarded feasible in 2050 due to economic and societal developments (Thornton, 2010). As an illustration, wheat prices increased by 113-116% in the United States between 2002 and 2007, with the largest increases during 2007, at the dawn of the global food crisis. The production costs for farmers to produce wheat only increased by 7% between 2002 and 2007 (Mitchell, 2008). Under such conditions, the importance of economic constraints is expected to decrease, and the importance of the bio-physical potential to produce food might increase.

Due to socio-economic and environmental constraints, farmers realise approximately 80% of the potential or limited production at most. The exploitable yield gap in a crop production system is defined as the difference between 80% of the potential or water-limited crop production and the actual production (Cassman *et al.*, 2003, Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013), whereas Van Ittersum *et al.* (2013) also mention a range of 75-85%. The exploitable yield gaps were assumed to be similar for crop *and* livestock production systems in Chapters 2, 5, and 6. Assuming production to plateau at 80% for feed crops (dry matter production) *and* for beef cattle (feed efficiency) implies that the actual production in feed-crop livestock systems is at most 64% (80% × 80%) of its potential or resource-limited production, and the corresponding theoretical yield gap is at least 36%.

The lowest yield gap of a feed-crop livestock system estimated in this thesis was 39% of the resource-limited production of a cow-calf-fattener system (farm type 11040) in the Charolais region. This farm type supplied the highest percentage of cereals in the diet (19%) of all twelve farm types investigated in Chapter 5. The actual feed efficiency in this system was 77% of the feed efficiency under resource-limitation. Actual feed efficiency was at most 82% of the feed efficiency under resource-limitation in farm type 31060 (18% cereals in the diet), which is still within the range mentioned by Van Ittersum *et al.* (2013). Hence, the hypothesis that livestock production (feed efficiency) can be increased to 75-85% of the resource-limited production is supported by the data from Chapter 5. Yield gaps tended to be smaller in systems feeding higher percentages of cereals in the diet. Future research may focus, therefore, on assessing yield gaps in feed efficiency of beef production systems feeding higher percentages of cereals (> 19%), or systems with intensive broiler or pig production to test the aforementioned hypothesis.

7.4.4 Synthesis

The first objective of this thesis was to develop a generic framework to assess the scope to increase production of feed-crop livestock systems per unit area based on concepts of production ecology. Such a framework was developed (Fig. 7.1), and applied successfully to beef production systems in the Charolais region of France. The scope to increase livestock production (feed efficiency) is an essential component of the framework, but could not be assessed generically at the start of this research. Therefore, a model was developed to estimate the bio-physical scope to increase livestock production generically. This model, named LiGAPS-Beef, allowed to simulate potential and feed-limited production of beef cattle, and allowed consequently to quantify the theoretical scope to increase livestock production (*i.e.* yield gaps). Hence, LiGAPS-Beef was the missing element to quantify the scope to increase beef production of feed-crop livestock systems. Yield gaps of feed-crop livestock systems with beef cattle were quantified in Chapters 5 and 6 with LiGAPS-Beef and crop growth models, contrary to the concise calculations used in Chapter 2

Table 7.1 Yield gaps of beef production systems (feed-crop livestock systems) in the Charolais region of France, as presented in Chapters 2, 5, and 6. Yield gaps in Chapter 2 are based on concise calculations, whereas yield gaps in Chapter 5 and 6 are based on simulations with LiGAPS-Beef and crop growth models. Yield gaps are separated in their feed crop component and their livestock component (feed efficiency).

	Concise calculations	Assessment with LiGAPS-Beef and crop growth models	
	Chapter 2	Chapter 5	Chapter 6
Relative yield gap $(Y_P - Y_A) / Y_P$			
Feed-crop livestock system	72 and 79%[a]	85% (80-88%)[b]	NA
Feed crop production	50 and 54%[a]	71% (67-74%)[b]	NA
Feed efficiency cattle	43 and 54%[a]	49% (37-57%)[b]	NA
Relative yield gap $(Y_L - Y_A) / Y_L$			
Feed-crop livestock system	NA	47% (39-55%)	41%[c]
Feed crop production	NA	26% (16-32%)	NA
Feed efficiency cattle	NA	28% (18-37%)	NA

[a] Relative yield gaps are based on beef production at herd level, and an *ad libitum* diet consisting of 65% wheat and 35% hay. This diet does not result in the highest production per hectare (Chapter 5, and section 7.4.2).
[b] Relative yield gaps are based on live weight production at herd level, and a diet consisting of silage grass.
[c] The relative yield gap is based on beef production from Charolais bull calves in the grazing season.
NA = not assessed.

(Table 7.1). The generic method allowed to analyse the specific factors attributing to yield gaps in beef production systems in the Charolais region of France (Fig. 7.2), and to identify improvement options to mitigate these yield gaps.

All in all, the accomplishment of the first (Chapter 2) and second objective of this thesis (Chapters 3 and 4) paved the road to accomplish the third objective (Chapter 5): the quantification and analysis of yield gaps of feed-crop livestock systems. The main achievement of this thesis, therefore, is the provision of a generic method to quantify and analyse yield gaps of feed-crop livestock systems.

7.5 Applications

The generic method to quantify and analyse yield gaps of feed-crop livestock systems can potentially be used for several other applications in future. Six applications described in this section are 1) mapping yield gaps, 2) simulating cattle kept for multiple purposes, 3) extending the model to other livestock species and to dairy cattle, 4) assessing the competition between food and feed production, 5) addition of indicators for sustainable intensification, and 6) assisting in livestock breeding.

7.5.1 Mapping yield gaps of feed-crop livestock systems

In this research, the scope to increase beef production was assessed for the Charolais region of France (Table 7.1). This assessment does, however, not provide much insights in the scope to increase beef production at regional, country, or global level, so global hotspots to increase beef production cannot be identified based on this thesis. The scope to increase crop production per unit area has been represented spatially in the Global Yield Gap Atlas (GYGA, www.yieldgap.org), for many crops in many countries. The GYGA allows to identify which areas in the world might be best suited for intensification of crop production.

To provide some more insight in the scope to increase the production of beef cattle in different countries, yield gaps were assessed for farms in Ireland and Uruguay, next to the yield gaps for farms in the Charolais region of France (Chapter 5). Charolais cattle were kept on farms in Ireland, and Hereford cattle were kept on farms in Uruguay. The location of the beef farms in Ireland was Cork (52.2°N, 8.2°E), and the location in Uruguay was Paysandú (32.3°S, 58.0°E). Cattle in Ireland grazed on pastures during spring, summer, and autumn, and were kept in stables during winter. Winter diets consisted of grass silage and concentrates. Cattle in Uruguay grazed year-round on natural pasture. The method to assess yield gaps in Ireland and Uruguay is described in Appendix 7A.

Benchmarking the actual live weight production against the potential production at feed-crop livestock systems level resulted in relative yield gaps between 81% and 97% (Fig. 7.3 A-C, Table 7.2). Benchmarking the actual live weight production against the resource-limited production resulted in relative yield gaps between 47% and 88% (Fig. 7.3 D-F, Table 7.2). Yield gaps were highest in Uruguay, because the potential production of grasses (33 t DM ha^{-1} year^{-1}) and the water-limited production

Table 7.2 Relative yield gaps of feed-crop livestock systems in France, Ireland, and Uruguay, and for their feed crop and cattle components. Actual production (Y_A) was benchmarked against the potential (Y_P) and resource-limited (Y_L) production. Minimum and maximum percentages are indicated between brackets. Data for France are from Chapter 5.

	France	Ireland	Uruguay[a]
Relative yield gap ($Y_P – Y_A$) / Y_P			
Feed-crop livestock system	85% (80-88%)	81% (77-83%)	97%
Feed crop production	71% (67-74%)	NA	93%
Feed efficiency cattle	49% (37-57%)	NA	60%
Relative yield gap ($Y_L – Y_A$) / Y_L			
Feed-crop livestock system	47% (39-55%)	56% (48-62%)	88%
Feed crop production	26% (16-32%)	NA	81%
Feed efficiency cattle	28% (18-37%)	NA	37%

[a] Minimum and maximum values for relative yield gaps are not available, since the actual production is based on the average national production of pasture-based beef farms, and not on multiple farms or farm types.
NA = Not Available. Actual feed crop production or feed efficiency were not given in Casey and Holden (2006).

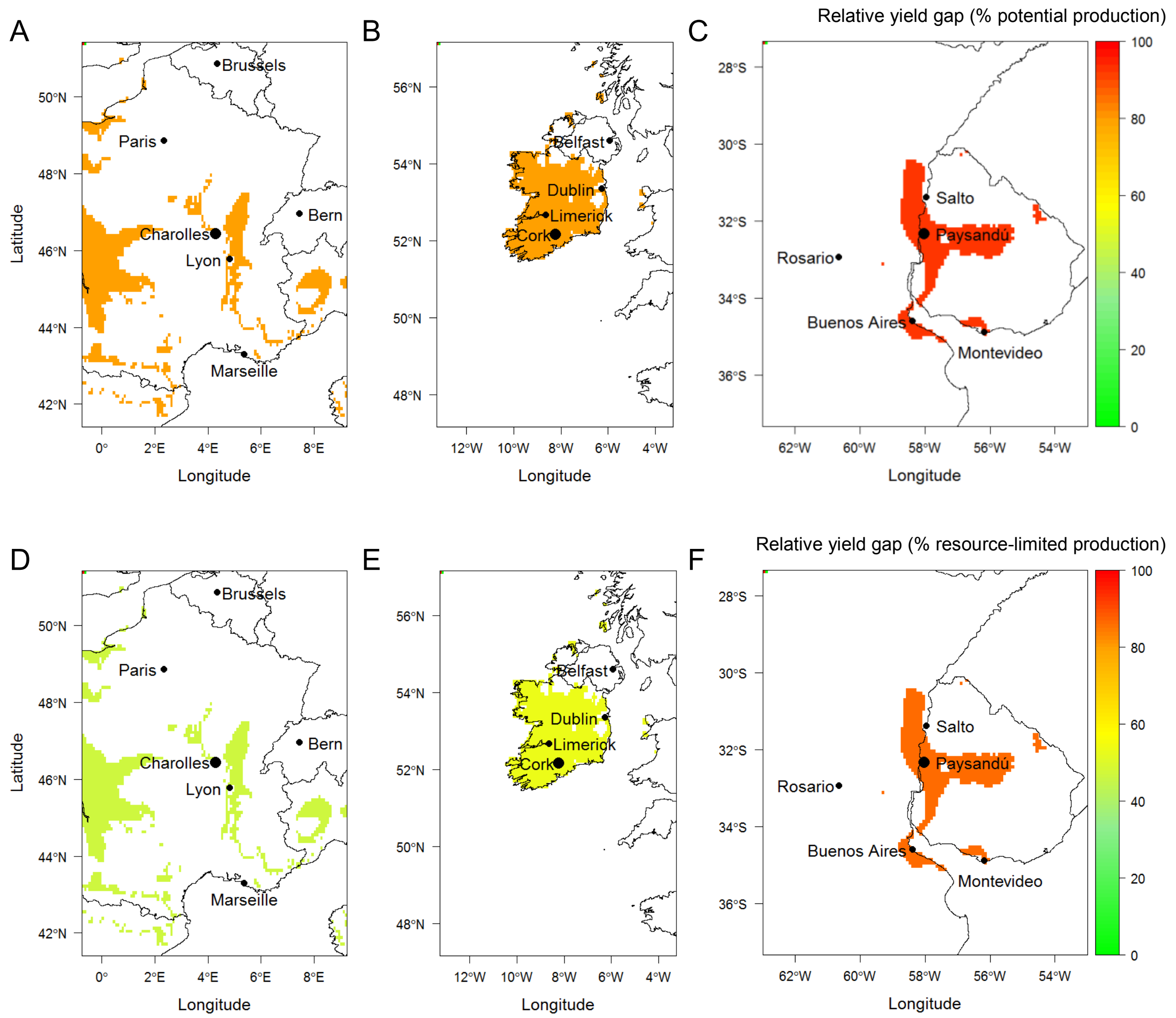

Figure 7.3 Relative yield gaps of beef production systems in France, Ireland, and Uruguay. Coloured areas indicate climate zones for which yield gaps were estimated. Actual production is benchmarked against potential production (A-C) and resource-limited production (D-F). Relative yield gaps are calculated as the difference between the benchmark and actual production, divided by the benchmark, and multiplied by 100%.

of grasses (23 t DM ha^{-1} year^{-1}) were high compared to the actual intake of natural pasture (2.2 t DM ha^{-1} year^{-1}). Benchmarking actual feed efficiency against the potential or feed-limited feed efficiency showed that relative yield gaps of cattle were higher in Uruguay than in France (Table 7.2). Potential live weight production was similar in France and Ireland. Resource-limited production was higher in Ireland than in France, which is related to the higher quality of the diet (Appendix 7A).

The yield gaps presented in this section indicate ample bio-physical scope to increase beef production. As the beef production systems investigated here are mainly rainfed, benchmarking against the resource-limited production seems most appropriate. After accounting for hard to avoid socio-economic and environmental constraints under resource-limited production (36% of the yield gaps in feed-crop livestock systems, see Section 7.4.4), the exploitable gaps are 11% in France, 20%

in Ireland, and 52% in Uruguay. These exploitable yield gaps correspond to 20% of the actual production in France, 45% of the actual production in Ireland, and 436% of the actual production in Uruguay.

The projected increase in global beef production from Alexandratos and Bruinsma (2012) is equivalent to 1.5% per year. According to FAO data and projections, the global feed efficiency of beef cattle increases by 0.5% per year (Wirsenius *et al.*, 2010), so increases in feed efficiency alone will not be sufficient. The increase in the live weight production per hectare per year in the past (1961-2010) was lower than the projected increase (1.5% per year) for major beef producing countries, such as Brazil (0.4% per year), China (1.2% per year), France (1.3% per year), the United States (1.3% per year), and Australia (1.4% per year) (Gerssen-Gondelach *et al.*, 2015). Hence, the land area for beef production has to be expanded if these historic trends continue, and if the projected increase in the global demand for beef appears to be accurate. To prevent this undesired expansion, yield gap analysis may be used to identify improvement options to increase the global beef production on the existing land area by 1.5% per year. Mapping and analysing yield gaps spatially may identify the regions best suited to increase beef production per hectare. Such information may be used subsequently by policy makers to prioritize interventions in the livestock sector.

7.5.2 Yield gap analysis for cattle kept for multiple outputs

Yield gaps of beef production systems were assessed in Chapters 2, 5, and 6. A number of additional steps must be taken to assess yield gaps in feed-crop livestock systems where cattle have one or more outputs next to beef. Firstly, the net energy (NE) and protein requirements must be assessed for each separate output of a herd. For example, the NE and protein requirements for milk production can be calculated from literature (NRC, 2000, CSIRO, 2007), and have been included in LiGAPS-Beef. Likewise, the NE and protein requirements for traction can be quantified (Van der Lee *et al.*, 1993). Formulas to quantify NE and protein requirements for rather qualitative outputs are not readily available. Outputs like social status and insurance, therefore, are hard to account for.

Secondly, the NE and protein requirements for outputs other than beef (*e.g.* milk production, traction) are calculated per herd unit, and used as input for LiGAPS-Beef. Thirdly, LiGAPS-Beef simulates the potential or feed-limited beef production while accounting for the estimated actual NE and protein requirements for the other outputs. The resulting yield gap indicates how much additional beef can be produced while maintaining the actual production of other outputs. Still, such a yield gap does not account for other outputs than beef. Fourthly, relative sensitivity analysis can be applied to study the effect of increasing and decreasing the NE and protein requirements for other outputs than beef. This method provides insight in the trade-offs between the production of outputs, and might allow to elucidate what combinations of outputs can be produced on top of the actual production.

7.5.3 Extension to other livestock types and species

Throughout this thesis, the generic benchmarking method for livestock production was illustrated for beef cattle (*Bos* sp.). Beef supplied 4.4% of the protein in the global diet in 2011 (Fig. 7.4). The share of protein from beef in the global human diet is smaller than the shares of protein from milk products, fish and seafood, poultry meat, or pork (Fig. 7.4). Extending LiGAPS-Beef to dairy cattle and other livestock species than beef cattle would allow to benchmark more livestock production systems, and cover a larger proportion of the animal-source protein in the global human diet.

Extension of LiGAPS-Beef to dairy cattle (LiGAPS-Dairy) is possible with a milk production module. Instead of simulating a fixed milk production as in LiGAPS-Beef, this module should simulate a variable milk production based on the defining and limiting factors, in interrelation with the variable live weight gain and beef production. LiGAPS-Dairy may also be applied to farm systems with dual-purpose cattle kept for milk and beef production. The structure of LiGAPS-Beef can also be used to develop models for sheep and goats kept for meat production. Besides meat, wool production is another output for sheep. LiGAPS-Beef does not simulate calf twins, so the model has to be adapted to account for twin and triplet lambs and kids.

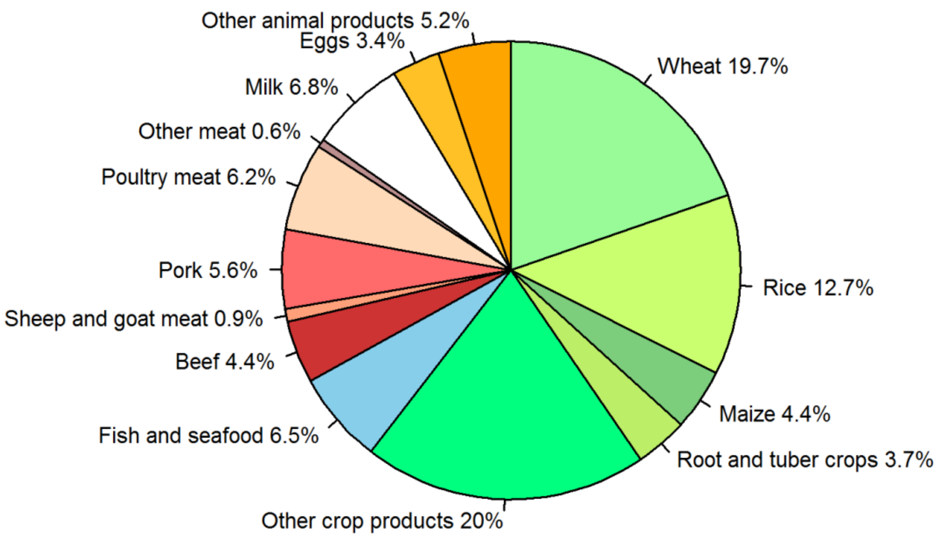

Figure 7.4 Relative contribution of crop and animal products to the protein supply in the average global diet in 2011 (80.5 g protein per capita per day). Other animal products include edible offals (1.4%). Source: FAO (2015).

Pigs are monogastric animals, and consequently the feed intake and digestion sub-model of LiGAPS-Beef, which applies to ruminants, requires adaptations. The concepts and structure of LiGAPS-Beef may be partially applicable to chicken also. As for pigs, the feed digestion model has to be adapted to account for the monogastric digestive system of chicken. The thermoregulation sub-model must be adapted too (Brouwer, 2014), as chicken are unable to increase the latent heat release via sweating (Turnpenny *et al.*, 2000b). The model for broilers may be extended with a module for egg production to simulate laying hens.

7.5.4 Quantifying food-feed competition

Human food crops and feed crops are cultivated both on arable land, resulting in competition between food and feed production. The production of plant-derived food and ASF were not compared on a hectare basis in this thesis, and the extent of food-feed competition was not assessed. The aim of this section, therefore, is to assess food-feed competition. Food-feed competition can be assessed by the land use ratio (LUR), which is a ratio comparing the production of human digestible protein (HDP) per unit of arable land from human food crops and ASF (van Zanten *et al.*, 2016a). The numerator of the LUR indicates how much plant-derived HDP can be produced if the arable land area in a feed-crop livestock system would be used for cultivation of food crops only. The denominator of the LUR indicates how much animal-source HDP can be produced from the same feed-crop livestock system. If the LUR is smaller than one, land of feed-crop livestock systems contributes more to HDP production under livestock production than it would under food crop production (Van Zanten *et al.*, 2016a).

The concept of the LUR was applied to two farm systems with Charolais cattle in the Charolais region of France, which were included in Chapters 2 and 5. The two systems correspond to farm types 11111 (cow-calf system) and 31041 (cow-calf-fattener system). Grassland was assumed to be unsuited for cultivation of food crops (Veysset *et al.* 2014). Further details about the calculation of the LUR are provided in Appendix 7B.

The LUR in the cow-calf system was lower than in the cow-calf-fattener system (Table 7.3). This result is explained by the lower fraction of wheat in the diet of the cow-calf system (5%) compared to the cow-calf-fattener system (17%), and consequentially a lower use of arable land per kg HDP produced. Given the actual LUR, both systems produce less HDP with beef cattle than they would with food crops. The cow-calf system had a LUR below one under resource-limited production (Table 7.3). This indicates that this system produces more HDP with beef cattle than it would with food crops, thanks to the large proportion of grassland area and an increased feed efficiency under resource-limited production compared to actual production.

Table 7.3 Beef production, human digestible protein (HDP) production, and land use ratios of a cow-calf system and a cow-calf-fattener system with Charolais cattle in the Charolais region in France.

		Actual production		Resource-limited production	
Farm characteristic	Unit	Cow-calf system[a]	Cow-calf-fattener system[a]	Cow-calf system	Cow-calf-fattener system
Feed efficiency[b]	kg beef t^{-1} DM feed	22.5	28.2	40.6	48.6
Beef production[b]	kg ha^{-1} agricultural land $year^{-1}$	118[c]	157	300	347
HDP production beef	kg ha^{-1} agricultural land $year^{-1}$	19.5	25.8	49.3	57.0
HDP production beef	kg ha^{-1} arable land $year^{-1}$	384	142	960	323
HDP production crops[d]	kg ha^{-1} arable land $year^{-1}$	704	795	950	950
Land use ratios	-	1.83	5.61	0.99	2.94

[a] The cow-calf system corresponds to farm type 11111, and the cow-calf-fattener system corresponds to farm type 31041 as specified in Reseaux d'Elevage Charolais (2014).
[b] Data adopted from Chapter 5.
[c] Calves are sold for fattening, and not slaughtered.
[d] The HDP production on arable land is obtained with soybeans, other crops (wheat, maize, potatoes) produce less HDP per hectare.

The LUR under resource-limited production was lower than under actual production (Table 7.3). The lower LUR under resource-limited production is mainly explained by a higher feed efficiency under resource-limited production than under actual production (Table 7.3). These results reveal that intensification from actual to resource-limited production reduced the LUR and thus the competition between food and feed production. In conclusion, the example for beef production systems in France indicates that combining concepts of production ecology with the concept of the LUR allows to assess food-feed competition. This approach is highly relevant to increase the number of people nourished per hectare of arable land within feed-crop livestock systems.

7.5.5 Adding indicators for sustainable intensification

Sustainable intensification is defined as increasing food production per unit of land, with less negative impacts on the environment (Garnett *et al.*, 2013, Godfray and Garnett, 2014). This thesis focussed on assessing the scope to increase livestock production per unit of land (kg live weight (LW) or beef ha^{-1} $year^{-1}$), which allows to calculate its reciprocal, the land footprint (m^2 year kg^{-1} LW or beef). So far, mitigation of the negative impacts on the environment was not investigated in this thesis. Nevertheless, the combination of LiGAPS-Beef and crop growth models allows to calculate the water use efficiency (kg LW or beef m^{-3} water) and its reciprocal, the water footprint (m^3 water kg^{-1} LW or beef). Water use can subsequently be separated in green water (derived from precipitation or groundwater charge) and blue water (derived from surface water or groundwater extraction), which allows to assess the green and blue water footprint (Hoekstra *et al.*, 2011).

Livestock production accounts for 18% of the total greenhouse gas emissions (Steinfeld *et al.*, 2006). A large part of the greenhouse gas emissions from beef production systems are attributed to enteric methane emissions (Beauchemin *et al.*, 2010, Dick *et al.*, 2015, Pashaei Kamali *et al.*, 2016). Including some more detail in the feed intake and digestion sub-model of LiGAPS-Beef will allow to simulate emissions of enteric methane under potential and resource-limited conditions. Subsequently, these results may be used, together with other results on greenhouse gas emissions at farm level, to calculate the carbon footprint (*e.g.* in CO_2-equivalents) per kg LW or beef produced.

As suggested in Chapter 5, LiGAPS-Beef and the crop growth models can be coupled to bio-economic models to assess the profitability of farms. The profit per kg live weight, per worker, or per farm can subsequently be used as indicators of the economic sustainability of beef production systems. Hence, the performance of beef production systems can also be benchmarked against other sustainability indicators than land use.

As indicated in Chapters 1 and 2, sustainable intensification needs to be accompanied by recognition that production activities feasible from a bio-physical perspective are not necessarily acceptable from an economic, social, cultural, environmental, legislative, or ethical perspective. Applying the concept of sustainable intensification to livestock production may raise ethical concerns about animal welfare in particular. At low livestock production levels, joint gains in production and animal welfare can be realised, for example by providing an adequate diet and controlling diseases effectively (McInerney, 1991 and 2004, Garnett *et al.*, 2013). However, at higher production levels, trade-offs between livestock production and animal welfare do exist. High livestock production can be accompanied by low animal welfare, even below the acceptable standards (McInerney, 1991 and 2004, Godfray and Garnett, 2014). Sustainable intensification of livestock production, therefore, certainly needs to come along with levels of animal welfare that are accepted by society or individual farmers. I concur, therefore, with Garnett *et al.* (2013) that techniques and options to increase livestock production should not be used if acceptable levels of animal welfare cannot be guaranteed.

7.5.6 Increasing potential production through breeding

Besides yield gap mitigation, increasing the potential production via breeding may contribute to intensification of agriculture also (Cassman, 1999, Evans and Fischer, 1999, Godfray *et al.*, 2010). Breeding has contributed significantly to increasing feed efficiency (kg ASF product kg^{-1} DM feed) observed in several livestock species over time (Rauw *et al.*, 1998, Havenstein *et al.*, 2003, Thornton, 2010). Already in the late

1960's, crop growth modelling was proposed as a valuable method to identify breeding objectives (Donald, 1968). Crop growth models have been used to identify important traits for crop production, and to design crops possessing an ideal combination of traits (*i.e.* an ideotype). Breeding objectives can subsequently be tailored to the ideotypes (Bouman *et al.*, 1996, Van Ittersum *et al.*, 2003, Yin *et al.*, 2003). Mechanistic livestock models are used to identify breeding objectives too (Wolfova *et al.*, 2005a, Wolfova *et al.*, 2005b, Doeschl-Wilson *et al.*, 2007). LiGAPS-Beef may be used, therefore, to assess the effects of breeding goals at herd level, such as increasing the carcass percentage, a better heat tolerance, or lower energy requirements for maintenance. As demonstrated in Chapter 5, the diet resulting in the highest feed efficiency at herd level is not necessarily the diet resulting in the highest live weight production per hectare at feed-crop livestock system level. Combining LiGAPS-Beef with crop growth models allows to assess the effects of breeding goals at feed-crop livestock system level. This combination allows to identify breeding objectives that improve the live weight production per hectare with the available feeds in a region.

7.6 Conclusions

The main conclusions from this research can be summarized as follows:

- Concepts of production ecology for livestock have been developed further to allow quantitative assessment of feed-crop livestock systems (livestock and corresponding feed production), which provides a generic framework to benchmark the actual production of feed-crop livestock systems against the potential and resource-limited production.
- The generic model LiGAPS-Beef simulates potential and feed-limited beef production based on concepts of production ecology, and accounts for (interactions among) the cattle genotype, climate, feed quality, and the available feed quantity, which allows to identify the most constraining bio-physical factors for growth. The model estimated live weight gain fairly well for different beef production systems in Australia, Uruguay, and the Netherlands.
- Combining LiGAPS-Beef with crop growth models based on concepts of production ecology is a powerful method for the quantification of yield gaps and the subsequent yield gap analysis in feed-crop livestock systems, as demonstrated for beef farms in the Charolais region of France.
- Beef production in the Charolais region of France can be increased substantially from a bio-physical perspective, because yield gaps of beef farms were on average 85% of the potential production per unit of agricultural area, and 47% of the resource-limited production. The main causes for these yield gaps are sub-optimal diets causing feed quality limitation and feed quantity limitation (41% of potential production), water-limitation in feed crops (31% of potential production), and cattle management (9% of potential production).

- Combining LiGAPS-Beef with crop growth models allows to explore future scenarios, such as grass-based beef production under climate change.
- The generic method to benchmark beef production at feed-crop livestock systems level provides opportunities to map yield gaps at (sub-)national and global level, to develop livestock models based on concepts of production ecology for other livestock than beef cattle, and to assess the competition for arable land between food and feed production.

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Appendix 1A

Compliance of available livestock models with yield gap analysis

This appendix contains a list of 32 mechanistic, dynamic livestock models simulating livestock production either at animal, herd, or flock level. The list is not meant as a complete inventory of all such livestock models available. Models simulating livestock at organ level (*e.g.* the rumen), farm level, or regional level were excluded, except for promising livestock sub-models that are part of a farm model (Rotz *et al.*, 1999), or of a household model (Lisson *et al.*, 2010). Feeding systems (*e.g.* from the National Research Council (NRC) or the Agricultural Research Council (ARC)) were not listed, as feeding systems usually require feed intake as an input for a fixed level of livestock production (Vermorel and Coulon, 1998). For each of these models, their compliance with the criteria to quantify yield gaps and to conduct yield gap analysis was investigated (Chapter 1).

Model evaluation was conducted to assess whether the genotype, climate, feed quality, and available feed quantity affected livestock production. The factor genotype was regarded to be included in a model if at least one breed-specific parameter affected production. The climate was included if at least one weather variable affected growth, even if the relation between climate and livestock production was assessed empirically (*e.g.* by using a temperature humidity index). Feed quality was reflected by the energy and protein content of feed, whereas essential amino acids, minerals, and vitamins were not taken into account. Livestock models complying with concepts of production ecology must predict feed intake based on the available feed quantity, and should not require feed intake as an input. The factor available feed quantity was included in a model if the feed intake of the model was predicted based on the available feed quantity.

Livestock production was simulated at herd or flock level if all animals necessary for production were included in the model, and if all life phases of animals were simulated. Animal-source food was regarded as a model output if the output could be consumed by humans, and if all relevant outputs (meat, milk, eggs) were simulated. The results of the model evaluation for their compliance to assess yield gaps generically are given in Table 1A.1.

Table 1A.1 Overview of mechanistic, dynamic livestock models simulating livestock production and eventually the production of animal-source food (ASF). Model compliance with the criteria to assess yield gaps generically are indicated with check marks. An asterisk for the factor climate indicates that the effect of climate on livestock production is included empirically in the model.

Animal species and type	Name of the model	Defining and limiting factors included in the livestock model					Herd or flock level	ASF output	Time step (days)	Model purpose is to:	Reference
				Feed quality							
		Genotype	Climate	Energy	Protein	Feed quantity					
Beef cattle	Texas A & M Cattle Production Systems Model	✓		✓	✓	✓	✓		30/31	Simulate feed intake and live weight gain of herds under different environmental and management conditions	Sanders and Cartwright (1979)
Beef cattle	BEEF / sub-model GRAZE	✓	✓*	✓	✓	✓	✓		0.01 / 1	Simulate the feed efficiency of a herd	Loewer *et al.* (1980), Loewer *et al.* (1983), Loewer *et al.* (1987a and 1987b)
Beef cattle	BEM	✓		✓		[a]	✓	✓	1	Simulate effects of feed efficiency with technological improvements in North America	Naazie *et al.* (1997)
Beef cattle	ABPSS	✓	✓*	✓	✓	[a]	✓		1	Predict nutrient requirements of cows and calves and assess effects of production traits and management	Pang *et al.* (1999)
Beef cattle		✓		✓	✓	✓	✓		1	Simulate effects of genotype, feed, and herd management on growth and body composition of cattle on rangelands	Tess and Kolstad (2000)
Beef cattle		✓		✓	✓	[b]		✓	1	Predict body composition	Hoch and Agabriel (2004)
Beef cattle		✓	✓*	✓	✓	[c]		✓	1	Simulate growth, feed intake, and body composition of cattle in feedlots	Tedeschi *et al.* (2004)
Dairy cattle	Sub-model DAFOSYM	✓		✓	✓	[a]			1	Predict feed intake, milk production, and manure excretion of herds consisting of six animal groups	Rotz *et al.* (1999)

[a] Feed intake is a model output calculated backwards from animal production, which makes the available feed quantity redundant as a model input.
[b] Digested nutrients are model input, and the corresponding feed intake and available feed quantity are not taken into account.
[c] Feed intake is either used as a model input used to predict production, or production is used as a model input to predict feed intake.

Table 1A.1 Continued.

Animal species and type	Name of the model	Defining and limiting factors included in the livestock model					Herd or flock level	ASF output	Time step (days)	Model purpose is to:	Reference
		Genotype	Climate	Feed quality		Feed quantity					
				Energy	Protein						
Dairy cattle	MOOSIM	✓	✓*	✓		✓			1	Predict milk yield and live weight change of dairy cows	Bryant *et al.* (2008)
Dairy cattle	LIVSIM	✓		✓	✓	✓	✓		30	Quantify the lifetime productivity and explore alternative feeding strategies of dairy cows	Rufino *et al.* (2009)
Cattle	CNCPS-C	✓	✓	✓	✓	[d]	✓		1	Estimate energy and nutrient requirements of cattle breeds under different feeding and management strategies	Fox *et al.* (2004)
Cattle	PC-HERD	✓		✓	✓	✓	✓		30	Assess production of a herd under different feeding and management strategies	Brouwer and Steenstra (1994)
Cattle and sheep	GRAZPLAN	✓	✓	✓	✓	[e]	✓		1	Support decision making, and predict intake and productivity of herds and flocks on pastures	Freer *et al.* (1997)
Sheep	Texas A & M Sheep Simulation Model	✓		✓	✓	✓	✓		15	Simulate sheep productivity in arid environments at animal and flock level with different feeding strategies and management	Blackburn and Cartwright (1987)
Sheep	CNCPS-S	✓	✓	✓	✓	?	✓		1	Predict energy and nutrient requirements of sheep	Cannas *et al.* (2004)
Sheep and goats	SRNS	✓	✓	✓	✓	?	✓		1	Predict energy and nutrient requirements of sheep and goats	Tedeschi *et al.* (2010)
Goats	PC-FLOCK	✓		✓	✓	✓	✓		7	Investigate the production and productivity for flocks with goat breeds kept for meat	Bosman *et al.* (1997)

[d] Feed intake is a model input or can be calculated via an empirical equation, which makes the available feed quantity redundant as a model input.

[e] Feed intake is calculated empirically from the relative size of an animal and lactation, and corrected for pasture biomass and dry matter digestibility.

Table 1A.1 Continued.

Animal species and type	Name of the model	Defining and limiting factors included in the livestock model					Herd or flock level	ASF output	Time step (days)	Model purpose is to:	Reference
		Genotype	Climate	Feed quality		Feed quantity					
				Energy	Protein						
Pigs			✓*	✓	✓	[f]		✓	1	Calculate live weight gain, feed efficiency, and body composition of growing pigs	Whittemore and Fawcett (1974, 1976)
Pigs		✓		✓	✓	[f]			1	Simulate growth and carcass weight of growing pigs from information on genotype, and feed quality	Moughan and Smith (1984) and Moughan *et al.* (1987)
Pigs		✓		✓	✓	[g]	✓		1	Simulate growth and total body composition based on genotype, feed, and management for growing pigs and sows	Pomar *et al.* (1991a, 1991b, 1991c)
Pigs				✓	✓	[h]			1	Simulate energy and protein metabolism in lactating sows	Pettigrew *et al.* (1992a, 1992b)
Pigs		✓	✓	✓	✓	✓			1	Assess effects of breed, temperature, and nutrition on growth rates, and lipid and fat accretion	Knap (2000)
Pigs		✓		✓	✓	[h]			1	Assess energy and protein utilisation for maintenance and growth of body tissues in growing pigs	Birkett and de Lange (2001a, 2001b)
Pigs		✓	✓	✓	✓	✓			1	Predict effects of genotype, climate, and nutrition on feed intake, growth, and body composition	Wellock *et al.* (2003)
Pigs		✓[i]		✓	✓	[h]		✓	0.01	Predict growth rate, chemical composition, and anatomical composition of growing pigs from digestible nutrient intake	Halas *et al.* (2004)
Pigs				✓		[j]			0.5	Predict the capacity for energy intake, maintenance requirements, and energy accretion in the body from net energy intake and body weights	Strathe *et al.* (2009)

[f] Feed intake is a model input, which makes the available feed quantity redundant as a model input.
[g] Feed intake is calculated empirically from a single equation, which makes the available feed quantity redundant as a model input.
[h] Feed and nutrient intake are model inputs, which makes the available feed quantity redundant as a model input.
[i] Parameters representing different genotypes are identified, but different genotypes are not simulated in this publication.
[j] Feed intake and energy intake are a function of metabolic body weight, which makes the available feed quantity redundant as a model input.

Table 1A.1 Continued

Animal species and type	Name of the model	Defining and limiting factors included in the livestock model: Genotype	Climate	Feed quality: Energy	Feed quality: Protein	Feed quantity	Herd or flock level	ASF output	Time step (days)	Model purpose is to:	Reference
Pigs	InraPorc	✓	✓*	✓	✓	[k]	✓	✓	1	Simulate live weight gain, feed intake, and body composition of growing pigs and sows	Van Milgen *et al.* (2008) and Dourmad *et al.* (2008)
Pigs	Davis Swine Model	✓		✓	✓	[l]			1	Predict protein and lipid retention, body composition, and manure production in growing pigs	Strathe *et al.* (2015)
Broilers			✓*	✓	✓	[m]		✓	1	Optimize diet composition by simulating energy, protein, and amino acid requirements	Talpaz *et al.* (1986)
Broilers	BPHL	✓		✓	✓	[n]		✓	1	Simulate broiler growth and carcass composition	King (2001)
Turkey		✓		✓	✓	✓		✓	1	Predict average weight gain for different genetic, environmental, and nutritional conditions	Rivera-Torres *et al.* (2011)
Multiple species	IAT[o]	✓		✓	✓	✓	✓		30/31	Predict growth and production for various livestock species in a smallholder farm	Lisson *et al.* (2010)

[k] Digested nutrients are model input, but feed intake is presented as well. *Ad libitum* feed intake is calculated from an empirical function of the metabolic body weight (body weight$^{0.75}$).
[l] Feed intake is calculated empirically from the body weight, which makes the available feed quantity redundant as a model input.
[m] Feed intake is a model output calculated from empirical growth curves and temperature, which makes the available feed quantity redundant as a model input.
[n] Feed intake is calculated from empirical equations, which makes the available feed quantity redundant as a model input.
[o] The IAT (Integrated Assessment Tool) is a household model. The part of the model related to livestock production was investigated.

Appendix 5A

Combining LiGAPS-Beef and LINGRA

Supplementary information Chapter 5: Yield gap analysis of feed-crop livestock systems: the case of grass-based beef production in France

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1 Extension and adaptation of models

This section describes the extension and adaptation of the crop growth models LINGRA (Light INterception an utilisation - GRAss) and LINTUL-2 (Light INTerception and UtiLisation), and the cattle growth model LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle). LINGRA and LiGAPS-Beef were combined to simulate resource-limited live weight production (water-limited growth of feed crops and feed-limited growth of cattle) in grass-based beef production systems with Charolais cattle in the Charolais area of France (Chapter 5).

1.1 Extension and adaptation of LINGRA

LINGRA simulates photosynthesis, grass growth, tillering, and leaf canopy dynamics of perennial ryegrass (*Lolium perenne* L.) under potential production and water-limited production (Schapendonk *et al.*, 1998). LINGRA simulates the green aboveground biomass and the dead biomass, but does not distinguish between vegetative and generative growth. Vegetative and generative growth, however, affect feed quality to a large extent (Höglind *et al.*, 2001, Barrett *et al.*, 2005). Since feed quality is an important input for LiGAPS-Beef, we included vegetative and generative growth in LINGRA to simulate grass quality.

LiGAPS-Beef simulates cattle for multiple years, and LINGRA was adapted to simulate multiple years of grass growth too. The tiller density is assumed to be fixed at the 1st of January for each year (13100 tillers m^{-2}). Each of the tillers present at the 1st of January is assumed to be sufficiently vernalized to become generative in the next growing season (Barrett *et al.*, 2005). Heading is assumed to occur at a developmental stage of 975 growing degree days (Table 1A.1), which allows to calculate the heading date of the grass. Tiller death rates, which are already included in LINGRA, are assumed to be equal for vernalized and non-vernalized tillers. The fraction tillers at or beyond the heading stage is calculated from the heading date (Eq. 1, Barrett *et al.*, 2005).

$$Eq.1\ \ F_{head}(t) = \frac{1}{\sqrt{2 \times 3.142}} \times SD \ \times e^{\frac{-(DOY(t)-HD)^2}{2 \times SD^2}}$$

Where F_{head} is the fraction tillers at or beyond heading, SD is the standard deviation of the heading date (days), DOY is the Julian day of the year, and HD is the heading date (Julian day). The number of generative tillers throughout the year is calculated from the tiller population present at the 1st of January, the cumulative tiller death rate, and the fraction of tillers at or beyond the heading stage (Eq. 2).

$$Eq.2\ \ GT(t) = T_{1^{st}\,Jan.} \times S(t) \times F_{head}$$

Where GT is the number of generative tillers (m^{-2}), $T_{1st\ Jan.}$ is the number of tillers present at the 1st of January, and S(t) is the probability of a tiller to survive up to time

Table 5A.1 Parameters used in the extension and adaptation of the grass growth model LINGRA.

Description parameter	Value	Unit	Equation number	Reference
Standard deviation heading	18	days	1	Barrett *et al.* (2005)
GDD for heading[a]	975	° days	1	P. Veysset, personal communication
Sink strength generative: vegetative tillers	3.5		3	Donaghy and Fulkerson (1998)
Base temperature ME decrease	12	°C	4	Lambert and Litherland (2000)
Decline ME in vegetative tillers	-0.005	MJ kg DM^{-1} $°C^{-1}$ day^{-1}	4	Derived from Lambert and Litherland (2000)
Decline ME in generative tillers	-0.010	MJ kg DM^{-1} $°C^{-1}$ day^{-1}	4	Derived from Lambert and Litherland (2000)
Minimum ME content	8	MJ kg DM	5	Lambert and Litherland (2000)
Maximum ME content	12	MJ kg DM	5	Lambert and Litherland (2000)
Minimum SLA	0.050	m^2 g^{-1} DM	-[b]	Barrett *et al.* (2005)
Maximum SLA	0.025	m^2 g^{-1} DM	-[b]	Barrett *et al.* (2005)
Minimum LUE	2.2	g DM MJ^{-1} PAR	-[b]	Barrett *et al.* (2005)
Maximum LUE	3.2	g DM MJ^{-1} PAR	-[b]	Barrett *et al.* (2005)

[a] Base temperature is 0°C, and the starting date is the 1st of February. Value is an average between 750 and 1200 GDD, which is the range observed for the Charolais area. The growing degree days for heading are used to calculate the heading date, a parameter in Equation 1.
[b] For the equation, see Barrett *et al.* (2005).
DM = dry matter; GDD = growing degree days; LUE = light use efficiency; ME = metabolisable energy; PAR = photosynthetic active radiation; SLA = specific leaf area

step t from the 1st of January, which was already included in the original version of LINGRA. The number of vegetative tillers is the total number of tillers minus GT. The number of growing degree days and the fraction of tillers at or beyond the heading stage are both set to zero at the 1st of January. Assimilates are distributed over roots and shoots in LINGRA. In our adapted version of the model, shoots consist of vegetative and, eventually, generative tillers. The sink strength of generative tillers is assumed to be 3.5 times the sink strength of vegetative tillers (Donaghy and Fulkerson, 1998, Barrett *et al.*, 2005). The fraction assimilates allocated to generative tillers (Eq. 3) and the fraction assimilates allocated to vegetative tillers add up to one.

$$Eq. 3 \quad FGT\ (t) = \frac{(GT(t)\ \times 3.5)}{(VT(t) +\ GT(t)\ \times 3.5)}$$

Where FGT is the fraction assimilates allocated to generative tillers, and VT is the number of vegetative tillers (m^{-2}). Decreases in the metabolisable energy (ME) content are dependent on temperature, and the fractions of vegetative and generative tillers (Lambert and Litherland, 2000) (Eq. 4).

$$Eq. 4 \quad MED\ (t) = \max(0, \frac{-(T_{max}(t) - T_{base})}{MER})$$

Where MED is the decrease in ME (MJ kg^{-1} dry matter (DM) day^{-1}) of the aboveground biomass, T_{max} is the maximum daily temperature (°C), T_{base} is the base temperature above which grass quality decreases (°C), and MER is the reduction in ME of vegetative or generative tillers (MJ ME kg^{-1} DM day^{-1} $°C^{-1}$). Newly-formed biomass over a day is assumed to be 12 MJ ME kg^{-1} DM. The average ME content of the green aboveground biomass at a specific day can be calculated from the ME content of the green aboveground biomass at the previous day, the ME decrease of the aboveground biomass at the previous day, and the newly-formed biomass at the previous day. The ME content is at least 8 MJ ME kg^{-1} DM (Eq. 5).

$$Eq. 5 \quad ME_{abg}\ (t+1) =$$

$$\max(ME_{min}, \frac{(ME_{abg}\ (t) - MED_v(t)) \times BVT(t) + (ME_{abg}\ (t) - MED_g(t)) \times BGT(t) + (GVT(t) + GGT(t)) \times ME_{new}}{(BVT(t) + BGT(t) + GVT(t) + GGT(t))})$$

Where ME_{abg} is the average ME content of the green aboveground biomass (MJ kg^{-1} DM), ME_{min} is the minimum ME content (MJ kg^{-1} DM), MED_v is the decrease in ME of vegetative tillers (MJ kg DM day^{-1}), BVT is the biomass of vegetative tillers (kg DM ha^{-1}), MED_g is the decrease in ME of generative tillers (MJ kg DM day^{-1}), BGT is the biomass of generative tillers (kg DM ha^{-1}), GVT is the growth of vegetative tillers (kg DM ha^{-1} day^{-1}), GGT is the growth of generative tillers (kg DM ha^{-1} day^{-1}), and ME_{new} is the ME content of the newly-formed biomass (MJ kg^{-1} DM).

Vegetative and generative tillers together constitute the green biomass. The dead biomass is simulated in the original version of LINGRA, and its quality is assumed to be equal to the minimum ME content. The decomposition rate of dead biomass is assumed to be 5% day^{-1}, irrespective of the environmental conditions (Woodward, 1998). Crude protein content is a function of the Julian day, which is adopted from Barrett *et al.* (2005) (Eq. 6).

$$Eq. 6 \quad CP = -1.9 \times 10^{-6} \times DOY^3 + 0.00148 \times DOY^2 - 0.3027 \times DOY + 27.526$$

Where CP is the crude protein content (% DM), and DOY is the (Julian) day of the year. The grass quality, reflected by the ME and CP content, is key input for LiGAPS-Beef, since feed quality is a limiting factor for cattle growth and production (Van de Ven *et al.*, 2003, Van der Linden *et al.*, 2015).

Several small adaptations were made in LINGRA. Firstly, the specific leaf area (SLA) and light use efficiency (LUE) were fixed in the original version of LINGRA, but have been converted into variables, following Barrett *et al*. (2005). Secondly, pastures used for grazing are assumed to be mown after the grazing season to eliminate differences in sward height. Mowing is assumed to remove all heads remaining at the end of the grazing season. The biomass of green leaves remaining after mowing is the minimum of the actual green leaf biomass and 1.5 t DM ha^{-1} year^{-1}. Thirdly, the critical leaf area index (LAI) indicates at what LAI the lowest green leaves in the sward are deteriorate due to shading. The default value for the critical LAI was 4 m^2 leaf m^{-2} soil, but this value was increased to 5.4 m^2 m^{-2}. The higher critical LAI resulted in a higher accumulation of aboveground biomass (up to 5 t DM ha^{-1} year^{-1}), which reflects the aboveground biomass of grasslands used for hay production better. Finally, it should be noted that LINGRA was adapted to simulate continuous grazing, which is a common grazing strategy in the Charolais area. Other grazing strategies, such as rotational grazing or strip grazing, were not considered.

1.2 Adaptation of LINTUL-2

The simple crop growth model LINTUL-2 was used to simulate potential and water-limited growth of spring wheat (Van Ittersum *et al.*, 2003). Nonetheless, wheat cultivated in the Charolais area of France is generally winter wheat. Yields of winter wheat are usually higher than yields of spring wheat, due to the higher leaf biomass and light interception during spring. Spring wheat was assumed to emerge at Julian day 60 in LINTUL-2, with an initial LAI of 0.01 m^{2}m^{-2}. To account for the difference between winter wheat and spring wheat, we increased the initial LAI at Julian day 60 to 0.50 m^2 m^{-2}, which represents the higher biomass of winter wheat in spring better.

The default light use efficiency (LUE, 3.0 g DM MJ^{-1} photosynthetic active radiation) was replaced by a function where the LUE was a function of the current atmospheric CO_2 concentration (Eq. 7). This function is the same as the function for LUE in LINGRA.

$$Eq. 7 \ LUE_C = LUE \ \times 1 + 0.5 \times log(CO_2/CO_{2\,ref.})$$

Where LUE_c is the LUE under the current atmospheric CO_2 concentration (3.2 g DM MJ^{-1} photosynthetic active radiation), CO_2 is the current atmospheric CO_2 concentration, which was set at 390 ppm, and $CO_{2\ ref.}$ is the reference CO_2 concentration, which was 360 ppm in LINTUL-2.

1.3 Adaptation of LiGAPS-Beef

LiGAPS-Beef simulates thermoregulation, feed intake and digestion, and energy and protein utilisation for metabolic processes, such as maintenance, growth, gestation, and lactation. LiGAPS-Beef allows to simulate potential production and feed-limited production (Van der Linden *et al.*, 2017a). This section describes the adaptations made in LiGAPS-Beef to simulate the mutual interaction between grass sward and cattle.

Selective grazing behaviour of cattle on pasture increases both the energy costs for locomotion and grazing, and the energy gain from a higher quality diet. Ruminants maximize net energy intake by balancing the energy costs for locomotion and the corresponding gains (Murray, 1991). Net energy requirements for locomotion and grazing are assumed to increase with decreasing pasture biomass (Freer *et al.*, 1997) (Eq. 8).

$$Eq.8 \quad NE_{loc}\,(t) = 1/(0.02 \times (BVT(t) + BGT(t) + BD(t)) + 60)$$

Where NE_{loc} is the net energy requirement for locomotion and grazing (MJ kg^{-1} total body weight (TBW) day^{-1}), and BD is the biomass of dead plant materials (kg DM ha^{-1}). Feed intake is reduced at low availability of aboveground biomass, which includes dead biomass. LiGAPS-Beef accounts for the maximum feed intake expressed in fill units (Jarrige *et al.*, 1986). To account for a low availability of aboveground biomass, the maximum feed intake in fill units in grassland is multiplied by an empirical intake multiplier calculated from a meta-analysis of grazing experiments (Jouven *et al.*, 2008) (Eq. 9).

$$Eq.9 \quad INTM\,(t) = 1 - exp^{(-0.00112 \times (BVT(t) + BGT(t) + BD(t))}$$

Where INTM is a dimensionless grass intake multiplier. Cattle select between green and dead biomass, which is assumed to result in a lower fraction of dead biomass in the diet than in the pasture (Eq. 10).

$$Eq.10 \quad FDB_{diet}\,(t) = \frac{(FDB_{pasture}\,(t)^4 + 0.3 \times FDB_{pasture}\,(t))}{1.3}$$

Where FDB_{diet} is the fraction dead biomass in the diet, and $FDB_{pasture}$ is the fraction dead biomass in the sward. Furthermore, cattle select within the green biomass for the highest quality components, such as the leaf lamina, and hence the ME content of the ingested green biomass is higher than the average ME content of the green biomass on the pasture. A lower availability of green biomass provides less

Table 5A.2 Breed and sex-specific parameters for Charolais cattle used as input for LiGAPS-Beef. Data are adopted from Van der Linden *et al.* (2017a).

Parameter	Unit(s)[a]	Sex		Sub-model[b]
		male	female	
Area : weight factor		1	1	T
Body core – skin conductance[c]	$W\ m^{-2}\ K^{-1}$	64.1	64.1	T
Coat length[d]	mm	12	12	T
Min. cond. body core – skin factor		1	1	T
Reflectance coat[e]		0.6	0.6	T
Sweating rate A[f]		3.08	3.08	T
Sweating rate B[f]		1.73	1.73	T
Sweating rate C[f]	°C	35.3	35.3	T
Birth weight[g]	kg TBW	48.1	45.9	E
Gompertz constant of integration[h]		1.6	1.6	E
Gompertz rate constant[h]		1.1	1.1	E
Gompertz reduction[h]	kg TBW	316.7	228.7	E
Lactation curve A[i]		-	0.276	E
Lactation curve B[i]		-	0.15	E
Lipid bone parameter[j]		11.6	11.6	E
Maintenance correction[k]		1	1	E
Max. carcass %[l]		64	62	E
Max. muscle : bone ratio[m]		4.4	4.1	E
Maximum adult weight[n]	kg TBW	1300	950	E
Min. % adult weight for gestation[o]		-	60	E

[a] This column is left blanc for unitless parameters.

[b] Refers to the sub-models in LiGAPS-Beef. T = thermoregulation sub-model; E = energy and protein utilisation sub-model.

[c] Maximum body-skin conductance under full vasodilatation, calculated from Turnpenny *et al.* (2000b). The parameter is constant with age and is valid for beef cattle.

[d] Seasonal changes in summer and winter coats are not taken into account. Coat length is adopted from Turnpenny *et al.* (2000b).

[e] Estimated from the breed coat colour based on da Silva *et al.* (2003).

[f] Sweating rate is calculated with the formula $x + A \times e^{(B \times (T_{skin}-C))} \times 0.628$, based on Gatenby (1986). Where x is the basal sweating rate, and T_{skin} is the skin temperature in °C. Parameters are estimated from Schleger and Turner (1965) and Gatenby (1986).

[g] Source: Simčič *et al.* (2006).

[h] Gompertz curves describing total body weight are written as $(a + (b - a + e) \times e^{(-c \times e^{(-d \times t)})}) - e$. Where a is the birth weight; b is the maximum adult weight; c is the constant of integration; d is the rate constant; t is time in days, and e is a reduction factor. Parameters c, d, and e are obtained by fitting Gompertz curves.

[i] The lactation curve is calculated with the formula $(t / 7 + 3) \times (A \times e^{(B \times (t / 7 + 3))})^{-1}$ (Jenkins and Ferrell, 1992). Where t is the time in days after parturition, A determines peak production, and B the shape of the milk production curve. Total milk production in a 240-day lactation period is assumed to be 1,600 L for Charolais cows.

[j] Lipid fraction in the bone is calculated as $W_b \times A \times \ln(W_b) / 100$. Where W_b is the bone weight, and A is the breed specific parameter. This formula is based on data of Field *et al.* (1974).

[k] *B. taurus* cattle are taken as a reference (1.00). As Charolais are *B. taurus* cattle, the NE requirements for maintenance are multiplied by 1.00.

[l] Charolais cattle have been bred for beef production, resulting in high carcass percentages. Males are assumed to have higher carcass percentages than females. Maximum carcass percentages of Charolais bulls are estimated from Pfuhl *et*

al. (2007) (60.4% at 18 months). Relations between empty body weight and carcass weight are given by Fox *et al.* (1976).
[m] Muscle:bone ratios were estimated from Berg and Butterfield (1968).
[n] Mature body weights under potential production are hard to estimate. Weights mentioned for Charolais are higher than the actual slaughter weights mentioned by Réseaux d'Élevage Charolais (2014) and Nguyen *et al.* (2012).
[o] The minimum percentage of the maximum adult weight for conception is 50% with ideal cattle management.
TBW = total body weight

opportunities for diet selection (Murray, 1991). In addition, the difference between the ME content of the green biomass and the minimum ME content of the green biomass is assumed to affect the opportunity for cattle to select a high quality diet (Eq. 11).

$$Eq.11 \quad ME_{gb}(t) = ME_{abg}(t) + (ME_{abg}(t) - ME_{min}) \times (1 - e^{\frac{-(BVT(t) + BGT(t))}{5000}})$$

Where ME_{gb} is the ME content of the green biomass selected by cattle. Subsequently, the average ME content of the diet is calculated from the fraction green and dead biomass in the diet (Eq. 12).

$$Eq.12 \quad ME_{tb}(t) = (1 - FDB_{diet}(t)) \times ME_{int}(t) + FDB_{diet}(t) \times ME_{min}$$

Where ME_{tb} is the ME content of the total biomass (green and dead) selected by cattle (MJ kg^{-1} DM). Net energy requirement for locomotion and grazing, the grass intake multiplier, and the ME content of the diet affect cattle production. Cattle reduce the aboveground biomass by defoliation, and the green biomass by trampling. The defoliation rate per hectare equals the total grass intake rate from all animals grazing this hectare. The reduction in green biomass due to trampling is a function of live weight (LW) and the green biomass on the pasture (Finlayson *et al.*, 2002) (Eq. 13). The green biomass trampled is assumed to end up in the pool of dead biomass.

$$Eq.13 \quad BLT(t) = 2.0 \times 10^{-6} \times LW(t) \times (BVT(t) + BGT(t))$$

Where BLT is the biomass loss due to trampling (kg DM ha^{-1} day^{-1}), and LW is the live weight of cattle (kg ha^{-1}). The version of LiGAPS-Beef used simulated potential and water-limited grass growth, but did not simulate for nutrient limitation. Hence, the effect of manure deposition on grass growth and grass intake was not taken into account, and neither was the effect of urine patches.

2 Model inputs and settings for LiGAPS-Beef, LINGRA, and LINTUL-2

2.1 Model inputs and settings for LiGAPS-Beef

The model LiGAPS-Beef requires data on the genotype, or breed, the climate, feed quality, feed quantity, and cattle management. The default parameters for the Charolais breed were adopted from the Supplementary Information of Van der Linden *et al.* (2017a) (Table 5A.2). One exception to the default parameters was the minimum percentage of the adult body weight required for conception. If calving is seasonal, like in the Charolais area, the default value for conception (60% of the adult body weight) results in the first calving at an age of three years. This age correspond to the actual age at first calving in the Charolais area. Nevertheless, the age at first calving can be two years with good cattle management in practice. Decreasing the default value to 50% can result in calving at two years of age. We set, therefore, the minimum percentage of the adult body weight required for conception at 50% under ideal cattle management.

Daily weather data used as input for LiGAPS-Beef were obtained for Charolles (46.4 °N, 4.3 °E), a city in the Charolais area, for the years 1998-2012 (Agri4Cast, 2013). The variables in the weather data files are described in Van der Linden *et al.* (2017a). Cattle are kept in stables during the winter period in the Charolais area, and are grazing outdoors during the grazing season. The daily weather data for outdoor conditions are corrected for the indoor conditions if cattle are kept in stables (Van der Linden *et al.*, 2017a). The turnout date on pasture in the farm types varied from Julian day 84 (25th of March) to Julian day 95 (5th of April), and the duration of the grazing season varied from 239-250 days (Table 5A.3).

Feed quality and the available feed quantity were different for the three main production levels (P_LA_L, P_PA_L, and P_PA_P), and their variants (P_LA_L – MMI, P_LA_L – M, P_PA_L – Hay, and P_PA_L – Silage) specified in Chapter 5. Feed quality is determined by the feed types consumed by cattle, which include fresh grass, hay, grass silage, maize silage, and wheat. The composition of these feed types is fixed (Table 5A.4), except for the quality of fresh grass, which is variable (Eqs 5 and 6).

Table 5A.3 Turnout date on pasture and duration of the grazing season in the twelve selected farm types in the Charolais area. Source: Réseaux d'Élevage Charolais (2014).

Farm type[a]	Turnout on pasture (Julian day)	Duration grazing season (days)
11021	84	250
11031	91	243
11065	91	243
11105	91	243
11111	84	250
11131	84	250
11140	95	239
21010	95	239
21020	84	250
31020	84	250
31041	91	243
31060	84	250

[a] Numbers of farm types correspond to the numbers used in Réseaux d'Élevage Charolais (2014).

Table 5A.4 Content and characteristics of the feed types used as input for LiGAPS-Beef. Feed components are given in g kg^{-1} DM (dry matter). Digestion and passage rates are given as fraction DM per hour.

Feed type	Included in production level	HIF	SNSC	INSC	DNDF	UNDF	SCP	DCP	UCP	kdINSC	kdDNDF	kdDCP	kPass	FU[a]	Pef[b]
Hay (good quality)[c]	P_pA_p, P_pA_l-Hay	0.318	100	150	346	148.2	48.2	74.3	49.5	0.300	0.040	0.085	0.035	1.120	1.00
Hay (actual quality)[d,e]	P_pA_l, P_lA_l, P_pA_l-M, P_pA_l-MMI	0.420	73[f]	73[f]	462[f]	198.0	20.3	28.0[f]	21.7[f]	0.300	0.040	0.085	0.035	1.370	1.00
Grass silage[c]	P_pA_l-Silage	0.290	128	81	397	49.1	124	89	6.3	0.150	0.060	0.120	0.031	0.924	1.00
Maize silage[c]	P_pA_l, P_lA_l, P_pA_l-M, P_pA_l-MMI	0.290	100	351[g]	271	239.0	54.9	23.0	4.0	0.250	0.040	0.040	0.030	1.000	0.93
Wheat[c]	All levels, except P_pA_l-Hay and P_pA_l-Silage	0.234	475	212	80	34.2	39.9	69.8	23.3	0.182	0.150	0.080	0.040	0.475	0.70

[a] FU obtained from Jarrige (1989). FUs for barley, concentrates, maize, soybean meal, and wheat are calculated as -2.276 × digestible DM (g kg^{-1}) + 2.545.
[b] Data from Mertens (1997).
[c] Data from Chilibroste *et al.* (1997)
[d] Data from Kolver (2000).
[e] Digestion and passage fractions of these feed types are assumed to be equal to good quality hay.
[f] Data calculated from Chilibroste *et al.* (1997)
[g] Value is increased from the value given in Chilibroste *et al.* (1997), to achieve a ME content corresponding to measured ME contents for maize silage.
HIF = heat increment of feeding (MJ heat MJ^{-1} metabolisable energy); SNSC = Soluble, non-structural carbohydrates; INSC = Insoluble, non-structural carbohydrates; DNDF = digestible neutral detergent fibre; UNDF = undegradable neutral detergent fibre; SCP = soluble crude protein; DCP = digestible crude protein; UCP = undegradable crude protein; kdINSC = digestion rate insoluble, non-structural carbohydrates, kdDNDF = digestion rate digestible neutral detergent fibre; kdDCP = digestion rate digestible crude protein; kPass = passage rate; FU = fill unit, pef = physical effectiveness factor (for neutral detergent fibre). For abbreviations of the production levels, see Table 5.2.

Table 5A.5 Metabolisable energy (ME) content of feed types, as simulated with the feed intake and digestion sub-model of LiGAPS-Beef. Minimum ME content is realised at high rumen fill, and maximum ME content at low rumen fill.

Feed type	Max. ME content ($MJ\ kg^{-1}\ DM$)	Min. ME content ($MJ\ kg^{-1}\ DM$)	Average ME content ($MJ\ kg^{-1}\ DM$)
Hay (good quality)	9.85	9.31	9.58
Hay (actual quality)	8.12	7.39	7.76
Grass silage	11.23	10.76	11.00
Maize silage	10.26	9.90	10.08
Wheat	12.86	12.81	12.84

Simulations with the feed intake and digestion sub-model indicated that wheat had the highest ME content of the feed types, and the hay fed in practice had the lowest ME content (Table 5A.5).

The actual diets were used as input to simulate the main production levels P_LA_L and P_PA_L. The percentage of cereals (wheat and maize grains) in the diet was assumed to be constant over the year, and for all animals in the herd, since more detailed data on the supplementation of cereals were not available. Cattle were assumed to have *ad libitum* access to hay when kept indoors during winter. Fresh grass was the main component of the diet in the grazing season, but hay was assumed to be supplemented if the aboveground biomass of the pasture was lower than 1,000 kg DM ha^{-1} $year^{-1}$. Cattle management was ideal for the main production levels P_LA_L and P_PA_L, and aimed to maximize LW production per hectare. With ideal cattle management, the optimum culling rate for cows was 50% per age cohort per year after the birth of the first calf. The total number of calves per cow is approximately two at this culling rate ($1 + 0.5^1 + 0.5^2 + 0.5^3 + \ldots + 0.5^8 \approx 2$). On average, one of these calves is a male calf, and the other is a female calf used as a replacement for the cow (Van der Linden *et al.*, 2015). The optimum slaughter weights of bulls (incremental steps of 50 kg LW) was 750 kg LW. The optimum calving date (incremental steps of 5 days) was Julian day 60 (1^{st} of March). The optimum stocking density for the farm types (incremental steps of 0.1 herd unit ha^{-1} pasture) varied between 2.3 – 3.3 herd units ha^{-1} pasture with P_LA_L, and between 3.9 – 6.4 herd units ha^{-1} pasture with P_PA_L. Given the ideal cattle management, calf mortality was zero, and the minimum calving interval was one year (Table 5A.6).

The *ad libitum* diet for the main production level P_PA_P consisted of 65% wheat and 35% high-quality hay to sustain potential growth of cattle (Van der Linden *et al.*, 2015). The optimum culling rate for cows was 50% per cohort per year after the birth of the first calf, and the optimum slaughter weight for bulls was 800 kg LW. The peak in calving date (set at Julian day 60) did not affect the LW production per hectare, because wheat and hay were available *ad libitum* throughout the year. Wheat and

Table 5A.6 Model settings to simulate the farm types with Charolais cattle for the production levels P_LA_L and P_PA_L. Data on the diet composition calculated and estimated from Réseaux d'Élevage Charolais (2014). Culling rates, selling and slaughter weights, peaks in calving, and stocking densities are optimized to maximize LW production per hectare.

Farm type[a]	Diet composition				Cattle management						Calf mortality (% calves born)	Calving interval (year)
	Fresh grass (%)	Hay (%)	Wheat (%)	Maize[b] (%)	Culling rate (% cows per cohort per year)	Selling or slaughter weights male calves (kg LW)	Selling or slaughter weights female calves (kg LW)[c]	Peak in calving (Julian day)	Stocking density P_LA_L (herd units ha^{-1} pasture)[d]	Stocking density P_PA_L (herd units ha^{-1} pasture)[c]		
11021	58.6	32.9	8.5	-	50	750	-	60	2.3	4.2	0	1.0
11031	62.1	28.7	9.2	-	50	750	-	60	2.4	4.2	0	1.0
11065	61.3	27.5	11.1	-	50	750	-	60	2.5	4.1	0	1.0
11105	63.8	30.1	6.1	-	50	750	-	60	2.4	4.1	0	1.0
11111	65.6	29.7	4.8	-	50	750	-	60	2.4	3.9	0	1.0
11131	49.8	28.7	12.9	8.7	50	750	-	60	3.1	5.9	0	1.0
11140	44.5	31.0	14.1	10.4	50	750	-	60	3.3	6.4	0	1.0
21010	57.1	34.4	8.5	-	50	750	-	60	2.5	4.2	0	1.0
21020	62.6	28.7	8.7	-	50	750	-	60	2.5	4.2	0	1.0
31020	53.9	34.6	11.4	-	50	750	-	60	2.6	4.8	0	1.0
31041	46.2	36.8	17.0	-	50	750	-	60	2.8	5.3	0	1.0
31060	48.7	29.1	13.8	8.3	50	750	-	60	3.1	5.9	0	1.0

[a] Numbers of farm types correspond to the numbers used in Réseaux d'Élevage Charolais (2014).
[b] Maize grains are assumed to be 50% of the maize dry matter.
[c] Female calves are not fattened, since all female calves have to replace cows at a culling rate of 50% per cohort per year.
[d] A herd unit consists of one cow and one male calf (Van der Linden *et al.*, 2015).
LW = live weight

Table 5A.7 Model settings to simulate the farm types with Charolais cattle for the production levels P_LA_L – MMI and P_LA_L – M. All data are actual farm characteristics calculated and estimated from Réseaux d'Élevage Charolais (2014). Calf mortality and calving interval are applicable to P_LA_L – MMI only.

Farm type[a]	Diet composition				Cattle management							Calf mortality (% calves born)	Calving interval (year)
	Fresh grass (%)	Hay (%)	Wheat (%)	Maize[b] (%)	Culling rate (% cows per cohort per year)	Selling or slaughter weights male calves (kg LW)	Selling or slaughter weights female calves (kg LW)	Peak in calving (Julian day)	Stocking density (livestock units ha^{-1} pasture)[c]	Stocking density P_LA_L – MMI (herd units ha^{-1} pasture)[d]	Stocking density P_LA_L – M (herd units ha^{-1} pasture)[d]		
11021	58.6	32.9	8.5	-	26	352	300	31	1.27	1.60	1.44	7	1.08
11031	62.1	28.7	9.2	-	24	420	423	40	1.21	1.45	1.27	8	1.10
11065	61.3	27.5	11.1	-	23	400	372	38	1.31	1.65	1.45	8	1.15
11105	63.8	30.1	6.1	-	22	470	390	67	1.36	1.80	1.50	10	1.15
11111	65.6	29.7	4.8	-	22	460	435	86	1.25	1.70	1.30	10	1.16
11131	49.8	28.7	12.9	8.7	25	699[e]	713[e]	10	1.53	1.49	1.31	8	1.08
11140	44.5	31.0	14.1	10.4	27	715[e]	678[e]	15	1.78	2.26	1.69	9	1.09
21010	57.1	34.4	8.5	-	24	330	300	15	1.36	1.81	1.65	8	1.09
21020	62.6	28.7	8.7	-	23	420	420	75	1.22	1.47	1.35	8	1.09
31020	53.9	34.6	11.4	-	25	395	350	25	1.45	1.93	1.71	8	1.09
31041	46.2	36.8	17.0	-	25	699[e]	718[e]	15	1.32	1.33	1.20	9	1.09
31060	48.7	29.1	13.8	8.3	30	707[e]	704[e]	1	1.81	2.50	1.64	8	1.21

[a] Numbers of farm types correspond to the numbers used in Réseaux d'Élevage Charolais (2014).
[b] Maize grains are assumed to be 50% of the maize dry matter.
[c] Livestock units are calculated based on Eurostat (2013).
[d] Herd units are calculated from the actual number of cattle per hectare of pasture.
[e] Calves are fattened on-farm. Live weight (LW) is calculated as 0.615/ carcass weight for male calves, and 0.575/carcass weight for female calves (Réseaux d'Élevage Charolais, 2014).

hay were harvested mechanically, so a stocking density was not applicable for the production level P_PA_P. For the production level P_PA_P, the genotype, climate, feed quality, and feed quantity were the same for all farm types. Hence, the live weight production was the same for all farm types for the production level P_PA_P. Logically, calf mortality was zero and the minimum calving interval was one year for the production level P_PA_P.

The diet, cattle management, calf mortality, and calving intervals corresponded to the actual conditions in the Charolais area for the production level P_LA_L – MMI (Table 5A.7). The diet and cattle management corresponded to the actual conditions in the Charolais area for the production level P_LA_L – M, but calf mortality was zero, and the minimum calving interval was one year. The stocking density, expressed in herd units (Van der Linden *et al.*, 2015), was calculated for P_LA_L – MMI and P_LA_L – M from the average number of heads per hectare to represent the actual stocking densities.

For the production levels P_PA_L – Hay and P_PA_L – Silage, the optimum culling rate of cows was 50% per cohort per year after the birth of the first calf, and the optimum slaughter weight was 800 kg LW. The peak in calving date (set at Julian day 60) did not affect the LW production considerably for the production levels P_PA_L – Hay and P_PA_L – Silage, since diets were available *ad libitum*. Grass for hay or silage production was harvested mechanically, so a stocking density was not applicable. Calf mortality was zero and the minimum calving interval was one year for the production levels P_PA_L – Hay and P_PA_L – Silage.

2.2 Model inputs and settings for LINGRA and LINTUL-2

The default parameters of LINGRA and LINTUL-2 were used, unless specified differently in Section 1 of this Appendix. Daily weather data for LINGRA and LINTUL-2 were obtained for Charolles (46.4 °N, 4.3 °E), a city in the Charolais area, for the years 1998-2012 (Agri4Cast, 2013). For both models, the water holding capacity of the soil was set at 0.15 cm^3 cm^{-3} for the Charolais area, which corresponds to a silty clay loam soil and a silt soil (Piedallu *et al.*, 2011). Soils were assumed to be at field capacity at the 1st of January. Water-limited production of hay, grass silage, and wheat was simulated under rainfed conditions, without any irrigation. Potential and water-limited production of hay, grass silage, and wheat were simulated for fifteen years in a row (1998-2012).

Grass (for hay production) was harvested if the aboveground DM production exceeded 4.3 t DM ha^{-1}, and the aboveground biomass was cut back to a LAI of 0.8 m^2 m^{-2}. The DM losses due to harvesting, processing, and feeding were assumed to be 20% for hay (Van der Linden *et al.*, 2015) and 10% for grass silage (Köhler *et al.*, 2013).

3 Economic data

Economic data used in this research were based on Réseaux d'Élevage Charolais (2014) (Table 5A.8). This source indicated the main revenues and costs, the inputs used on farms, land use, yields of feed crops, herd dynamics, cattle management, live weight production, and labour requirements for the twelve farm types included in this research. These data allowed to calculate the revenues from beef production, the operational profit, and the operational profit with the bovine and grassland premium (Prime Herbagère Agro-Environnementale, PHAE) per hectare of feed crops, per livestock unit, and per kg LW. These data were used to construct a correlation matrix (Fig. 5.6 in Chapter 5).

Table 5A.8 Economic data for the twelve farm types, in k€ $year^{-1}$ (source: Réseaux d'Élevage Charolais (2014)).

Farm type[a]	Farm revenues[b]	Operational costs[c]	Fixed costs[d]	Gross farm surplus[e]	Revenues from beef production[f]	Operational costs for beef cattle	Operational costs for forage production	Bovine premium	PHAE premium	ICHN premium	Decoupled aid
Farm 11021	88.0	23.5	30.9	33.6	48.9	19.2	2.6	9.2	5.1	9.3	11.5
Farm 11031	143.5	33.6	55.0	54.9	87.1	28.3	2.3	13.8	7.6	3.4	23.0
Farm 11065	152.5	45.1	54.0	53.4	95.3	38.4	3.1	14.4	7.6	3.4	23.1
Farm 11105	139.7	35.0	52.5	52.2	93.7	32.7	2.3	13.7	7.6	3.4	21.3
Farm 11111	277.2	71.3	114.6	91.3	193.5	68.2	3.1	29.1	7.6	3.4	43.6
Farm 11131	216.2	71.3	75.8	69.1	151.6	56.3	10.0	15.5	-	3.4	33.7
Farm 11140	240.8	85.2	72.9	82.7	168.5	66.1	13.6	18.3	-	6.8	40.5
Farm 21010	129.5	38.4	52.6	38.5	63.3	22.1	4.0	11.5	-	3.4	20.7
Farm 21020	160.5	40.2	59.6	60.7	88.2	27.4	3.7	13.0	7.6	3.4	23.7
Farm 31020	202.5	69.0	83.8	49.7	61.3	22.4	6.3	10.3	-	5.3	36.6
Farm 31041	353.1	120.7	117.1	115.3	134.5	59.0	5.3	14.7	-	6.8	68.2
Farm 31060	407.7	118.8	127.3	161.6	210.1	77.3	9.3	21.7	-	6.8	68.8

[a] Numbers of farm types correspond to the numbers used in Réseaux d'Élevage Charolais (2014).
[b] Including premiums, operating aid, and revenues from the production of food crops.
[c] Includes operational costs for cattle, feed crops, and food crops.
[d] Fixed costs include fixed costs for the production of cattle, feed crops, and food crops. Fixed costs for cattle and feed crops are not indicated separately.
[e] Gross farm surplus is defined as the farm revenues, including premiums, minus the operational and fixed costs.
[f] Excludes the PHAE premium, the IHCN premium, the bovine premium, and operating aid.
PHAE = Prime Herbagère Agro-environnementale (grassland premium); ICHN = Indemnité Compensatoire des Handicaps Naturels (compensatory allowance for mountainous and less-favoured areas).

Appendix 7A

Mapping yield gaps of beef production systems

This Appendix describes the materials and methods used to estimate yield gaps of beef production systems in France, Ireland, and Uruguay. Besides, the Appendix contains additional results, and discusses the results in more detail than in the general discussion (Chapter 7).

Materials and methods

Production levels and yield gaps for beef production systems in the Charolais area of France were adopted from Chapter 5. The methods described in Chapter 5 were applied to five conventional beef farms in southern Ireland also (Casey and Holden, 2006). The cattle breed was not mentioned explicitly for farms in Ireland. Charolais cattle were selected subsequently, because the Charolais breed is the most common beef breed in Ireland (Table A1). Cattle grazed approximately 250 days per year, and were housed during the winter season (Casey and Holden, 2006). Pastures were assumed to consist of perennial ryegrass (*Lolium perenne* L.) only. Cattle were fed grass silage and some concentrates while being housed. Concentrates consisted of many constituents from many different countries (Casey and Holden, 2006). For simplicity, concentrates were assumed to consist of wheat only, and this wheat was assumed to be cultivated in southern Ireland also.

Data for an average, pasture-based farm in Uruguay were adopted from Becoña *et al.* (2014). Cattle grazed natural pasture year-round, and concentrate supplementation was negligible (Becoña *et al.*, 2014). The cattle breed was not mentioned explicitly for farms in Uruguay. Hereford cattle were selected subsequently, because the Hereford breed is the most common beef breed in Uruguay (Table A1). The diet under potential production was high-quality grass silage (metabolisable energy (ME) content = 11.1 MJ per kg DM (dry matter)) and the diet under resource-limited production corresponded to the average pasture quality (ME content = 8.6 MJ per kg DM) (Becoña *et al.*, 2014). Diets were assumed to be available *ad libitum* under potential and resource-limited production. Feed efficiency (kg live weight t^{-1} DM) was simulated with LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems), for diets consisting of grass silage and natural pasture. Weather data for Uruguay included the year 2001 only (Table A1). Potential and water-limited yields for natural pastures were assumed to

Table A1. Cattle breeds, weather data, and feeding strategies of beef production systems in France, Ireland, and Uruguay.

	France	Ireland	Uruguay
Cattle breed	Charolais	Charolais	Hereford
Region	Charolais area	Southern Ireland	Western Uruguay
Location weather data	Charolles	Cork	Paysandú
Latitude (°)[a]	46.4	52.2	-32.3
Longitude (°)[a]	4.3	-8.2	-58.0
Weather data used[b]	1998-2012	1998-2012	2001
Code climate zone GYGA[c]	4702	3901	6602
Housing	Winter season	Winter season	No housing
Pasture	Perennial ryegrass	Perennial ryegrass	Natural pasture
Winter feeding	Hay	Silage	Natural pasture
Actual production obtained for	Farm types	Individual farms	Average pasture-based farm
Reference farm description	Réseaux d'Élevage Charolais (2014)	Casey and Holden (2006)	Becoña *et al.* (2014)

GYGA = Global Yield Gap Atlas.
[a] Negative latitudes indicate the southern hemisphere, and negative longitudes indicate the west of the prime meridian.
[b] Simulations with LiGAPS-Beef started in each of the fifteen years in the period 1998-2012 for France, but simulations in Ireland started in 1998 only. Weather data for Uruguay were replicated to simulate animals living for multiple years.
[c] See www.yieldgap.org and Van Wart *et al.* (2013) for an explanation of the climate zones and their codes.

correspond with the yields of perennial ryegrass, and were simulated with the grass growth model LINGRA (Light INterception and utilisation - GRAss) (Schapendonk *et al.*, 1998). Under resource-limited production, the percentage of pasture intake was assumed to be 50% of the total pasture production (Beretta *et al.*, 2006). Finally, the feed efficiency was multiplied by the dry matter intake (t DM ha^{-1} $year^{-1}$) to assess live weight production per hectare per year under potential and resource-limited production.

Results and discussion

Potential production of feed crop-livestock systems was highest for Uruguay, and similar for France and Ireland (Fig. A1 A-C). Resource-limited production was highest in Ireland and lowest in France (Fig. A1 D-F), and actual production was highest in Ireland, and lowest in Uruguay (Fig. A1 G-I).

As indicated in Chapter 2, yield gaps of feed-crop livestock systems can be split up in their livestock component (feed efficiency) and feed crop component (dry matter intake or production). Yield gaps for feed crop production in France and Uruguay were larger than for the cattle production (feed efficiency), except for resource-limited production in France (Table A2). The yield gaps of the beef production systems in the Charolais area of France were discussed extensively in Chapter 5. Yield gaps in Ireland were assessed for feed-crop livestock systems only, but were not assessed for feed crop production or feed efficiency, as actual data were not available (Table A2). Although potential production in France and Ireland was similar (Fig. A1 A and

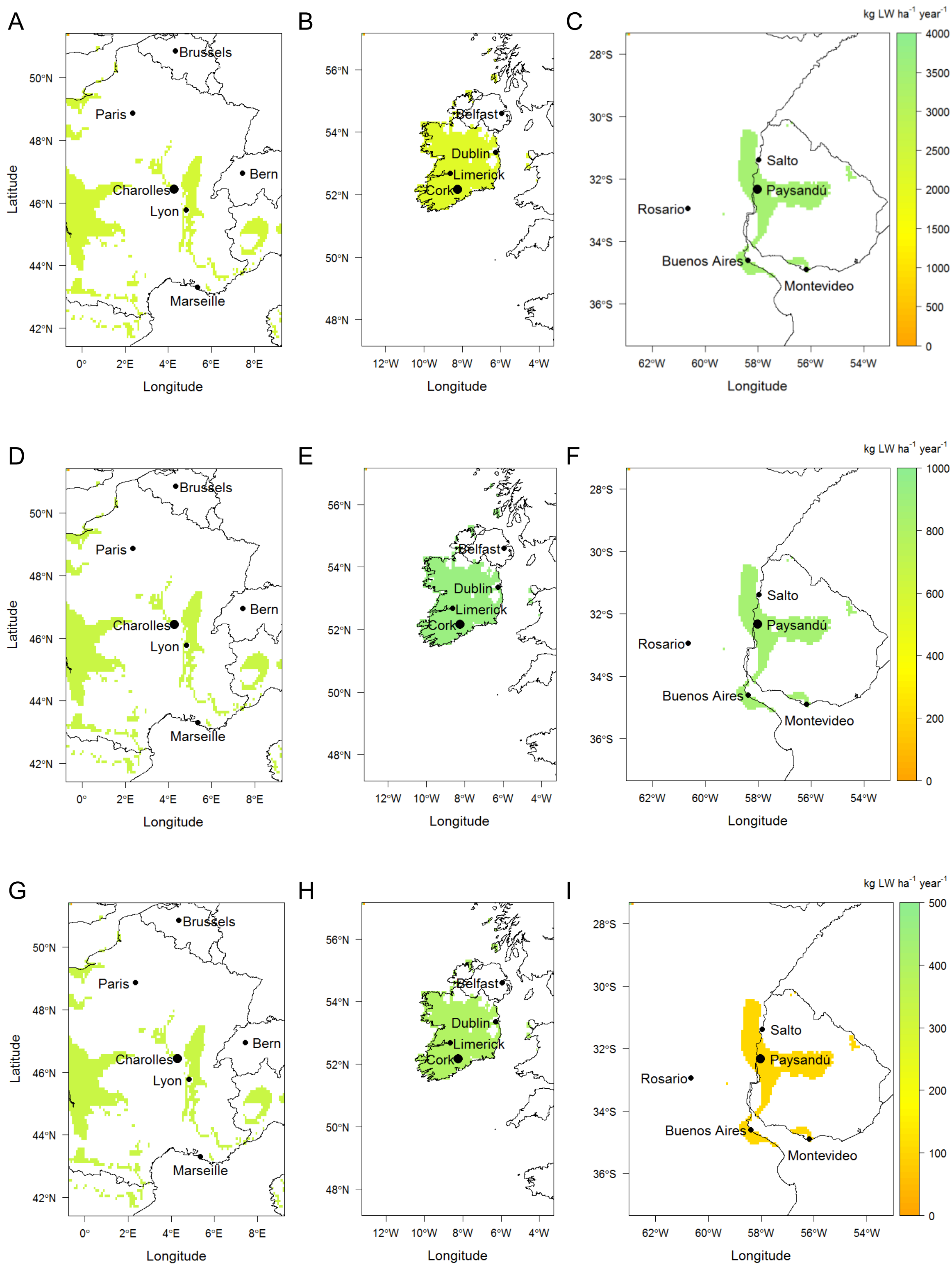


Figure A1. Potential (A-C), resource-limited (D-F), and actual production (G-I) of beef production systems in France, Ireland, and Uruguay. Production is expressed as live weight (LW) per hectare per year, including all land required to produce feed crops. Note scales are different for potential, resource-limited, and actual production.

B), resource-limited production was higher in Ireland than in France (Fig. A1 D and E). This is mainly explained by a higher feed efficiency in Ireland (120 kg LW t^{-1} DM) than in France (89 kg LW t^{-1} DM), and is hardly explained by differences in feed intake (7.6 vs 7.4 t^{-1} DM ha-1 $year^{-1}$ respectively). The higher feed efficiency in Ireland is explained by a higher average ME content of the diet. The grass silage fed in Ireland during the winter season had a higher ME content than the hay fed in France. In addition, the ME content of the pasture simulated with the combination of LiGAPS-Beef and LINGRA was higher in Ireland than in France, due to more favourable temperatures and higher rainfall.

The large yield gaps in feed crop production in Uruguay (latitude: 32°S) are caused by the high yield of grass silage under potential production (32.8 t DM ha^{-1} $year^{-1}$ grass; 29.5 t ha^{-1} $year^{-1}$ grass silage), and the high grass intake under water-limited production (11.7 t DM ha^{-1} $year^{-1}$), whereas actual intake is much lower (2.2 t DM $ha^{-1}$$year^{-1}$). In Australia (latitude 36°S), irrigated and well-fertilized phalaris (*Phalaris aquatica*) yielded 32 t DM ha^{-1} $year^{-1}$, tall fescue (*Festuca arundinacea*) yielded 29 t DM ha^{-1} $year^{-1}$, and perennial ryegrass yielded 23 t DM ha^{-1} $year^{-1}$ (Greenwood *et al.*, 2006). Hence, the DM production of pasture simulated for Uruguay is comparable to the results of this experiment in Australia, which is conducted at a similar latitude. The ME content of grass silage (11.1 MJ kg^{-1} DM) corresponded also to the ME contents of forages found in the experiment of Greenwood *et al.* (2006) also. Although a potential LW production of 3,520 kg LW ha^{-1} $year^{-1}$ (Figure A1 C) and a corresponding yield gap of 97% (Table 2) seem extraordinary, such numbers might be accurate from a bio-physical perspective.

Table A2. Relative yield gaps for feed crop-livestock systems in France, Ireland, and Uruguay, and for their feed crop and cattle components. Actual production (Y_A) was benchmarked against the potential (Y_P) and resource-limited (Y_L) production. Minimum and maximum percentages are indicated between brackets. Data for France are from Chapter 5. This table corresponds to Table 7.2 in the General Discussion of this thesis.

	France	Ireland	Uruguay[a]
Relative yield gap ($Y_P – Y_A$) / Y_P			
Feed crop-livestock system	85% (80-88%)	81% (77-83%)	97%
Feed crop production	71% (67-74%)	NA	93%
Feed efficiency cattle	49% (37-57%)	NA	60%
Relative yield gap ($Y_L – Y_A$) / Y_L			
Feed crop-livestock system	47% (39-55%)	56% (48-62%)	88%
Feed crop production	26% (16-32%)	NA	81%
Feed efficiency cattle	28% (18-37%)	NA	37%

NA = Not Available. Actual production of feed crops and the actual feed efficiency were not given in Casey and Holden (2006).
[a] Minimum and maximum values for relative yield gaps are not available, since the actual production is based on the average national production of pasture-based beef farms, and not on multiple farm types or farms.

Pasture biomass was assumed to be available *ad libitum* under resource-limited production. Cattle in Uruguay grazing natural pastures are known, however, to lose weight in winter, when feed availability is limited (Beretta, 2006). Hence, the resource-limited production may be overestimated, as feed quantity limitation was not taken into account.

The yield gaps presented in Table A2 suggest ample scope to increase live weight production per unit area. Farmers are not expected to close yield gaps fully, as this is not cost-effective, not feasible in practice, or prohibited by environmental legislation (Cassman *et al.*, 2003, Lobell *et al.*, 2009, Van Ittersum *et al.*, 2013). The exploitable yield gap in crop production is the difference between 75-85% of potential or water-limited production (Van Ittersum *et al.*, 2013). In Chapters 2, 5, and 6, production in crop *and* livestock systems was assumed to be maximally 80% of the benchmark production, so the actual production of feed crop-livestock systems is at most 64% (80% × 80% = 64%) of the benchmark production. Hence, the relative yield gap is at least 36% due to economic, social, and environmental factors. As the beef production systems investigated here are mainly rainfed, benchmarking against the resource-limited production seems most appropriate. Relative yield gaps of feed crop-livestock systems, benchmarked against the resource-limited production, were all higher than 36% (Table A2). This finding suggests scope to increase LW production, especially in Uruguay.

The Global Yield Gap Atlas (GYGA, www.yieldgap.org) presents yield gaps for many crops in many countries, at national level and sub-national level, for different climate zones and soil types. The results of the GYGA are generated using a bottom-up approach (Van Bussel *et al.*, 2015). The approach to map yield gaps in beef production systems presented here is bottom up, but does not meet the protocol of the GYGA fully. According to the GYGA protocol, model simulations are valid in a circular buffer zone with a radius of 100 km from a weather station. A buffer zone is clipped at country borders and at borders of the climate zone. In addition, the GYGA protocol prescribes that climate zones and buffer zones must contain minimum percentages of the national area used for a specific agricultural activity. Furthermore, the most prevalent soil types are used to estimate crop yield within a buffer zone (Van Bussel *et al.*, 2015). The results for livestock production presented here, however, did not account for such buffer zones and for the percentage of national area for feed production covered by a climate zone or a buffer zone, as well as different soil types. Hence, the results are still location-specific, but this explorative exercise can be developed further to quantify yield gaps at regional, national, and global level.

Concentrates in France and Ireland were assumed to consist of wheat only, which was produced in the close proximity of the cattle farm. Concentrates can consist, however, of crop products imported from different countries all across the world

(Casey and Holden, 2006). Simulating potential and water-limited crop production for each crop constituent of the diet is laborious. In addition, models for specific crops may not be available, or not calibrated for the local conditions where these crops are grown, or input data may be scarce (*e.g.* weather data). Assuming (some of) the diet constituents are produced locally may be more straightforward, especially if diets contain low fractions of imported foreign concentrates.

Appendix 7B

Quantification of food-feed competition

This Appendix describes the calculation of the land use ratio (LUR). The concept of the LUR was applied to two farm systems with Charolais cattle in the Charolais area of France, under resource-limited and actual production. The two systems correspond to farm types 11111 (a cow-calf system acquiring most of its income beef production) and 31041 (a cow-calf-fattener system acquiring most of its income from crop production). Both farming systems are described in Réseaux d'Élevage Charolais (2014). Actual beef production, concentrate consumption, and land use were obtained from Réseaux d'Élevage Charolais (2014). Data reflecting resource-limited production were obtained from Chapter 5. All concentrates were assumed to be represented by wheat.

Grasslands in the Charolais area are not suited for tillage, and cannot be used to cultivate arable crops (Veysset *et al.*, 2014a). Farmland suited for tillage is ploughed and used for arable production (Veysset *et al.*, 2014a). We assumed, therefore, that the arable land for wheat production fed as concentrates could be used for human food crops also, and that the grassland is not suited to be converted in arable land. The maximum human digestible protein (HDP) production from arable land in France was 839 kg ha^{-1} $year^{-1}$ under soybean production (Van Zanten *et al.*, 2016b). One kg of beef contains 164.4 g HDP (Van Zanten *et al.*, 2016b). Wheat production was assumed to be 5.0 t DM ha^{-1} $year^{-1}$ for farms specialised in beef production, and 5.6 t DM ha^{-1} $year^{-1}$ for farms specialised in crop production in the Charolais area (Veysset *et al.*, 2014a). Wheat production was 5.9 t DM ha^{-1} $year^{-1}$ for France as a whole (Van Zanten *et al.*, 2016b). We assumed, therefore, that the maximum HDP production from food crops on arable land was 16.1% lower for farm type 11111 and 5.3% lower for farm type 31041 compared to the average in France. The LUR was calculated subsequently according to Van Zanten *et al.* (2016b). The values for the LUR are presented in Table 7.3 of the general discussion (Chapter 7) of this thesis.

Summary

Global livestock production is expected to increase significantly towards 2050. As expansion of the land area used for feed production is not desired, the question is to what extent, and how actual livestock production can be increased on the existing agricultural land area. Concepts of production ecology provide a generic, bio-physical framework to assess the scope to increase crop and livestock production per unit agricultural land (*i.e.* yield gap). These concepts distinguish potential (*i.e.* maximum theoretical) production, limited production, and the actual farmers' production (Figure). Limited production is determined by water- and nutrient limitations in crops, and by drinking water and feed-limitation (*i.e.* feed quality and quantity limitation) in livestock. Yield gaps in crops are the difference between potential, or water-limited production and actual production, whereas yield gaps in livestock are the difference between potential, or feed-limited and actual production (Figure).

Similar to crop production, the bio-physical potential and feed-limited livestock production levels are fairly conservative over time, and provide a stable benchmark for actual livestock production under the different agro-ecological conditions across

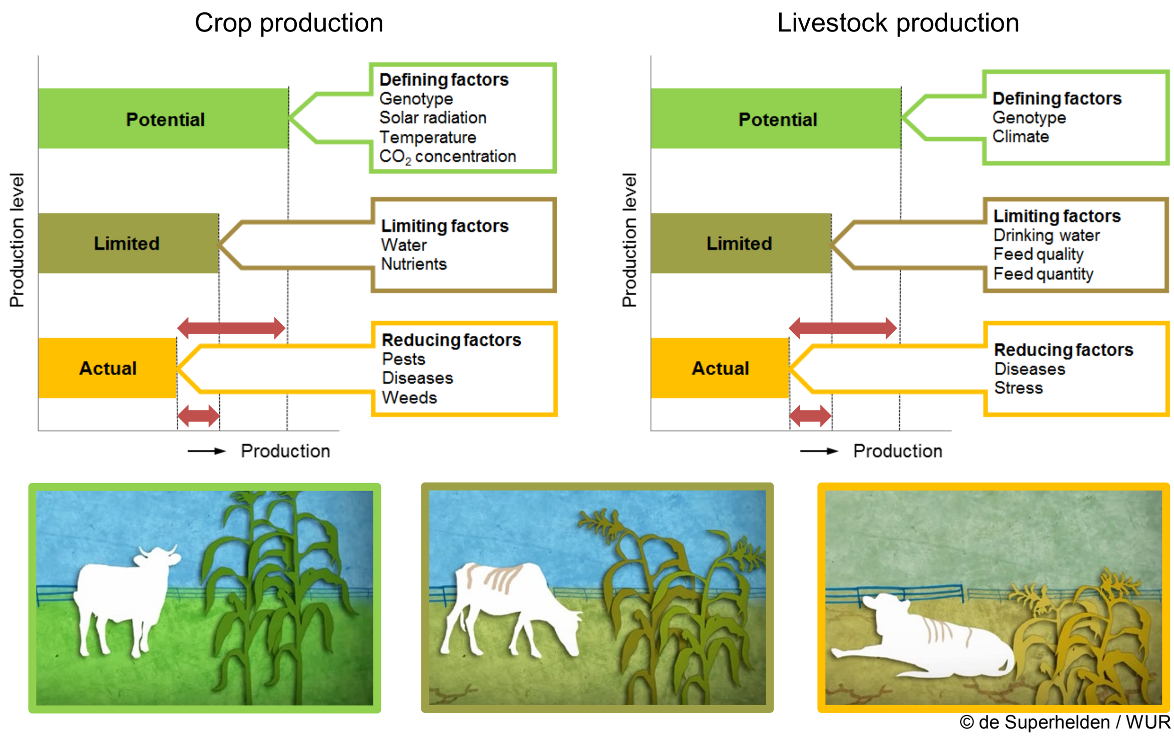


Figure Concepts of production ecology distinguish potential, limited, and actual production levels in crop and livestock production systems, with their corresponding growth defining, limiting, and reducing factors. Yield gaps are indicated by red arrows.

the globe. The fraction of the bio-physical potential that is actually produced per unit area depends on variable, in time, socio-economic, cultural, environmental, legislative, and ethical constraints. Future constraints are likely to differ markedly from the current ones, but predicting how these constraints will affect agricultural production in 2050 is impossible. Methods assessing the bio-physical potential, therefore, are suited to assess the scope to increase livestock production in future if constraints other than the bio-physical are absent.

Although generic methods are available to assess the bio-physical scope to increase production in cropping systems, such methods were not available for livestock systems at the start of this research. In addition, little insight is provided in the opportunities to reduce yield gaps in different livestock systems, with their corresponding feed crop production (referred to as feed-crop livestock systems).

The objectives of this thesis were 1) to develop a generic framework to assess the scope to increase production in feed crop-livestock systems, 2) to develop a generic livestock model simulating potential and feed-limited livestock production, and 3) to apply this framework and model to feed-crop livestock systems, and conduct yield gap analyses.

Concepts of production ecology provide a generic framework to assess potential crop production and crop production limited by water and nutrients. In **Chapter 2**, these concepts of production ecology are specified in more detail for livestock systems to assess potential and feed-limited production. In addition, the feed efficiency (*i.e.* kg animal-source food per t dry matter intake) of a herd or flock under potential and feed-limited conditions appears suitable to benchmark livestock production only, whereas the potential and limited production of animal-source food per unit agricultural area is required to benchmark the entire feed-crop livestock system. Concepts of production ecology were subsequently applied to beef production systems in the Charolais region of France. Potential production was broadly quantified with simple calculations. Yield gaps were 79% of the potential production per unit agricultural area for a cow-calf system, and 72% for a cow-calf-fattener system, indicating ample scope to increase the actual production, *i.e.* approximately by a factor 5 and 4 respectively. The simple calculations, however, did not account for the effect of climate, feed quality and available feed quantity, and revealed the need for a generic livestock model simulating potential and feed-limited production.

Chapter 3 describes the mechanistic, dynamic model LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle), which aims to simulate potential and feed-limited production of beef cattle under different agro-ecological conditions. Inputs for the model are parameters on the cattle genotype, daily weather data, and data about feed quality and the available feed quantity. The model consists of sub-models for thermoregulation, feed intake and digestion, and energy and protein utilisation. It simulates live weight and beef production from individual animals, and scales up to herd level. Next to cattle production, (interactions among) the most constraining bio-physical factors for growth are simulated. The applicability of the model was illustrated by simulating potential and feed-limited production for beef cattle in France and Australia. Model evaluation against independent experimental data indicated that the thermoregulation sub-model and the feed intake and digestion sub-model simulated heat release and feed digestion fairly well.

An evaluation of the entire LiGAPS-Beef model was conducted in **Chapter 4**. The model was calibrated, and subsequently evaluated with independent experimental data from beef production systems in Australia, Uruguay, and the Netherlands. Live weight gain in the three systems was estimated fairly well by LiGAPS-Beef (mean absolute error = 15.4% of measured live weight gain), indicating that the model can be used for the aim it was developed for. Sensitivity analysis revealed the most sensitive input parameters, such as energy requirements for maintenance, conversion of digestible energy to metabolisable energy, body area, and the efficiency of protein accretion in body tissues. Identification of the most sensitive parameters may allow more targeted measurements to improve the models' input data and accuracy.

In **Chapter 5**, LiGAPS-Beef was applied to twelve grass-based beef production systems in the Charolais region of France. LiGAPS-Beef was combined with the grass growth model LINGRA (Light INterception and utilisation – GRAss) to simulate the interaction between grazing cattle and the sward. Hay production was simulated with LINGRA, and wheat with a similar crop growth model. Resource-limited production was defined as the combination of water-limited production of feed crops and feed-limited production of cattle. Yield gaps were 85% (80-88%) of the potential production per unit agricultural area, and 47% (39-55%) of the resource-limited production, showing considerable scope to increase production. The part of the yield gap between potential and resource-limited production was explained by feed quality and quantity limitation (41% of potential production) and water-limitation in feed crops (31%). The part of the yield gap between resource-limited and actual production was explained by the combination of sub-optimal selling or slaughter weights, culling rates, calving dates, age at first calving, and stocking densities (9% of potential production), the combination of sub-optimal calving intervals and calf mortality (2%), and growth-reducing factors (3%). Due to socio-economic and environmental constraints, farmers are expected to realise at most 80% of the potential and water-limited production of feed crops, and at most 80% of the potential and feed-limited feed efficiency of livestock in practice. Hence, farmers are expected to realise at most 64% of the potential or resource-limited production (*i.e.* relative yield gap is at least 36%) in feed-crop livestock systems. Improving grassland management and an earlier start of the grazing season were proposed as improvement options to increase live weight production per hectare. Until 2015, intensification was not encouraged by subsidies provided to farmers who kept their stocking densities below threshold values. Since 2015, these thresholds have been abolished, which provides scope to increase stocking densities and the live weight production per hectare. Chapter 5 demonstrates that combined models for feed crop and livestock production based on concepts of production ecology can quantify potential and resource-limited production of feed-crop livestock systems, and their corresponding yield gaps. Furthermore, combining LiGAPS-Beef and crop growth models allowed to disentangle yield gaps of feed-crop livestock systems, and to identify improvement options for intensification, given the socio-economic constraints and conditions.

Chapter 6 assesses the effects of climate change on beef production from bulls in the Charolais region of France. Combining LiGAPS-Beef and LINGRA, the beef production per hectare of grassland was simulated under a reference climate (1999-2006), under the smallest projected climate change in 2050 (representative concentration pathway (RCP) 2.6), and under the largest projected climate change in 2050 (RCP 8.5). Under the reference climate, the yield gap for bull production was 41% of resource-limited production. The resource-limited beef production per hectare was 6% higher under the RCP 2.6 than under the reference climate, and 14% higher under RCP 8.5. The generic method and models based on concepts of production ecology can thus be used to simulate the effects of climate change on the theoretical, bio-physical production of beef per unit area.

The results of this thesis can be used to assess yield gaps of beef production systems at multiple levels. In addition, LiGAPS-Beef provides a template for the development of models for dairy cattle and other livestock species. Future efforts may focus on assessing yield gaps in feed-crop livestock systems with multi-purpose animals, and on quantifying the competition between food and feed production. Given the widespread consensus on the need for sustainable intensification, more sustainability indicators may be included in LiGAPS-Beef, such as water use and greenhouse gas emissions, and, indirectly, animal welfare.

From the results of this thesis, it can be concluded that:

1) A generic framework based on concepts of production ecology is available now to assess the bio-physical scope to increase production in feed-crop livestock systems per unit area under different agro-ecological conditions.

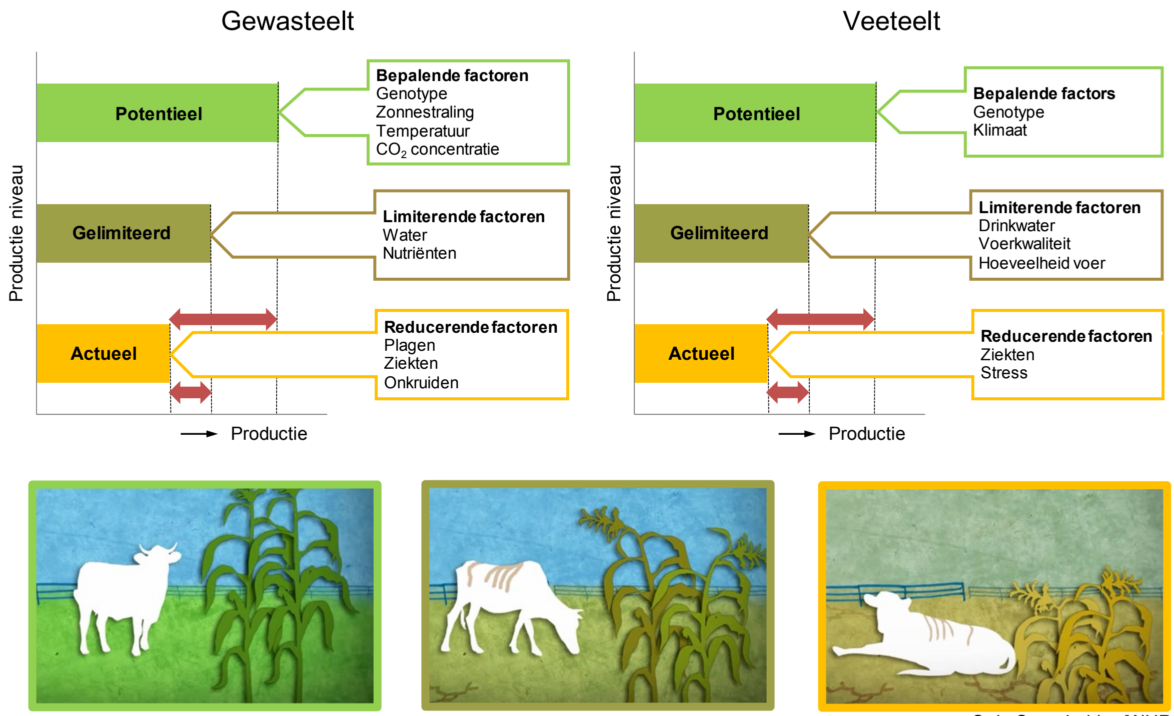
2) The mechanistic model LiGAPS-Beef simulates potential and feed-limited production of beef cattle fairly well for different beef production systems under different agro-ecological conditions, which makes the model a suited tool to benchmark the actual beef and live weight production against the potential and feed-limited production.

3) Combining LiGAPS-Beef with crop growth models allows to quantify yield gaps in feed-crop livestock systems. Beef production systems in the Charolais region of France have considerable scope to increase production per hectare, but socio-economic constraints did not favour yield gap mitigation.

4) The application of mechanistic crop and livestock models based on concepts of production ecology has proven to be successful for analysing yield gaps in feed-crop livestock systems with beef cattle in the Charolais region of France, and for identifying improvement options to mitigate these yield gaps. At global level, the application of this generic method can provide insight in options to reduce or halt the expansion of agricultural land used for feed crop production, and to decrease the competition between food and feed production on arable land.

Samenvatting

De wereldwijde productie in de veehouderij zal naar verwachting significant stijgen tot 2050. Omdat verdere uitbreiding van het areaal dat nodig is voor de productie van veevoer niet gewenst is, is de vraag in hoeverre, en op welke manier de actuele productie in de veehouderij kan toenemen op het bestaande areaal. Concepten van productie ecologie bieden een generiek en biofysisch raamwerk om in te schatten hoeveel de productie van gewassen en vee per eenheid landbouwgrond kan toenemen. Deze extra hoeveelheid wordt ook wel de ‘yield gap’ genoemd. Concepten van productie ecologie onderscheiden potentiële (maximale theoretische) productie, gelimiteerde productie, en de actuele productie die wordt gerealiseerd in de praktijk (Figuur). De gelimiteerde productie wordt bepaald door water- en nutriëntentekorten bij gewassen, en door drinkwater en beperkingen in voerkwaliteit en voerhoeveelheid bij vee. Yield gaps in gewassen zijn het verschil tussen de potentiële productie, of de watergelimiteerde productie, en de actuele productie, terwijl yield gaps in de veeteelt het verschil zijn tussen potentiële productie, of voergelimiteerde productie, en de actuele productie (Figuur).



Figuur Concepten van productie ecologie onderscheiden potentiële, gelimiteerde, en actuele productieniveaus voor de productie van gewassen en vee, met de daarbij horende bepalende, limiterende, en reducerende factoren voor groei. Yield gaps zijn aangeduid met de rode pijlen.

Net zoals in de gewasproductie zijn de potentiële en gelimiteerde productieniveaus in de veeteelt biofysisch van karakter, en vrij constant op de lange termijn. Daarom bieden deze productieniveaus een stabiel ijkpunt voor de actuele productie onder verschillende agro-ecologische omstandigheden in de wereld. Het gedeelte van het biofysische potentieel dat daadwerkelijk wordt geproduceerd per oppervlakte-eenheid is afhankelijk van sociaaleconomische, culturele, milieukundige, juridische, en ethische beperkingen. De huidige beperkingen zullen waarschijnlijk aanzienlijk verschillen van die in 2050, maar hoe deze beperkingen de productie zullen beïnvloeden valt niet te voorspellen. Methoden om het biofysisch potentieel te berekenen zijn daarom geschikt om in te schatten hoeveel de productie in de veeteelt verhoogd kan worden in de toekomst als er geen andere beperkingen dan de biofysische zouden zijn.

Hoewel er generieke methoden beschikbaar zijn om in te schatten hoeveel de gewasproductie kan worden verhoogd, waren zulke methoden nog niet beschikbaar voor de veeteelt bij de start van dit onderzoek. Zo werd er ook weinig inzicht geboden in de mogelijkheden tot het verkleinen van de yield gaps van verschillende veehouderijsystemen met de daarbij horende productie van voedergewassen (hier voedergewas-vee systemen genoemd).

De doelen van deze thesis waren om 1) een generiek raamwerk te ontwikkelen om in te schatten hoeveel de productie van voedergewas-vee systemen kan worden verhoogd, 2) een generiek model voor vee te ontwikkelen dat de potentiële en voergelimiteerde productie simuleert, en 3) dit raamwerk en model toe te passen op voedergewas-vee systemen, en de yield gaps daarvan te analyseren.

Concepten van productie ecologie bieden een generiek raamwerk om de potentiële gewasproductie en de door water en nutriënten gelimiteerde gewasproductie in te schatten. In **Hoofdstuk 2** worden de concepten van productie ecologie in meer detail uitgewerkt voor de veehouderijsystemen, om zo de potentiële en voer-gelimiteerde productie in te schatten. De voerefficiëntie (kg product van dierlijke afkomst per ton voeropname) van een kudde of toom onder potentiële en voer-gelimiteerde omstandigheden blijkt een geschikt ijkpunt voor de productie van vee alleen, terwijl de potentiële en gelimiteerde productie van dierlijk voedsel per eenheid landbouwgrond nodig is als ijkpunt voor het hele voedergewas-vee systeem. Concepten van productie ecologie werden vervolgens toegepast op boerderijsystemen die rundvlees produceren in de Charolais regio in Frankrijk. De potentiële productie werd gekwantificeerd met basale berekeningen. De yield gap was 79% van de potentiële productie per eenheid landbouwgrond voor een koe-kalf systeem, en 72% voor een koe-kalf-afmesterij systeem, wat aangeeft dat er een omvangrijke ruimte is om de actuele productie te verhogen, met respectievelijk een factor van circa 5 en 4. Het klimaat, de voerkwaliteit, en de beschikbare hoeveelheid voer waren echter niet meegenomen in de basale berekeningen. Hierdoor werd de urgentie om een generiek model voor vee op basis van de concepten van productie ecologie te ontwikkelen nog eens onderstreept.

Hoofdstuk 3 beschrijft het mechanistische en dynamische model LiGAPS-Beef (Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle, oftewel veesimulator voor de generieke analyse van dierlijke productie systemen – vleesrunderen), dat als doel heeft om de potentiële en voergelimiteerde productie van vleesrunderen te simuleren onder verschillende agro-ecologische omstandigheden. Input voor het model zijn parameters die het genotype van de runderen reflecteren, dagelijkse weergegevens en gegevens over de voerkwaliteit en de beschikbare hoeveelheid voer. Het model bestaat uit submodellen voor thermoregulatie, voeropname en vertering, en energie- en eiwitbenutting. Het simuleert het levend gewicht en de vleesproductie van individuele dieren en schaalt op naar het niveau van een kudde. Naast de productie van de runderen, worden ook de (interacties tussen de) meest beperkende biofysische factoren voor de groei gesimuleerd. De toepasbaarheid van het model werd geïllustreerd door het simuleren van de potentiële en de voergelimiteerde productie van vleesrunderen in Frankrijk en Australië. Evaluatie van het model met onafhankelijke experimentele gegevens gaf aan dat het submodel voor thermoregulatie en het submodel voor voeropname en vertering respectievelijk het afgeven van warmte en de vertering van voer redelijk goed simuleerden.

Een evaluatie van het volledige model LiGAPS-Beef wordt beschreven in **Hoofdstuk 4**. Het model werd gekalibreerd en vervolgens geëvalueerd met onafhankelijke experimentele gegevens van rundveehouderijsystemen in Australië, Uruguay, en Nederland. De toename in levend gewicht in deze drie systemen werd redelijk goed ingeschat door LiGAPS-Beef. De gemiddelde absolute fout was 15.4% van de gemeten gewichtstoename, wat aangeeft dat het model gebruikt kan worden voor het doel waarvoor het ontwikkeld is. Een gevoeligheidsanalyse identificeerde de meest bepalende parameters voor modelresultaten, zoals de energiebehoefte voor lichaamsonderhoud, de omzetting van verteerbare energie in metaboliseerbare energie, de lichaamsoppervlakte, en de efficiëntie van eiwitaanzet in lichaamsweefsels. De identificatie van de meest bepalende parameters kan leiden tot nauwkeurige meting van de benodigde inputgegevens en tot verbetering van de precisie van het model.

In **Hoofdstuk 5** wordt LiGAPS-Beef toegepast op twaalf boerderijsystemen met vleesrunderen die voornamelijk worden gevoed met gras. Deze boerderijen bevinden zich in de Charolais regio in Frankrijk. LiGAPS-Beef werd gecombineerd met het grasgroeimodel LINGRA (Light INterception and utilisation – GRAss, oftewel licht onderschepping en benutting – gras) om de interactie tussen runderen en grasproductie te simuleren, inclusief hooi. De productie van tarwe werd met een gelijksoortig gewasgroeimodel gesimuleerd. De resource-gelimiteerde productie van het systeem werd gedefinieerd als de combinatie van watergelimiteerde productie van voedergewassen en de voergelimiteerde productie van de runderen. De yield gaps waren 85% (80-88%) van de potentiële productie per eenheid landbouwgrond en 47% (39-55%) van de resource-gelimiteerde productie. Dit laat zien dat er aanzienlijke mogelijkheden zijn om de productie te verhogen. Het gedeelte van de yield gaps tussen de potentiële en de resource-gelimiteerde productie werd verklaard door beperkingen in voerkwaliteit en voerhoeveelheid (41% van de potentiële productie) en door waterlimitatie in voedergewassen (31%). Het gedeelte van de yield gaps tussen de resource-gelimiteerde en de actuele productie werd verklaard door de combinatie van suboptimale verkoop- of slachtgewichten, vervangingspercentages, datum van afkalven, de leeftijd van koeien bij de eerste keer afkalven en de veebezetting van grasland (9% van de potentiële productie), evenals de combinatie van een suboptimale tussenkalftijd en kalversterfte (2%) en de reducerende factoren (3%). Sociaaleconomische beperkingen zorgen ervoor dat boeren in praktijk niet meer dan 80% van de potentiële of watergelimiteerde productie van voedergewassen realiseren en ook niet meer dan 80% van de potentiële of voer-gelimiteerde productie van het vee. De verwachting is daarom dat boeren maximaal 64% van de potentiële of voer-gelimiteerde productie realiseren in voedergewas-vee systemen (de relatieve yield gap is dus minimaal 36%). Verbetering van het graslandmanagement en een vroegere start van het weideseizoen werden voorgesteld als opties om de productie van het levend gewicht per hectare te verhogen in de Charolais regio. Tot 2015 werd intensivering niet gestimuleerd door het verstrekken van subsidies voor boeren die de veebezetting onder een drempelwaarde hielden. Vanaf 2015 zijn deze drempelwaardes afgeschaft, zodat er ruimte is om de veebezetting en de productie van levend gewicht per hectare te verhogen. Hoofdstuk 5 laat zien dat gecombineerde modellen voor de productie van voedergewassen en vee, op basis van concepten van productie ecologie, de potentiële en resource-gelimiteerd productie kunnen kwantificeren, en de daarbij horende yield gaps. De combinatie van LiGAPS-Beef en gewasgroeimodellen maakte het ook mogelijk om de yield gaps van voedergewas-vee systemen te ontrafelen en om opties voor intensivering te onderscheiden, gegeven de sociaaleconomische beperkingen en omstandigheden.

Hoofdstuk 6 voorspelt de effecten van klimaatverandering op de vleesproductie van stieren in de Charolais regio in Frankrijk. De vleesproductie per hectare grasland werd gesimuleerd met een referentieklimaat (1999-2006), met de minimaal verwachte klimaatverandering in 2050 (representative concentration pathway (RCP) scenario 2.6), en met de maximaal verwachte klimaatverandering (RCP scenario 8.5). De yield gap voor de stieren was 41% van de resource-gelimiteerde productie met het referentieklimaat. De resource-gelimiteerde productie was 6% hoger met RCP 2.6 dan met het referentieklimaat, en 14% hoger met RCP 8.5. De generieke methode en modellen die zijn gebaseerd op concepten van productie ecologie kunnen dus gebruikt worden om de effecten van klimaatverandering op de theoretische, biofysische productie van vlees per oppervlakte-eenheid te simuleren.

Op basis van de resultaten in deze thesis kan geconcludeerd worden:

1) Er is nu een generiek raamwerk beschikbaar op basis van concepten van productie ecologie om in te schatten hoeveel de productie van voedergewas-vee systemen per oppervlakte-eenheid kan toenemen onder verschillende agro-ecologische omstandigheden.

2) Het mechanistische model LiGAPS-Beef simuleert potentiële en voergelimiteerde productie van vleesrunderen redelijk goed onder verschillende agro-ecologische omstandigheden. Daarmee is het model een geschikt instrument is om de biofysische ijkpunten te bepalen waarmee de actuele productie vergeleken kan worden.

3) Het combineren van LiGAPS-Beef met gewasgroeimodellen maakt het mogelijk om yield gaps in voedergewas-vee systemen te kwantificeren. Boerderijen met vleesrunderen in de Charolais regio in Frankrijk kunnen hun productie per hectare aanzienlijk verhogen, maar sociaaleconomische factoren verhinderden de verkleining van yield gaps.

4) De toepassing van mechanistische gewas- en veemodellen, gebaseerd op concepten van productie ecologie, laat zien dat het mogelijk is om de yield gaps in voedergewas-vee systemen met vleesrunderen in de Charolais regio in Frankrijk te analyseren, en opties te identificeren om deze yield gaps te verkleinen. De toepassing van deze methode op wereldschaal kan opties aandragen om de uitbreiding van het landbouwareaal voor voedergewassen te stoppen of te verminderen, en om de competitie tussen voedselgewassen en voedergewassen op akkerland te verminderen.

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In October 2012, I started my PhD project with the working title ‘Benchmarking animal production in farming systems in diverse agri-ecological environments’. During this multidisciplinary project, I interacted with many people that directly or indirectly helped, supported, and inspired me. Their valuable contributions shaped this thesis, and made the four years of my PhD project an enjoyable and pleasant time.

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During my PhD project I covered a broad array of topics. Thanks are also to the colleagues within Wageningen University & Research that contributed to this thesis. I acknowledge Jan Dijkstra, Walter Gerrits, Henk van Lingen, and Wilbert Pellikaan for their helpful comments and suggestions on animal nutrition, Henry van den Brand for his advices on modelling thermoregulation in animals, Wopke van der Werf, Lia Hemerik, and Dirk van Apeldoorn for making me acquainted with the programme language R, and Michiel Wallis de Vries for sharing experimental data. Farahnaz Pashaei Kamali, thanks for the collaboration – it was a good opportunity for me to learn more about the economics of farming systems.

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During my PhD research I interacted with many fellow PhDs in the Animal Production Systems group, the Plant Production Systems group, and other groups of Wageningen University. Although I will not spell out all of your names here, your accompany was highly appreciated and valued. Thank you all for the chats in the coffee and lunch breaks. Iris Boumans en Cindy Klootwijk, dank dat jullie al jaren zulke fantastische kamergenoten zijn. Corné Rademaker, dank voor de filosofische discussies die mij hielpen om mijn biofysische onderzoek in een breder perspectief te plaatsen.

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Aart van der Linden

Wageningen, the Netherlands
11th of January, 2017

About the author

Aart van der Linden was born on the 31st of January 1989 in Bilthoven, the Netherlands. He started studying Plant Sciences at Wageningen University in 2007, specializing in plant production, ecology, and crop management. Aart wrote a BSc thesis at the Plant Production Systems group of Wageningen University, entitled ‘Input-output relations of *Miscanthus* cropping systems in Europe for liquid biofuel purposes’. During this thesis, he worked with the crop growth model LINTUL, and developed an interest in crop growth modelling.

Aart proceeded his studies with a MSc Plant Sciences at Wageningen University, specializing in crop science. He carried out a MSc thesis at the Centre for Crop Systems Analysis of Wageningen University, where he conducted a greenhouse experiment to investigate the effects of nitrogen on zinc uptake and transport in rice. This work led to the thesis ‘Nitrogen-zinc interactions in rice (*Oryza sativa* L.): can nitrogen increase zinc grain concentrations?’ In addition, Aart conducted a four-month internship at the Agriculture and Horticulture group of Massey University, New Zealand. He used the grass growth model LINGRA to simulate effects of drought stress in perennial ryegrass. Aart obtained his MSc degree in September 2012.

Aart started his PhD research at the Animal Production Systems group and the Plant Production Systems group of Wageningen University in October 2012. His PhD project was part of the IPOP project ‘Mapping for Sustainable Intensification’. Supervised by Simon Oosting, Gerrie van de Ven, Imke de Boer, and Martin van Ittersum, his aim was to extend concepts of production ecology to livestock production, and to assess the scope to increase feed and livestock production under different agro-ecological conditions. The results of this research, described in this thesis, were presented at international conferences, and were published or will be published in peer-reviewed journals. During his PhD project, Aart was one of the founders of the PhD discussion group ‘Sustainable Intensification of Agricultural Systems’, and he was a member of the WIAS Science Day committee in 2015.

Since the completion of the PhD thesis in December 2016, Aart works as a postdoctoral researcher in the Animal Production Systems group and Plant Production Systems group of Wageningen University.

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Publications

Publications in double refereed journals

Van der Linden A, Oosting SJ, van de Ven GWJ, de Boer IJM, van Ittersum MK, 2015. A framework for quantitative analysis of livestock systems using theoretical concepts of production ecology. Agricultural Systems 139, 100-109.

Pashaei Kamali F, van der Linden A, Meuwissen MPM, Cunha Malafaia G, Oude Lansink AGJM, de Boer IJM, 2016. Environmental and economic performance of beef farming systems with different feeding strategies in southern Brazil. Agricultural Systems 146, 70-79.

Van der Linden A, van de Ven GWJ, Oosting SJ, van Ittersum MK, de Boer IJM. LiGAPS-Beef, a mechanistic model to explore potential and feed-limited beef production 1. Model description and illustration. Under review.

Van der Linden A, van de Ven GWJ, Oosting SJ, van Ittersum MK, de Boer IJM. LiGAPS-Beef, a mechanistic model to explore potential and feed-limited beef production 2. Model evaluation. Under review.

Van der Linden A, Oosting SJ, van de Ven GWJ, Veysset P, de Boer IJM, van Ittersum MK. Yield gap analysis of feed crop-livestock systems: the case of grass-based beef production in France. Under review.

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Kerr GA, Chapman DF, Thom ER, Matthew C, van der Linden A, Baird DB, Johnston E, Corkran JR, 2012. Evaluating perennial ryegrass cultivars: improving accuracy. Proceedings of the New Zealand Grassland Association 74, 127-135.

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Van der Linden A, Oosting SJ, van de Ven GWJ, van Ittersum MK, de Boer IJM, 2014. A mechanistic model to explore potential beef production of cattle breeds in contrasting climates. Book of Abstracts of the 65th Annual Meeting of the European Association of Animal Production, Wageningen Academic Publishers, ISBN 9789086862481, p. 94.

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Van der Linden A, van de Ven GWJ, Oosting SJ, van Ittersum MK, de Boer IJM, 2016. Manual and programming code for LiGAPS-Beef, digital library Wageningen University & Research, http://dx.doi.org/10.18174/386763.

Education Certificate

With the educational activities below, the PhD candidate has complied with the educational requirements set by the graduate school Wageningen Institute of Animal Sciences (WIAS) of Wageningen University & Research, which comprises a minimum of 30 ECTS (European Credit Transfer and accumulation System). One ECTS equals a study load of 28 hours.

The Graduate School WAGENINGEN INSTITUTE of ANIMAL SCIENCES

The basic package — 3.0 ECTS

International conferences — 3.7 ECTS

- 1st International Conference on Global Food Security, Noordwijkerhout, the Netherlands, September 29 - October 2, 2013
- 65th Annual Meeting of the European Federation of Animal Science, Copenhagen, Denmark, August 25-29, 2014
- 5th International Symposium for Farming System Design, Montpellier, France, September 7-9, 2015
- LiveM 2016 Conference, Potsdam, Germany, June 14-16, 2016

Seminars and workshops — 2.2 ECTS

- WIAS Science Day, Wageningen, the Netherlands (2013-2016)
- International Dairy Nutrition Symposium 'Feed Efficiency in Dairy Cattle', Wageningen, the Netherlands, November 21, 2013
- 1st Wageningen PhD Symposium, Wageningen, the Netherlands, December 10, 2013

Presentations — 5.0 ECTS

- 1st International Conference on Global Food Security, 2013, poster
- 1st Wageningen PhD Symposium, 2013, oral presentation
- 65th Annual Meeting of the European Association of Animal Production, 2014, oral presentation
- 5th International Symposium for Farming System Design, 2015, oral presentation (keynote speaker)
- WIAS Science Day, 2016, oral presentation
- LiveM 2016 Conference, 2016, oral presentation

In-depth studies — 21.2 ECTS

- Bayesian statistics, Wageningen University, 2012

Ecological modelling in R (CSA 50306), Wageningen University, 2012

Animal nutrition and physiology (ANU 30806), Wageningen University, 2013

Tropical farming systems with livestock, Wageningen University, 2013

Spatio-temporal analysis and big data processing using free and open source software, University of Twente, 2014

Analysis and design of sustainable agricultural systems: concepts, methods and applications, Montpellier SupAgro, 2015

PhD discussion group 'Sustainable intensification of agricultural systems', Wageningen University, 2013-2016

Professional skills support courses	**1.8 ECTS**

Techniques for writing and presenting a scientific paper, Wageningen University

PhD competence assessment, Wageningen University

PhD workshop carousel, Wageningen University

Research skills training	**1.5 ECTS**

Review Research Master Cluster proposals (2x)

Review manuscripts Agricultural Systems (2x)

Supervision of practicals and excursions	**6.0 ECTS**

Systems Approach in Animal Sciences (APS 20806), 2013, 2014, 2015

Global and Sustainable Animal Production in the 21st Century (APS 21803), 2014

Introduction to Animal Sciences (YAS 10306), 2014

Introduction Quantitative Agroecology (CSA 10806), 2015, 2016

Supervision of BSc and MSc theses	**3.0 ECTS**
Organisation of seminars and courses, boards and committees	**3.5 ECTS**

Member WIAS Science Day committee, 2014-2015

Board member PhD discussion group 'Sustainable intensification of agricultural systems', 2013-2014

Co-organiser monthly lunch meetings of the Wageningen Centre for Agro-ecology and Systems Analysis (WaCASA), 2014-2016

Total completed training and supervision plan	**50.9 ECTS**

List of abbreviations

ABPSS	Alberta Beef Production Simulation System, a model simulating beef production systems (Pang *et al.*, 1999).
ADG	Average Daily Gain (kg live weight per animal per day)
AGBOM	Australian Government Bureau Of Meteorology
ARC	Agricultural Research Council, a former research organisation in the United Kingdom.
ASF	Animal-Source Food
B.	*Bos* (genus includes domestic and wild cattle species)
BEEF	Beef Energy and Economic evaluator for Farms, a whole-farm model of a beef enterprise (*e.g.* Loewer *et al.*, 1980).
BEM	Beef Efficiency Model, a model simulating a beef cattle herd (Naazie *et al.*, 1997).
BPHL	Bromley Park Hatcheries Limited, a broiler model (King, 2001).
B×S	¾ Brahman × ¼ Shorthorn cattle
CAP	Common Agricultural Policy, agricultural policy of the European Union.
CNCPS-C	Cornell Net Carbohydrate and Protein System – Cattle, model assesses feed requirements (Fox *et al.*, 2004).
CNCPS-S	Cornell Net Carbohydrate and Protein System – Sheep, model assesses feed requirements (Cannas *et al.*, 2004).
CP	Crude Protein
CSIRO	Commonwealth Scientific and Industrial Research Organisation, a governmental research organisation in Australia.
DAFOSYM	DAiry FOrage SYstem Model, a dairy farm model (Rotz *et al.*, 1999).
DCP	Degradable Crude Protein
DE	Digestible Energy
DM	Dry Matter
DNDF	Degradable Neutral Detergent Fibre
EBW	Empty Body Weight, excludes the weight of digesta in the digestive tract.
$EBW^{0.75}$	Empty Body $Weight^{0.75}$, corresponds to the metabolic body weight.
FAO	Food and Agriculture Organisation of the United Nations

FCR	Feed Conversion Ratio (kg dry matter feed per kg animal-source food, or kg dry matter feed per kg live weight). The feed conversion ratio is the reciprocal of the feed efficiency.
FE	Feed Efficiency (kg animal-source food per ton dry matter feed, or kg live weight per ton dry matter feed)
FM	Fresh Matter
FU	Fill Unit, as defined by Jarrige *et al.* (1986).
GDD	Growing Degree Days
GE	Gross Energy
GJ	Gigajoule
GYGA	Global Yield Gap (and water productivity) Atlas, http://www.yieldgap.org.
ha	hectare
HDP	Human Digestible Protein
HIF	Heat Increment of Feeding (megajoule heat per megajoule metabolisable energy)
IAT	Integrated Assessment Tool, a household model for smallholders with livestock (Lisson *et al.*, 2010).
ICHN	Indemnité Compensatoire des Handicaps Naturels / compensatory allowance for permanent natural handicaps. This allowance is destined for farmers in mountainous and less-favoured areas in France to preserve landscapes and promote sustainable farming.
INRA	Institut National de la Recherche Agronomique / national institute for agricultural research, research institute in France.
INSC	Insoluble, Non-Structural Carbohydrates
ISO	International Organisation for Standardization
LAI	Leaf Area Index (m^2 leaf per m^2 soil)
LCT	Lower Critical Temperature
LiGAPS-Beef	Livestock simulator for Generic analysis of Animal Production Systems – Beef cattle, a mechanistic, dynamic model simulating potential and feed-limited production of beef cattle (Chapter 3).
LiGAPS-Dairy	Livestock simulator for Generic analysis of Animal Production Systems – Dairy cattle, a hypothetical model simulating potential and feed-limited production of dairy cattle.
LINGRA	Light INterception and utilisation – GRAss, a mechanistic, dynamic model simulating potential and water-limited production

	of perennial ryegrass (*Lolium perenne* L.) (Schapendonk *et al.*, 1998).
LINTUL-2	Light INTerception and UtiLisation-2, a mechanistic, dynamic model simulating potential and water-limited production of spring wheat (*Triticum* sp.).
LIVSIM	LIVestock SIMulator, a mechanistic, dynamic model simulating milk and live weight production of dairy cattle in the highlands of East Africa (Rufino *et al.*, 2009).
LU	Livestock Unit
LUE	Light Use Efficiency (g dry matter per megajoule photosynthetic active radiation)
LUR	Land Use Ratio, a ratio to quantify the competition between food and feed production. Defined and described by Van Zanten *et al.* (2016b).
LW	Live Weight, corresponds to the total body weight.
LWG	Live Weight Gain (kg per animal per day)
MAE	Mean Absolute Error
MAFF	Ministry of Agriculture, Fisheries and Food, a (former) ministry in the United Kingdom.
ME	Metabolisable Energy
MJ	Megajoule
NA	Not Available, or Not Assessed
NE	Net Energy
NIWA	National Institute for Water and Atmospheric research, research institute in New Zealand.
NRC	National Research Council, a non-profit, non-governmental research organisation in the United States.
NS	Non-Significant
OECD	Organisation for Economic Co-operation and Development
PAR	Photosynthetic Active Radiation
pef	physical effectiveness factor (for neutral detergent fibre) (Mertens, 1997).
PE&RC	Production Ecology & Resource Conservation, a graduate school connected to the Plant Sciences Group of Wageningen University, the Netherlands.
PHAE	Prime Herbagère Agro-Environnementale / agri-environmental grassland payment

P_LA_L	Plants water-Limited, Animals feed-Limited. This production level is also referred to as the resource-limited production of a feed-crop livestock system.
P_LA_L – M	Plants water-Limited, Animals feed-Limited with actual cattle Management
P_LA_L – MMI	Plants water-Limited, Animals feed-Limited with actual cattle Management, calf Mortality, and calving Intervals
P_PA_L	Plants Potential, Animals feed-Limited. Feed crop production is potential, and cattle production is feed-limited.
P_PA_L – Hay	Plants Potential, Animals feed-Limited with an *ad libitum* diet of Hay
P_PA_L – Silage	Plants Potential, Animals feed-Limited with an *ad libitum* diet of grass Silage
P_PA_P	Plants Potential, Animals Potential. Cattle are fed an *ad libitum* diet of 65% wheat and 35% hay *ad libitum*. The yields of wheat and grass for hay making correspond to the potential yields.
RCP	Representative Concentration Pathway, a scenario for the concentration of greenhouse gases in the atmosphere.
RMSE	Root Mean Square Error
SCP	Soluble Crude Protein
SLA	Specific Leaf Area (m^2 leaf per g dry matter)
SNSC	Soluble, Non-Structural Carbohydrates
SRNS	Small Ruminant Nutrition System, model assesses feed requirements and is based on the Cornell Net Carbohydrate and Protein System (CNCPS) for sheep (Tedeschi *et al.* 2010).
t	tonne (1000 kg)
TBW	Total Body Weight, includes the weight of digesta in the digestive tract. Corresponds to live weight.
THI	Temperature Humidity Index
TLU	Tropical Livestock Unit, equivalent to an animal of 250 kg live weight (Van de Ven *et al.*, 2003).
TNZ	Thermo-Neutral Zone
UCP	Undegradable Crude Protein
UCT	Upper Critical Temperature
UN	United Nations
UNDF	Undegradable Neutral Detergent Fibre

WIAS	Wageningen Institute of Animal Sciences, a graduate school of the Animal Sciences Group of Wageningen University, the Netherlands.

Colophon

The research described in this thesis is part of the Wageningen UR strategic programme ‘Mapping for sustainable intensification’, 2012-2016, funded by the strategic funds of Wageningen UR, and the PE&RC and WIAS graduate schools of Wageningen University (http://www.wur.nl/en/About-Wageningen/Strategic-Plan/Strategic-plan-2011-2014/Mapping-for-Sustainable-Intensification.htm).

Updates and applications of LiGAPS-Beef will be published on the model portal of the Plant Production Systems group of Wageningen University, the Netherlands (http://models.pps.wur.nl/content/ligaps-beef).

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