Natural resources and
bioeconomy studies
41/2018

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Doctoral Dissertation

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Doctoral programme in Sustainable Use of Renewable Natural Resources
Doctoral School in Environmental, Food and Biological Sciences
University of Helsinki

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public examination in Room K110, C-building (Latokartanonkaari 5) of the University of Helsinki on September 28th 2018, at 12 o' clock.

Natural Resources Institute Finland, Helsinki 2018

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ISBN: 978-952-326-615-5 (Print)
ISBN: 978-952-326-616-2 (Online)
ISSN 2342-7647 (Print)
ISSN 2342-7639 (Online)
URN: http://urn.fi/URN:ISBN:978-952-326-616-2

Author: Katariina Manni
Publisher: Natural Resources Institute Finland (Luke), Helsinki 2018
Year of publication: 2018
Cover photo: HKScan Finland Oy
Printing house and: publishing sales: Juvenes Print, http://luke.juvenesprint.fi

Abstract

Katariina Manni

Beef production in Finland is mostly based on dairy breeds. To compensate for the lack of domestic beef, slaughterhouse pricing favours lean and heavy carcasses. Higher carcass weights increase the probability of increasing fatness. It is necessary to control fatness because consumers generally favour low-fat products. In addition, excessive fat accumulation decreases the efficiency of feed utilization. High-fat carcasses are undesirable for the meat industry because the value of fat is low compared with that of red meat. Consequently, slaughterhouses have implemented price penalties for fat carcasses. For these reasons, carcass fat score is an important production parameter that affects the profitability of farms and the entire beef chain. On the other hand, very low-fat carcasses may decrease the eating quality of the meat. Thus, the target is to produce heavy low-fat carcasses without impairing eating quality of the meat. There is need to establish beef production methods to satisfy demand for such carcasses. One way to reduce carcass fatness and improve feed conversion could be to utilize steadily or periodically restricted energy intake and the ability of animals to exhibit compensatory growth.

The main objective of this thesis was to elucidate the effects of different restricted energy intake strategies on performance of growing dairy bulls, especially growth rate, feed efficiency, carcass fatness and meat quality. Energy intake was restricted by restricting concentrate or total diet dry matter (DM) intake (DMI), either periodically or during the whole growing period. The target was to achieve steady, increased or decreased growth patterns with diets based on grass silage and barley grain.

The objectives of the first experiment were to determine the effects on animal performance and meat quality when energy intake and growth rate were manipulated by controlling energy intake through changing barley allowance and allocation and offering grass silage *ad libitum*. Barley allocation regimes were steady, increased and decreased at two concentrate intake levels, where barley as a proportion of DM was either 0.23 or 0.43. Higher energy intake increased live weight gain (LWG). Over the total growing period, periodic energy intake did not affect LWG. Effects on feed efficiency were not found. Higher energy intake did not affect carcass fatness, but periodic energy intake decreased it. Higher energy intake increased meat fat content and tenderness. Periodic energy intake reduced tenderness compared with steady energy feeding. The responses to different energy feeding strategies demonstrated that there were no major effects on performance of animals. Observed effects on meat quality were minor and one explanation may be low carcass and meat fat content in all treatments.

The objective of the second experiment was to determine the effects on animal performance when growth rate was manipulated by controlling energy intake through changing total diet DMI. The treatments consisted of four feed allocation regimes: steady, restricted, increased and decreased energy intake. Restricted energy feeding was conducted by restricting DMI by 20% of the intake in the steady feeding treatment. In the increased and decreased treatments, the DMI was restricted similarly but either during the early or late part of the growing period. Average barley proportion of DMI was 0.42 and when DMI was not restricted, silage was offered *ad libitum*. Restricted feeding strategies decreased LWG and increased the number of growing days required to reach the same carcass weight. Compensatory growth was recorded. There were no significant differences in average feed efficiency attributable to the treatments over the total experimental period. Restricted DMI decreased carcass fat score. The results indicated that silage intake *ad libitum* and when supplemented with concentrate resulted in the most effective beef production but it also increased carcass fat score.

The objective of the third experiment was to determine the effects on animal performance when growth rate was manipulated by controlling energy intake through changing concentrate proportion in total mixed ration. The treatments comprised four feed allocation regimes, which were steady, restricted, increased and decreased energy intake. Barley proportion of DM was 0.30 in the steady feeding treatment. When energy intake was restricted, barley was removed from the diet. When barley was supplemented in the diet during the early or late part of the growing period, its proportion on a DM basis was 0.60 and 0.58, respectively. There was a trend of increased LWG by increasing energy intake. When comparing increased and decreased energy intake, carcass fat score increased and decreased, respectively. Energy intake strategies had no effect on feed efficiency over the whole growing period. Although good quality grass silage as a sole feed could support moderate to high levels of performance of growing cattle, including barley in the diet further improved the performance of the animals.

The results of this thesis confirm that increasing energy intake is a feasible method for increasing growth rate and shortening the growing period of dairy bulls, but it also increases carcass fatness. The responses to periodic energy intake demonstrated the great ability of growing bulls to adapt to different kinds of feeding regime without major effects on performance. However, it may reduce carcass fatness. This provides flexibility in selecting feeding strategies based on feed availability and prices, resulting in potential benefits to the economy of beef production. However, when targeting effective rotation time of beef production, high energy feeding during the entire growing period is required. Different feeding regimes had no major effects on meat quality, but did highlight the challenge of improving beef quality through modifying the diet.

Keywords: beef production, dairy bull, restricted feeding, feed efficiency, compensatory growth, meat quality

Tiivistelmä

Katariina Manni

Tämän väitöskirjatyön tarkoituksena oli selvittää energiansaannin rajoituksen vaikutuksia maitorotuisten sonnien tuotantotuloksiin, erityisesti kasvuun, rehun hyväksikäyttöön, ruhon rasvoittumiseen ja lihan laatuun. Energiansaantia säädeltiin rajoittamalla väkirehun tai kokonaiskuiva-aineen syöntiä joko jaksoittain tai koko kasvatuskauden ajan. Tavoitteena oli tasainen, nopeutuva tai hidastuva kasvu nurmisäilörehuun ja ohraan perustuvilla ruokinnoilla.

Työn taustalla oli tarve löytää keinoja ruhojen rasvoittumisen ehkäisemiseksi. Lihan alituotannosta johtuvan teuraspainojen nousun myötä ruhojen rasvoittumisen todennäköisyys lisääntyy. Taustalla on kuluttajien halu käyttää vähärasvaista lihaa. Lisäksi rasvoittuminen heikentää rehun hyväksikäyttöä ja rasvan arvo teurastamoteollisuudelle on murto-osa punaisen lihan arvosta. Toisaalta rasvaisuuden vähentyminen saattaa heikentää lihan syöntilaatua. Tässä työssä etsittiin ruokintavaihtoehtoja, joilla voidaan tuottaa painavia mutta vähärasvaisia ruhoja heikentämättä lihan syöntilaatua.

Ensimmäisessä osakokeessa tutkittiin energiansaannin rajoituksen ja jaksotuksen vaikutusta lihanautojen tuotantotuloksiin ja lihan laatuun. Koeruokintojen väkirehun osuus oli 0,23 tai 0,43 kuiva-aineesta. Väkirehu annettiin tasaisesti koko kasvatuskauden ajan tai jaksottamalla se kasvatuskauden alku- tai loppujaksolle. Nurmisäilörehua oli koko ajan vapaasti saatavilla. Sonnien päiväkasvu nopeutui energiansaannin lisääntyessä, mutta energiansaannin jaksotus ei vaikuttanut koko kasvatuskauden keskimääräisiin kasvuihin. Energiansaanti tai sen jaksottaminen ei vaikuttanut rehun hyväksikäyttöön. Lisääntynyt energiansaanti ei vaikuttanut ruhojen rasvaisuuteen, mutta energiansaannin jaksotus vähensi rasvoittumista. Energiansaannin lisääntyminen lisäsi lihan rasvapitoisuutta ja mureutta, mutta energiansaannin jaksotus heikensi mureutta. Energiaruokintojen vaikutukset sonnien tuotantotuloksiin ja lihan laatuun olivat kaiken kaikkiaan melko vähäiset. Kaikki ruhot olivat melko vähärasvaisia, mikä saattaa osaltaan selittää ruokintojen vähäistä vaikutusta lihan laatuun.

Toisessa osakokeessa tutkittiin energiansaannin rajoituksen ja jaksotuksen vaikutusta lihanautojen tuotantotuloksiin rajoittamalla kokonaiskuiva-aineen syöntiä. Kokeessa oli neljä ruokintaa, joissa energiansaanti oli joko tasainen, rajoitettu, lisääntyvä tai vähentyvä. Ruokintaa rajoitettaessa sonnit saivat 80 % tasaisesti saaneiden sonnien kuiva-aineen syönnistä. Jaksotetusti energiaa saaneiden sonnien kuiva-aineen syöntiä rajoitettiin joko alku- tai loppukasvatuskaudella samoin kuin rajoitetulla ruokinnalla. Keskimääräinen ohran osuus oli 0,42 kuiva-aineesta. Kun energiansaantia ei rajoitettu, nurmisäilörehua annettiin vapaasti. Energiansaannin rajoitus hidasti sonnien päiväkasvua ja pidensi kasvatusaikaa. Kun energiansaantia lisättiin alkujakson rajoituksen jälkeen, sonnit kasvoivat kompensatorisesti. Energiaruokintastrategioilla ei ollut vaikutusta keskimääräiseen rehun hyväksikäyttöön. Energiansaannin rajoitus koko kasvatuskauden ajan vähensi ruhojen rasvoittumista. Vapaa nurmisäilörehuruokinta täydennettynä väkirehulla oli tehokkain tapa saavuttaa teuraspaino, mutta se myös lisäsi ruhojen rasvaisuutta.

Kolmannessa osakokeessa tutkittiin energiansaannin rajoituksen ja jaksotuksen vaikutusta lihanautojen tuotantotuloksiin muuttamalla väkirehun osuutta seosrehuruokinnassa. Kokeessa oli neljä ruokintaa, joissa energiansaanti oli joko tasainen, rajoitettu, lisääntyvä tai vähentyvä. Tasaisesti energiaa saaneiden sonnien ruokinnassa ohran osuus oli 0,30 kuiva-aineesta koko kasvatuskauden ajan. Energiansaantia rajoitettiin antamalla sonneille pelkää nurmisäilörehua. Jaksotettaessa energian saantia ohraa annettiin vain alku- tai loppukasvatuskaudella, jolloin ohran osuus oli alkujaksolla 0.60 ja loppujaksolla 0,58 kuiva-aineesta. Suuntaus oli, että päiväkasvu nopeutui energiansaannin lisääntyessä. Verrattaessa jaksotettuja energiansaanteja toisiinsa, energiansaannin lisääminen kasvatuskauden lopussa lisäsi ja rajoittaminen vähensi ruhojen rasvoittumista. Energiaruokintastrategioilla ei ollut vaikutusta keskimääräiseen rehun hyväksikäyttöön. Vaikka hyvälaatuisella nurmisäilörehulla päästiin melko hyviin kasvutuloksiin, ohran lisääminen ruokintaan paransi sonnien tuotantotuloksia.

Energiansaannin lisääminen on yksi keino nopeuttaa maitorotuisten sonnien kasvua ja lyhentää kasvatusaikaa, mutta samalla ruhojen rasvoittuminen lisääntyy. Jaksotettu energiansaanti saattaa olla keino vähentää ruhojen rasvoittumista. Kaiken kaikkiaan tulokset osoittivat sonnien sopeutuvan erilaisille ruokinnoille ilman suuria vaikutuksia tuotantotuloksiin. Tämä tuo joustoa ruokintastrategioiden valintaan, mikä mahdollistaa rehujen saatavuuden ja hintojen huomioimisen osana ruokinnan suunnittelua. Tämä saattaa tuoda taloudellista hyötyä naudanlihantuotantoon. Toisaalta nopea eläinten kiertonopeus on taloudellisesti tärkeää ja se edellyttää runsasta energiansaantia koko kasvatuskauden ajan. Erilaiset ruokintastrategiat eivät vaikuttaneet merkittävästi lihan laatuun. Toisaalta tämä korostaa sitä, että käytäntöön soveltuvilla ruokinnoilla on rajalliset mahdollisuudet vaikuttaa lihan laatuun.

Avainsanat: naudanlihantuotanto, maitorotu, sonni, rajoitettu ruokinta, rehun hyväksikäyttö, kompensatorinen kasvu, lihan laatu

Acknowledgements

I would like to express my sincere gratitude to my supervisors, Research Professor Marketta Rinne and Research Professor Arto Huuskonen at the Natural Resources Institute Finland (Luke) for their guidance and support during this work. They helped and supported me whenever needed, irrespective of day of the week or time of day. My collaboration with Marketta started already many, many years ago when she supported me with my MSc thesis. I am grateful for this collaboration and also the friendship that has lasted all these years. Arto´s contributions and valuable comments on this doctoral thesis were substantial. Collaboration with Marketta and Arto has been pleasant and their scientific expertise has been precious. They have been the best possible supervisors I could have ever had.

I wish to thank Professor Aila Vanhatalo at the Department of Agricultural Sciences, University of Helsinki, for guidance and support during this work and for valuable comments on the thesis manuscript.

I appreciate the collaboration with co-authors Professor Pekka Huhtanen at the Swedish Agricultural University and Senior Specialist Erkki Joki-Tokola at Luke. I especially want to thank Pekka for his guidance and encouragement during all the years I have worked with my doctoral studies. I want to warmly thank Erkki for all the guidance and support in study II.

My special gratitude goes to the reviewers appointed by the Faculty, Professor Odd Magne Harstad and Principal Research Scientist, PhD Aidan Moloney, for their useful and constructive comments for improving the manuscript of this thesis.

I am grateful to Jonathan Robinson for the linguistic revision of this thesis.

I want to thank all persons who took care of the experimental animals and helped with the experimental arrangements. I also want to thank Taina Jalava and the laboratory staff at Luke, Jokioinen, for the laboratory analyses and considerable advice.

The financial support from the Foundation of Henrik and Ellen Tornberg is gratefully acknowledged. This financial support enabled me to complete this thesis.

I want to thank Degree Programme Manager Jukka Korhonen at Häme University of Applied Sciences for allowing me study leave to finish this thesis.

I want warmly to thank my parents Sirkka-Liisa and Veli-Matti Manni for encouragement and support during all these years when I have worked with my doctoral studies. I appreciate that you have always believed in me.

Finally, my deepest gratitude I want to express to my beloved Jukka Salonen for all unselfish support and help you have given to me. Thank you for your patience, flexibility and understanding during those long days and evenings, weekends and holidays, when I worked with this thesis. Without your support this PhD project might have never been finished. My heartfelt thanks to you.

List of original publications

This thesis is based on the following publications:

I Manni, K., Rinne, M. & Huhtanen, P. 2013. Comparison of concentrate feeding strategies for growing dairy bulls. Livestock Science 152: 21–30.

II Manni, K., Rinne, M., Joki-Tokola, E. & Huuskonen, A. 2017. Effects of different restricted feeding strategies on performance of growing and finishing dairy bulls offered grass silage and barley based diets. Agricultural and Food Science 26: 91–101.

III Manni, K., Rinne, M. & Huuskonen, A. 2016. Effects of barley intake and allocation regime on performance of growing dairy bulls offered highly digestible grass silage. Livestock Science 191: 72–79.

IV Manni, K., Rinne, M., Huuskonen, A. & Huhtanen, P. 2018. Effects of contrasting concentrate feeding strategies on meat quality of growing and finishing dairy bulls offered grass silage and barley based diets. Meat Science 143: 184–189.

The above-mentioned publications were reprinted with the kind permission of copyright owners Elsevier Science (I, III, IV) and Agricultural and Food Science (II).

The publications are referred to in the text by their Roman numerals.

All experiments were conducted at the Natural Resources Institute Finland (Luke; formerly MTT Agrifood Research Finland).

Contribution

The contributions of all authors to the original articles of this thesis are presented in the following table:

	I	II	III	IV
Planning the experiment	MR, PH	EJT, MR, PH	AH, KM, MR	MR, PH
Data analysis	KM, MR, PH	AH, KM, MR	AH, KM, MR	AH, KM, MR, PH
Calculating and interpreting the results	KM, MR, PH	AH, KM, MR	AH, KM, MR	AH, KM, MR, PH
Manuscript preparation	KM, MR, PH	AH, EJT, KM, MR	AH, KM, MR	AH, KM, MR, PH

AH = Arto Huuskonen, EJT = Erkki Joki-Tokola, KM = Katariina Manni, MR = Marketta Rinne, PH = Pekka Huhtanen

Abbreviations

General abbreviations:

AAT	amino acids absorbed from the small intestine
CP	crude protein
DM	dry matter
DMI	dry matter intake
DOM	digestible organic matter
D value	digestible organic matter in dry matter
FCR	feed conversion rate
iNDF	indigestible neutral detergent fibre
LL	longissimus lumborum
LW	live weight
LWG	live weight gain
ME	metabolizable energy
MEI	metabolizable energy intake
NDF	neutral detergent fibre
PBV	protein balance in the rumen
SEM	standard error of the mean
SR	substitution rate
TMR	total mixed ration
VFA	volatile fatty acids
WSC	water soluble carbohydrates

Abbreviations of the treatments in publications I-IV:

I, IV:

L	low energy feeding, barley proportion of dry matter 0.23, grass silage *ad libitum*
H	high energy feeding, barley proportion of dry matter 0.43, grass silage *ad libitum*
LSR	low energy feeding, steady barley ration
LIR	low energy feeding, increased barley ration
LDR	low energy feeding, decreased barley ration
HSR	high energy feeding, steady barley ration
HIR	high energy feeding, increased barley ration
HDR	high energy feeding, decreased barley ration

II:

A	steady energy feeding, barley proportion of dry matter 0.41, grass silage *ad libitum*
R	restricted steady energy feeding, dry matter intake 0.80 of dry matter intake in A
I	increased energy feeding, first R and then A
D	decreased energy feeding, first A and then R

III:

GS	restricted steady energy feeding, grass silage alone *ad libitum*
SC	steady energy feeding, barley proportion of dry matter 0.30
IC	increased energy feeding, first grass silage alone *ad libitum* and then barley proportion of dry matter 0.58
DC	decreased energy feeding, first barley proportion of dry matter 0.60 and then grass silage alone *ad libitum*

Contents

1. Introduction

1.1. Background

1.1.1. Rationale to establish alternative feeding strategies in beef production

Improving economic profitability represents a principal challenge in beef production and it is important that innovative production methods are assessed in order to improve profitability. In general, feed costs are a major component of total variable costs in most beef production systems (Patjas 2004) and reducing feed costs without diminishing animal performance would greatly improve profitability of beef production.

Beef production in Finland is mostly based on dairy breeds (Niemi & Ahlstedt, 2015). Most of the beef cattle are bulls, but heifers are also raised for beef production. Steers are not used. Because of the decrease in the size of the dairy cattle population and no change in beef consumption, there is an undersupply of domestic beef in relation to consumption and the gap is foreseen as growing in the future. To compensate for the reduction in numbers of slaughtered animals, slaughterhouse pricing systems favour heavy carcasses. Simultaneously, however, higher carcass weights increase the probability of increasing fatness according to data from Finnish slaughterhouses, reported by Herva et al. (2011) and Huuskonen et al. (2014c), and from elsewhere (Steen & Kilpatrick 2000, Kirkland et al. 2006, Nogalski et al. 2014).

Market demand in Finland concerning carcass fat differs from those beef markets where marbled beef is favoured and the target is to achieve a required fat score (Platter et al. 2005, Murphy et al. 2018). In Finnish beef production it is necessary to control the fatness of heavy carcasses because consumers generally favour low-fat products. In addition, high-fat carcasses represent additional expenditure for the meat industry (Herva et al. 2011). Consequently, carcass weight, fat score and conformation are included in the pricing system of Finnish slaughterhouses. Heavy and lean carcasses are favoured in price setting and there are penalties associated with fat carcasses. The Finnish beef industry has stated that optimally two thirds of carcasses should have a EUROP fat score of 2 and one third a score of 3 (Herva et al. 2011). Additionally, excessive fat accumulation decreases the efficiency of feed utilization (Murphy & Loerch 1994). For these reasons, carcass fat score is an important production parameter that affects the profitability of farming and the entire beef chain. On the other hand, very low-fat carcasses may decrease the eating quality of beef (Hocquette et al. 2010). The challenge is to produce heavy but low-fat carcasses without impairing eating quality of beef. The need is to establish methods to produce carcasses that meet demand criteria.

It is generally agreed that increased energy intake of growing cattle increases carcass fatness (Nogalski et al. 2014, Huuskonen & Huhtanen 2015). One way to reduce carcass fatness and/or improve feed conversion could be to utilize steady or periodically restricted energy intake and the ability of animals to exhibit compensatory growth (Hicks et al. 1990, Carstens et al. 1991, Murphy & Loerch 1994, Steen & Kilpatrick 2000).

1.1.2. Restricted energy intake strategies for manipulating growth rates of beef cattle

If the feed and nutrient intake is steady (in relation to metabolic live weight) during the whole growing period, growth rate accelerates until puberty and slows when approaching maturity, resulting in a typical sigmoid growth curve (McDonald et al. 1988). Mature size is generally assumed to be the point at which muscle mass reaches a maximum (Owens et al. 1993). If the growth rate is manipulated by altering the amount and/or quality of feeds offered during growing and finishing periods, the shape of the growth curve can be altered (Carstens 1995, Hornick et al. 2000).

If energy intake is first restricted and then realimented, animals may exhibit compensatory growth which enables them to reach the weight of animals whose growth was not restricted. However, full recovery is rarely observed (Hornick et al. 2000). Numerous mechanisms interact to produce accelerated growth rate after growth restriction. These mechanisms include reduction in energy density of tissue growth, reduced energy requirement for maintenance and increase in feed intake and gut fill (Carstens 1995, Hornick et al. 2000).

Many factors may affect compensatory growth. Consequently, the recorded effects on animal performance vary (Steen & Kilpatrick 2000, Cummins et al. 2007, Moloney et al. 2008a, b). Age during restriction, severity and duration of the growth restriction, rate of gain during recovery, length of recovery period and quality of feed during recovery are elements that influence animal performance during compensatory growth (Nicol & Kitessa 1995).

The implications of compensatory growth are important in beef production systems where seasonal variation in feed intake occurs. In such systems beef production may be based on restricted feed and/or nutrient intake during winter and then access to high quality pasture during the grazing season. Alternatively, calves are raised in semi-natural low quality pastures and finished intensively in feedlots. In intensive beef production systems, such as those in the Nordic countries, animals are typically confined and there is no clear division of pre-slaughter period into growing and finishing periods but only one continuous growing period with intensive feeding. Feeding is typically based on *ad libitum* grass silage intake supplemented with grain and/or by-products of the food industry. In this type of system, compensatory growth is currently not used and the possible benefits of it are unclear.

Restricting energy intake during the whole or final part of the growing period until slaughter may affect the performance of beef animals. If energy intake is restricted during the whole growing period, growth rate typically decreases (Hicks et al. 1990, Murphy & Loerch 1994). In the experiment of Murphy & Loerch (1994; exp. 1) carcass fatness decreased but in other experiments no differences in fatness were recorded (Hicks et al.

1990; exp. 1, 2, Steen & Kilpatrick 2000). Typically, increased energy intake increases carcass fatness (Huuskonen & Huhtanen 2015) and restricting energy intake during the late part of the growing period could represent a method for reducing carcass fatness (Steen & Kilpatrick 1995). However, this kind of energy supply pattern has been studied only to a limited extent. Restricted feed intake during the whole growing period could also potentially improve feed efficiency and thus reduce feeding costs, as was reported earlier (Hicks et al. 1990, Murphy & Loerch 1994, Schmidt et al. 2005).

1.1.3. Possibilities to affect meat quality by manipulating energy intake

Beef quality aspects are receiving greater attention among consumers (Verbeke et al. 2010). Eating quality consists of a combination of tenderness, flavour and juiciness, the most important characteristics by which consumers judge meat quality (Grunert et al. 2004). Although colour is weakly correlated with the eating characteristics of meat, in the purchase phase it is a crucial factor that affects visual evaluation and consumer choice (Priolo et al. 2001, Grunert et al. 2004, Killinger et al. 2004). Attention has also been paid to meat healthiness, especially to the amount and type of fat (Lusk & Parker 2009, Huuskonen et al. 2010, Pesonen et al. 2013).

Meat quality can be manipulated via alterations to diet and/or feeding strategy (Vestergaard et al. 2000, Sami et al. 2004, Moloney et al. 2008b). The challenge is that variation in breed, animal background, growth rate, duration of finishing period and age, weight and fatness at slaughter etc. (Matthews 2011) may obscure the effects among experiments. However, manipulating growth rate could be a strategy to improve meat tenderness. Numerous studies have suggested that there is a relationship between the high rate of muscle protein degradation at slaughter and increased tenderness of meat, as reviewed by Andersen et al. (2005). This appears to represent the link between feeding strategy and tenderness within specific muscles (Therkildsen et al. 2008).

It is generally assumed that intramuscular fat in particular improves sensory quality traits of beef, including tenderness, juiciness and flavour (Hocquette et al. 2010). In addition, a thin fat cover may expose carcasses to cold shortening during chilling, which decreases meat quality, especially tenderness (French et al. 2001).

When targeting low-fat carcasses, as in Finnish beef production, the challenge is that in the meanwhile it may reduce the eating quality of beef. In addition, there is a paucity of published information of the effects of different energy feeding strategies on meat quality of low-fat dairy bulls.

1.2. Objectives and hypotheses of the study

The objective of the work reported in this thesis was to determine if restricting the growth of dairy bulls by manipulating feed energy intake during the whole growing period, or periodically during the early or late phase, could benefit feed efficiency and carcass and meat quality. Manipulation of the growth was conducted by restricting either concentrate or dry matter (DM) intake (DMI). The target was to achieve steady, increased or decreased growth patterns with diets based on grass silage and barley grain. The specific research questions were:

- Does continuously or periodically restricted energy intake of growing dairy bulls affect
    - growth pattern
    - growth rate
    - feed efficiency
    - carcass quality
    - meat quality?
- Do the bulls exhibit compensatory growth after restricted and then increased energy intake in an intensive beef production system?

It was hypothesized that:

1. By restricting feed intake, feed conversion rate improves.
2. By restricting feed energy intake steadily during the whole growing period carcass fatness decreases but also meat quality, particularly tenderness, decreases.
3. Increasing and decreasing energy feeding strategies result in different growth patterns of dairy bulls, but their average growth rates do not differ over the whole experimental period.
4. By restricting feed energy intake during the early part of the growing period and realimenting thereafter, bulls exhibit compensatory growth.
5. As a result of compensatory growth, feed conversion rate of dairy bulls improves and carcass fatness decreases without negative effects on carcass conformation and meat quality.

2. Materials and methods

2.1. Animals, feeding management and experimental procedures

The study comprised three experiments (1, 2 and 3; Table 1) that were documented in four publications (I–IV). Publications I and IV were based on the same experiment. The experiments are presented in this thesis in the order in which they were performed, not in the order in which they were published as single papers. The experimental procedures used are described in detail in publications (I-IV) and only brief summaries are presented here.

Table 1. Summary of experiments reported in this thesis.

Exp.[1]	Pub.[2]	Number of bulls in the experiment	Number of bulls per treatment	Initial live weight (LW), kg	LW at modified feeding, kg	Final LW, kg	Length of the experimental period, d	Total barley intake, kg dry matter (DM)	Measurements	Feeding methods	Treatments Early part	 Late part	Abbreviation
1	I, IV	53									Barley proportion of total DMI		
			9	93	405	558	424	639	Daily DM intake (DMI), microbial N synthesis, growth rate, carcass weight and quality, meat quality	Separate feeding Grass silage *ad libitum* Barley 39 (L[3]) or 74 (H[4]) g DM/kg $LW^{0.60}$	0.23	0.23	LSR[5]
			9	95	360	554	440	681			0	0.44	LIR[6]
			9	93	403	539	438	662			0.44	0	LDR[7]
			8	94	395	558	404	1190			0.43	0.42	HSR[8]
			9	95	389	565	409	1121			0.23	0.58	HIR[9]
			9	95	409	552	402	1187			0.62	0.25	HDR[10]
2	II	32	8	124	436	578	377	1180	Daily DMI, growth rate, carcass weight and quality	Separate feeding Grass silage *ad libitum* and barley *93 g DM/kg* $LW^{0.60}$ or restricted DMI 80% of total DMI in A	Grass silage *ad libitum* , barley proportion 0.41	Grass silage *ad libitum* , barley proportion 0.42	A[11]
			8	123	430	559	494	1215			Restricted DMI, barley proportion 0.43	Restricted DMI, barley proportion 0.46	R[12]
			8	122	436	604	464	1220			Restricted DMI, barley proportion 0.43	Grass silage *ad libitum* , barley proportion 0.37	I[13]
			8	122	438	559	409	1166			Grass silage *ad libitum* , barley proportion 0.40	Restricted DMI, barley proportion 0.43	D[14]
3	III	33	8	233	444	642	366	0	Daily DMI, growth rate, carcass weight and quality	Grass silage alone or grass silage and barley in total mixed ration *ad libitum*	Grass silage only	Grass silage only	GS[15]
			7	222	474	659	366	926			Barley proportion 0.30	Barley proportion 0.30	SC[16]
			9	231	442	712	366	1151			Grass silage only	Barley proportion 0.58	IC[17]
			9	232	483	656	366	844			Barley proportion 0.60	Grass silage only	DC[18]

[1] Experiment; [2] Publication; [3] Low energy feeding; [4] High energy feeding; [5] Low and steady energy feeding; [6] Low and increased energy feeding; [7] Low and decreased energy feeding; [8] High and steady energy feeding; [9] High and increased energy feeding; [10] High and decreased energy feeding; [11] Steady energy feeding; [12] Restricted energy feeding; [13] Increased energy feeding; [14] Decreased energy feeding; [15] Restricted energy feeding; [16] Steady energy feeding; [17] Increased energy feeding; [18] Decreased energy feeding.

The objective was to study the effects of continuously and periodically restricted energy intake on performance (I, II, III) and meat quality (IV) of growing and finishing dairy bulls. The target was to achieve three different growth patterns: steady, increased and decreased. In addition, the effects were studied of two concentrate levels (I, IV), restricted DMI (II) and grass silage used as a sole feed (III).

Experiments started at different ages and live weights (LW) of the experimental animals. Experiments 1 and 2 comprised both growing and finishing periods. Calves were weaned when the experiments started. In experiment 3, age and LW at the beginning of the experiment were typical for farms specialized in finishing bulls from the age of approximately six-months to slaughter. Slaughter weight in experiment 3 was typical for current slaughter weight. Slaughter weights in experiments 1 and 2 enabled study of the effects of restricted energy intake at lower carcass weights. A rather long restricted energy intake period was chosen to establish possible differences between restricted and unrestricted treatments. By using a long restricted energy intake period, the differences between the treatments could be seen more clearly.

Experiments were conducted in the experimental barns of the Natural Resources Institute Finland (Luke) (formerly MTT Agrifood Research Finland) in Jokioinen (60 °N, 23 °E) (I, IV) and in Ruukki (64 °N, 25 °E) (II, III). Animals were managed according to Finnish legislation regarding the use of animals in scientific experimentation.

In the first experiment (I, IV) all animals were born in the Jokioinen Estates dairy herd while in other experiments (II, III) animals were purchased from local dairy farms. During the feeding experiments, the bulls were placed in an insulated barn in adjacent tie-stalls and fed individually. The bulls had free access to water. Feeding was based on grass silage and the concentrate used was rolled barley. Grass silage was prepared from mixed timothy (*Phleum pratense* L.) and meadow fescue (*Festuca pratensis* Huds.) swards (I, II, IV) and from a pure timothy sward (III). All grass silages were pre-wilted and ensiled with a formic acid based additive. The daily ration included mineral mixture. Grass silage and concentrate were offered either separately (I, II, IV) or a total mixed ration (TMR) was used (III).

In experiment 1 (I, IV), daily growth rate was manipulated by controlling energy intake through changing barley allowance and allocation. Grass silage was offered *ad libitum*. The experiment comprised 54 Ayrshire bulls, initial LW 94 (s.d. ±9.1) kg. During the experiment, one animal was eliminated for a reason unrelated to the experimental treatments. At the beginning of the experiment the animals were allotted to nine blocks by age and LW and within the block randomly allotted to six experimental treatments in a 2×3 factorial arrangement. The treatments consisted of two levels of concentrate feeding (39 and 74 g barley DM/kg $LW^{0.60}$; low (L) and high (H), respectively) and three concentrate allocation regimes, steady (SR), increased (IR) and decreased (DR) within both concentrate levels. The aim was that the total amount of consumed barley within the concentrate level during the whole experimental period was the same for SR, IR and DR. Bulls were slaughtered after reaching the target LW of 550 kg.

In experiment 2 (II), daily growth rate was manipulated by controlling energy intake through changing DMI. The experiment comprised 32 Ayrshire bulls, initial LW 123 (s.d. ±8.9) kg. At the beginning of the experiment the animals were allotted to eight blocks by LW and within the blocks they were randomly allotted to four experimental treatments. The treatments consisted of four feed allocation regimes. In steady energy feeding (A) grass silage was fed *ad libitum* and supplemented with barley at 93 g DM/kg $LW^{0.60}$ during the whole growing period. In restricted energy feeding (R), DMI was fed at 80% of DMI in treatment A at corresponding LW during the whole growing period. In increasing energy feeding (I) the bulls were fed similarly as group R up to LW 430 kg and then as group A until slaughter. In decreasing energy feeding (D) the bulls were fed similarly as group A up to LW 430 kg and then as group R until slaughter. Bulls were slaughtered after reaching the estimated carcass weight of 300 kg.

In experiment 3 (III), highly digestible grass silage was used, and growth rate was manipulated by controlling energy intake through changing concentrate proportion in the range of 0 to 0.60 DM. The animals were fed *ad libitum* either grass silage alone or TMR composed of grass silage and barley. The experiment comprised 20 Holstein and 16 Nordic Red bulls, initial LW 230 (s.d. ±36.9) kg. The population structure of the Nordic Red dairy cattle is a mixture of the Finnish Ayrshire, Danish Red and Swedish Red cattle (Makgahlela et al. 2013). During the experiment three Holstein bulls were eliminated for reasons unrelated to the experimental treatments. At the beginning of the experiment the animals were allotted to nine blocks by LW and breed and within the blocks they were randomly allotted to four experimental treatments. The treatments consisted of four feed allocation regimes, which were 1) grass silage alone (GS) during the whole growing period or concentrate as follows: 2) steady (SC; TMR contained grass silage proportion of DM 0.70 and barley 0.30 during the whole growing period), 3) increased (IC; grass silage alone during the first six months and then TMR contained grass silage proportion of DM 0.42 and barley proportion 0.58 during the later six months) and 4) decreased (DC; TMR contained grass silage proportion of DM 0.40 and barley proportion 0.60 during the first six months and grass silage alone during the later six months). Because barley was given as a constant proportion in DM of TMR instead of related to LW of the animals, total barley intake varied among treatments. Realized intakes of barley were 0, 66, 79 and 62 g/kg $LW^{0.60}$ for GS, SC, IC and DC, respectively. The bulls were slaughtered after 366 days in the experiment.

2.2. Experimental measurements and calculations

The individual feed intakes were recorded daily. Silage sub-samples for chemical analyses were collected daily (I) or twice a week (II, III), then pooled for periods of four weeks and stored at -20 °C before analyses. Barley sub-samples for chemical analyses were collected daily (I) or weekly (II, III) and then pooled for periods of eight weeks.

Silage samples were analysed for DM, ash, crude protein (CP), neutral detergent fibre (NDF), *in vitro* digestible organic matter (DOM) in DM (D value) and fermentation quality (pH, lactic acid, volatile fatty acids (VFA) and ammonia-N content of total N) (I, II, III, IV). Additionally, crude fat, crude fibre (I, IV), indigestible NDF (iNDF), ether extract, starch (III), water soluble carbohydrates (WSC) (I, IV, III), formic acid and soluble N content of total N (II, III) were analysed. Concentrate samples were analysed for DM, ash and CP (I, II, III, IV). Additionally, crude fat and crude fibre (I, IV), NDF (II, III), iNDF, ether extract and starch (III) were analysed.

The metabolizable energy (ME) concentration of the silage was calculated as 0.016 × D value (g/kg DM). The ME values of barley were calculated based on chemical composition and tabulated digestibility coefficients (Luke 2018). The supply of amino acid absorbed from the small intestine (AAT) and protein balance in the rumen (PBV) were calculated according to Finnish Feed Tables (Luke 2018). Feed conversion rate (FCR) was calculated as total daily DMI and MJ ME per live weight gain (LWG) (I, II, III) and also as CP and per carcass gain (II, III).

Total urine collection was conducted to calculate microbial N synthesis in the rumen based on urinary excretion of purine derivatives (I). Quantitative urine collection was undertaken in 6 blocks resulting in a total of 24 animals before the level of concentrate was changed in treatments IR and DR. The adjustment period in the metabolism crates was 2 days and the total urine collection was conducted for 5 days. Daily samples were combined per animal for analyses of allantoin and uric acid. The equation used to describe the quantitative relationship between absorption of microbial purines (X mmol/d) and excretion of purine derivatives, allantoin and uric acid in urine (Y mmol/d) was: $X = (Y - 0.385 \times W^{0.75}) / 0.85$. Intestinal flow of microbial N (g N/d) was calculated from amount of the microbial purines absorbed (X mmol/d) and the equation used was: Microbial N supply (g/d) = $[(X \times 70) / (0.83 \times 0.116 \times 1000)] = 0.727 \times X$.

The animals were weighed on 2 consecutive days at the start of the experiment and on 2 consecutive days before they were slaughtered (I, II, III, IV). During the experiments animals were weighed every 28 days (I, II, IV) or in the middle of the experiment when diets were changed (III). The LWG and carcass gain were calculated as the difference between the initial and final weights and divided by the number of growing days. Carcass weight at the beginning of the experiment was assumed to be 0.50 × initial LW. Dressing proportion was calculated from the ratio of carcass weight to final LW. When used, cold carcass weight (II, III) was estimated as 0.98 of the hot carcass weight. Carcass conformations and carcass fat scores were determined visually according to the EUROP classification (EC 2006).

Two muscle samples for meat quality measurements were cut from *longissimus lumborum* (LL), on the left side of carcasses immediately after the carcasses cross-section between the 7th and 8th lumbar vertebra three days post-slaughter (IV). The samples were used to determine pH, colour, drip loss, sarcomere length, chemical composition, sensory analysis and shear force. The ultimate pH and meat colour (L* brightness, a* redness and b* yellowness) were measured on the sampling day 3 days post-slaughter. For drip loss, LL steaks were packed on the sampling day 3 days post-slaughter in plastic bags and suspended in a cold room at 2 °C for 4 days. Drip loss was calculated as the difference between initial weight and weight after suspension. For measuring sarcomere length, muscle samples were cut on the sampling day, preserved in formalin and stored at room temperature. Sarcomere lengths were measured by laser diffraction and length (µm) was calculated using equation: $(632.8 \times 10^{-3} \times D \times (T / D)^2 + 1) / T$, where 632.8×10^{-3} is the wavelength of the radiation (µ), D equals the distance (mm) from the specimen-holding device to the screen (in the present experiment a constant value of 100 mm was used) and T equals the separation (mm) between the zero and the maximum. Samples were analysed for DM, N and crude fat. The CP concentration was calculated as N × 6.25. Shear force measurement was a modification of the Warner-Bratzler method. Trained sensory panellists evaluated the meat samples for tenderness, juiciness and flavour on a seven-point scale.

2.3. Statistical methods

All experiments were set up according to a complete randomized block design with animal as an experimental unit. The results were subjected to analysis of variance using GLM (I, II, IV) or MIXED (III) procedures of SAS (version 9.3., SAS Institute Inc., Cary, NC).

The results were shown as least squares means with standard error of the mean (SEM). The normality of analysed variables was checked using graphical methods: box-plot and scatter plot of residuals and fitted values. Relationships between LWG, carcass composition and meat quality were analysed using partial correlations and individual animal data using CORR procedures of SAS (IV).

The comparisons between diets were conducted using orthogonal contrasts (I, IV). The concentrate feeding regime imposed at the moment of microbial N synthesis measurements was evaluated using a polynomial linear contrast (I). Differences between the treatment means were tested using Tukey´s test (II, III). Tukey´s test was also used in I. This enabled separate comparison of steady, increased and decreased treatments. The results of Tukey´s tests in I were not reported but are referred to in this thesis and the differences were considered statistically significant at $p < 0.05$. As a consequence of using results of Tukey´s test, some results and conclusions may differ from those in the publication where results were analysed by using contrasts (I).

When two breeds were used, breed was a part of the blocking structure and therefore was not added to the statistical model (III). Thus, breed does not explain the differences among treatments.

3. Results and discussion

Grass silage is a typical feed in Finnish beef production and good quality grass silage is the basis of the feeding. A reasonable LWG can be achieved with highly digestible grass silage as the sole feed (Randby et al. 2010). However, typically, grass silage is supplemented with concentrates, generally cereal grains. The main reason is to increase energy intake and improve performance of growing animals.

3.1. Feeds

The average chemical composition and nutritional values of grass silages used as experimental feeds are presented in Table 2. The grass silages used were of average nutritional quality produced in Finland when compared with the average values for grass silages analysed in the laboratory of Valio Ltd. (dairy company) in 2014-2017 (Table 2). The D values ranged from 652 to 703 g/kg DM. Recommendation of D value for growing bulls according to Finnish feeding guidelines is 680–710 g/kg DM if cultivated area does not limit grass silage production (Huuskonen 2010). If the need is to maximize grass silage yield, target D value can be lower. However, decreased energy content must be compensated for by increasing concentrate allowance in the feed to sustain the same LWG as with using higher digestibility grass silage. The contents of NDF were typical for Finnish grass silages. The silages used were made using formic acid based additives, resulting in restricted fermentation as indicated by low fermentation end products and high WSC concentrations (McDonald et al. 1991). Fermentation characteristics were good, as indicated by low pH value and low concentrations of VFA and proportion of ammonia-N in total N.

Table 2. The average nutritional values and chemical compositions of experimental grass silages (data in I–IV) and mean values at farm level production, analysed in the laboratory of Valio Ltd. (dairy company) in Finland in 2014–2017.

	Grass silage			
	I, IV	II	III	Average in Finland[1]
Number of samples	20	17	12	73824
Dry matter (DM), g/kg	287	306	234	335
In DM, g/kg DM				
Organic matter	916	921	937	ND[2]
Crude protein	127	161	161	141
Neutral detergent fibre	555	575	556	539
Digestible organic matter	677	652	703	680
Feed values				
Metabolizable energy, MJ/kg DM	10.8	10.4	11.3	10.9
Metabolizable protein, g/kg DM	79	81	86	81
Protein balance in the rumen, g/kg DM	8	42	33	20
Fermentation quality of silage				
pH	4.25	3.95	3.97	4.17
Lactic acid, g/kg DM	45	47[3]	55[3]	46[3]
Volatile fatty acids, g/kg DM	25	14	12	13
Water soluble carbohydrates, g/kg DM	95	ND	50	72
Ammonia nitrogen, g/kg in total N	47	42	52	44

[1] Mean values of grass silages analysed by Valio Ltd. in Finland in 2014-2017.

[2] ND = Not determined.

[3] Including formic acid.

The barley used had typical chemical compositions and feed values, corresponding to the average values in the Finnish Feed Tables (Luke 2018).

3.2. Feed intake and nutrient supply

It is well established that DMI (kg/day) is related to LW and increases as animals gain weight, as was reported in the meta-analysis of Huuskonen et al. (2013). Supplementing grass silage with concentrate is one method for increasing DM and energy intake of growing cattle (Randby et al. 2010, Pesonen et al. 2013). However, concentrate level and forage intake potential interact, which affects DMI so that greater responses to concentrate feeding are expected when forages with low intake potential are used (Keady et al. 2004, Huuskonen et al. 2013). In addition, several other factors relating to animals, feed, management, housing and environment influence the regulation of feed intake (Ingvartsen 1994).

In the work embodied in this thesis, energy restriction of growing dairy bulls was conducted using three methods: Restricting barley intake (I, IV) or totally removing barley supplementation (III) but providing grass silage *ad libitum* or by restricting both barley and grass silage intake (II).

3.2.1. Effects of continuous energy restriction

The effects of restricted energy intake methods on ME intake (MEI) are shown in Figure 1. When energy intake was restricted by decreasing barley allowance and silage intake was *ad libitum*, silage intake increased, but daily DMI was not significantly affected and consequently MEI decreased (I: LSR vs. HSR, III: GS vs. SC). The result was similar to that reported by Huuskonen et al. (2014b) where concentrate proportions were 0.33 and 0.66 of DM. This is in contrast to many experiments for silage-fed growing cattle where increasing levels of concentrate increased DMI, resulting in increased MEI, although silage intake simultaneously decreased (Caplis et al. 2005, Keane et al. 2006, Randby et al. 2010). When DMI was restricted during the whole growing period, average daily DM and energy intake decreased by 27% (II: R vs. A). When observed over the whole growing period, the differences in total DMI were minor (I: HSR vs. LSR; 13 kg, II: A vs. R; 126 kg, III: SC vs. GS; 172 kg).

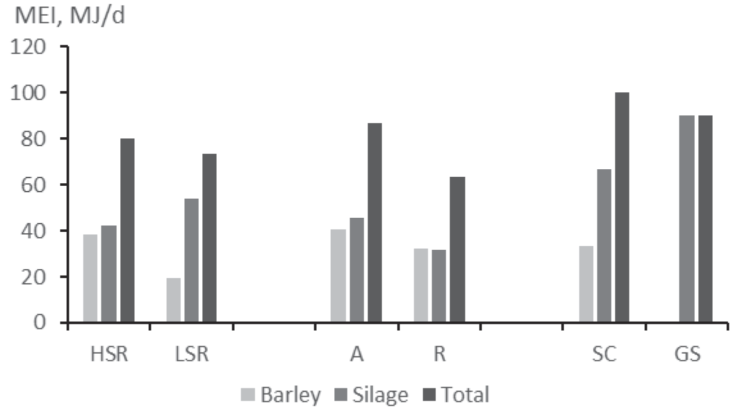

Figure 1. Average daily metabolizable energy intake from barley, silage and total dry matter (MEI; MJ/d) over the whole growing period (data in I–III). HSR = high steady energy intake and LSR = low steady energy intake (I), A = steady energy intake and R = restricted steady energy intake (II), SC = steady energy intake and GS = restricted steady energy intake (III).

Substitution rate (SR) is typically used to express the decrease in silage DMI per kg increase of concentrate DMI. The level of concentrate and silage feed value (intake potential) are the major factors affecting the SR (McNamee et al. 2001). Usually SR increases with increasing silage digestibility (Steen et al. 2002, Randby et al. 2010) and concentrate intake (Steen et al. 2002, Caplis et al. 2005, Keane et al. 2006, Huuskonen et al. 2007) (Table 3). With moderate levels of concentrate proportion, relatively high SR, 0.81, demonstrated high digestibility/intake potential of grass silage (III: GS vs. SC). The SR was higher than often reported at low or moderate concentrate levels, as in experiments of Caplis et al. (2005) and Keane et al. (2006), but similar as in those of Randby et al. (2010), Pesonen et al. (2013) and Huuskonen et al. (2014b) (Table 3). When average concentrate proportion of DM increased from 0.23 to 0.43 and digestibility of grass silage was moderate, SR was 0.76 (I: LSR vs. HSR).

Table 3. Substitution rates from some earlier experiments and from the data of this thesis (I, III).

Reference	Substitution rate	D value of the silage, g/kg DM[1]	Concentrate proportion on DM basis
Caplis et al. (2005)	0.36[2]	704[3]	0 vs. 0.31
	0.64[2]	704[3]	0.31 vs. 0.55
Huuskonen et al. (2007)	1.02	668	0.30 vs. 0.50
	1.26	668	0.50 vs. 0.70
Huuskonen et al. (2014b)	0.85[2]	669	0.33 vs. 0.66
Keane et al. (2006)	0.43[2]	647[3]	0 vs. 0.43
	0.58[2]	647[3]	0.43 vs. 0.73
Pesonen et al. (2013)	0.81[4]	672	0.20 vs. 0.50
	0.60[5]	672	0.20 vs. 0.50
Pesonen et al. (2014)	1.05	685	0.33 vs. 0.66
Randby et al. (2010)	0.63	747	0 vs. 0.27
	0.75	708	0 vs. 0.27
	0.33	647	0 vs. 0.27
Steen et al. (2002)	0.62	743	0.20 vs. 0.40
	0.91	743	0.40 vs. 0.60
	0.48	643	0.20 vs. 0.40
	0.65	643	0.40 vs. 0.60
I	0.76	677	0.23 vs. 0.43
III	0.81	703	0 vs. 0.30

[1] Dry matter.

[2] Calculated from separate feeding treatment.

[3] For this experiment, the D value (g/kg DM) was estimated from DM digestibility (DMD; g/g). First organic matter (OM) digestibility (OMD) was calculated from DMD using an unpublished formula OMD = 0.0193 + 0.994 × DMD, and then D value was calculated as (1000 – ash) × OMD.

[4] Hereford bulls.

[5] Charolais bulls.

Intake models for growing cattle (Huuskonen et al. 2013) and dairy cows (Keady et al. 2004, Huhtanen et al. 2008) have demonstrated that there is an interaction between concentrate level and forage intake potential: concentrate supplementation increases total DMI more with diets based on low rather than high intake potential forages. This suggests that metabolic constraints increase more with increased concentrate feeding with forages of high compared to low intake potential. The results presented above support this. According to Nadeau et al. (2002), LW, age of the animal, concentrate intake, silage NDF concentration and silage DM concentration are the factors that have significant effects on silage DMI.

Based on the meta-analysis of data from the feeding experiments, Huuskonen & Huhtanen (2015) established that energy intake was clearly the most important variable affecting LWG of growing cattle, whereas the results showed only marginal effects of protein supply on growth. In addition, according to many experiments with growing dairy bulls (Huuskonen et al. 2007, Huuskonen et al. 2008, Huuskonen 2011), protein supplementation had no effects on the dressing proportion, carcass conformation or carcass fat score. According to Huuskonen et al. (2014a) advantages of using AAT in estimating protein supply and requirements are questionable for growing cattle above 200 kg LW; microbial protein and rumen-undegraded protein from high quality forages and grain-based energy supplements can meet the requirements. In that case, protein supplementation is not needed for growing and finishing dairy bulls as concluded by Huuskonen (2011). In the data of this thesis restrictively fermented grass silage of high or medium digestibility and barley-based concentrates were used, and so there was no need for protein supplementation.

However, N is required for ruminal fermentation and amino acids for host animal, including for muscle tissue synthesis. Ruminants derive most of the absorbed amino acids from microbial N synthesised in the rumen. Microbial N synthesis is driven by the amount of fermentable substrate in the rumen when the N requirements of the microbes are met.

No effect was found of the level of concentrate (from 0 to 0.57) on the microbial N synthesis in the rumen per kg DOM intake (I). The results from other experiments have been variable. In cattle, Owens et al. (2008) reported no effect, Rooke et al. (1985) found a positive effect and Jaakkola & Huhtanen (1993) reported a curvilinear effect with a positive response to moderate increase in concentrate feeding whereas Harstad & Vik-Mo (1985) reported gradually reduced efficiency of microbial synthesis in sheep when the amount of barley increased.

Increased concentrate level increased microbial N flow per day similarly as in Jaakkola & Huhtanen (1993) and Owens et al. (2008). This may be a consequence of increased DM and DOM intake and higher LW with increased concentrate level. There was a linear decrease in dietary PBV value with increasing concentrate proportion, but it was not correlated with microbial N synthesis. This suggests that the N supply probably did not restrict microbial N synthesis even at the highest concentrate level, when the minimum PBV concentration of -10.8 g per kg DMI was reached during these measurements.

According to the Finnish feeding recommendations, PBV values down to -10 g/kg DM are accepted for growing cattle above 200 kg LW (Luke 2018). Based on the meta-analysis of the feeding experiments, Huuskonen et al. (2014a) found that PBV below -20 g/kg DM had only minimal influence on LWG response to increased CP. They concluded that recommended PBV could even be lower than the current -10 g/kg DM without harmful effects on LWG. For the data reported in this thesis, the lowest average PBV value per kg DMI was -5 g and CP concentration in this treatment was 126 g/kg DM (I: HIR). This should provide the rumen microbes with sufficient N and consequently, supply of AAT is sufficient. Based on these results it was concluded that AAT supply was not a limiting factor in the experiments and did not influence the results obtained.

3.2.2. Effects of periodic energy restriction

When energy intake was restricted periodically by restricting DMI, total daily DM and ME intake decreased over the whole growing period (II: I or D vs. A). When energy intake was restricted periodically by restricting only barley intake, it did not affect DM and ME intake over the whole growing period (I: L and H; IR or DR vs. SR, III: IC or DC vs. SC). When barley intake was restricted or removed from the diet and grass silage was offered *ad libitum*, bulls increased silage intake significantly (I: exception HDR vs. HSR, no statistically significant difference, III). The results demonstrated the ability of the bulls to compensate periodically for restricted barley intake by increasing silage intake during the restriction when good quality grass silage was available *ad libitum*.

Increased energy intake. Feed intake during compensatory growth may vary, as was found in the data for this thesis and also in earlier experiments. Similarly as in the data for this thesis (II: I vs. A, III: IC vs. SC), DMI increased during compensatory growth (Sainz et al. 1995, Cummins et al. 2007), but not always (I: L and H; IR vs. SR, Carstens et al. 1991, Keogh et al. 2015). Differences in the severity and duration of feed intake restriction and the length of unrestricted nutrient intake period before slaughter may be factors that cause variation in the effects of compensatory growth. Both Saubidet & Verde (1976) and Yambayamba & Price (1991) reported that the more severe the feed restriction, the more the animals increased feed intake during the compensatory growth. This was also found in the present thesis (II vs. I).

When silage intake was *ad libitum* during the restriction period, the restriction was not very severe (I). In consequence, DMI decreased by only 11% and 7% and energy intake by 14% and 10% (I: L and H; IR vs. SR, respectively). Increasing barley intake during realimentation increased DMI only slightly, by 2% and 3% and energy intake by 6% (I: L and H; IR vs. SR, respectively). Realimentation period before slaughter was rather long, which may partly explain the lack of substantial differences in DMI.

Severity of restriction increased when both barley and grass silage intake were restricted (II). During restriction, DM and energy intake decreased by 23% (II: I vs. A). During realimentation, bulls increased grass silage intake significantly and as a result, DM and energy intake increased by 12% and 9%, respectively. Despite increased DMI, bulls were not able to compensate fully for DM and energy intake, resulting in 14% and 15% lower intakes over the whole growing period, respectively.

When grass silage was used as a sole feed during the early part of the growing period, grass silage intake was 29% higher but DM and energy intake decreased by 10% and 14%, respectively (III: IC vs. SC). During realimentation, when barley was included in the diet, DM and energy intake increased by 17% and 23%, respectively (III: IC vs. SC). Probably the increased DMI during the late part of the growing period resulted from increased barley intake, but compensatory growth, and possibly larger rumen capacity due to earlier forage only diet, may have contributed to it.

Decreased energy intake. When concentrate intake in the diet increased during the early part of the growing period, DM or energy intake did not increase (I: L and H; DR vs. SR, III: DC vs. SC). This indicated that the need of ME was fulfilled. An especially high-concentrate diet, up to 0.60 of diet DM, with highly digestible grass silage may have metabolically limited silage intake (III). Huuskonen (2009a) suggested that probably the capacity to use energy is the limiting factor in intake regulation of young dairy bulls with concentrate proportion over 0.50 of diet DM. During the late part of the growing period, when concentrate proportion was duplicated, DM and energy intake increased significantly (III: IC vs. SC).

Possible effects of high concentrate intake. It is well known that high concentrate levels with increased starch intake may lead to low rumen pH and increase the risk of diseases such as rumen acidosis developing (Krause & Oetzel 2006), which decreases intake. Also reduced NDF digestibility may limit DMI in some cases. Reduced NDF digestibility has been associated with high concentrate intakes (Huuskonen et al. 2007, 2014b). Decreased NDF digestibility typically increases rumen fill and satiety and consequently the bulls have no more capacity to increase DMI. However, in the experiment of Manninen et al. (2010), when concentrate was offered *ad libitum* three months pre slaughter, DMI increased, although the digestibility of NDF in the diet decreased.

When the total amount of barley was included in the diet during the early or late part of the growing period, starch concentration in the diet was 343 g/kg DM and the diet contained 222 g forage NDF per kg DM (III). Huuskonen et al. (2014b) outlined that a starch level of 400 g/kg DM is not too high for growing bulls when the diet contains forage NDF at least 180 g/kg DM. These criteria were fulfilled and based on this starch or NDF intake did not limit DMI (III).

Based on the meta-analysis of Huuskonen et al. (2013), LW was the most important variable predicting DMI. However, when dietary NDF concentration was included in the model, intake prediction improved clearly. Thus, Huuskonen et al. (2013) concluded that when poor-quality forage is used, primarily physical constraints limit DMI and capacity of DMI is related to LW. When more concentrated diets are used, the importance of physical constraints on DMI decrease and DMI is regulated mainly by metabolic requirements.

When observing dietary NDF concentrations at the highest concentrate levels either during the early or late part of the growing period, average diet NDF concentrations were 314, 363, 350 and 351 g/kg DM (I: HDR, HIR, III: DC, IC, respectively). Based on the meta-analysis of Huuskonen et al. (2013), maximum DMI was achieved at NDF concentration of 345-414 g/kg DM at LW of 200-600 kg. Based on this, deficiency of NDF may have limited DMI (I: HDR). It is noteworthy that the model of Huuskonen et al. (2013) was based on experiments where the same diet was fed during the whole growing period and the model may result in biased predictions for animals during compensatory growth.

3.3. Growth rate and feed efficiency

A typical growth curve is sigmoid, where growth becomes slower after the high LWG during the early part of the growing period (Lawrence & Fowler 2002). However, when growth has been manipulated by restricting feed and/or nutrient intake, the growth curve has changed (Rossi et al. 2001, Cummins et al. 2007, Moloney et al. 2008b).

Typically, feed conversion (kg DM/kg LWG, MJ ME/kg LWG) is more efficient in young animals and declines as LW and DMI increase, cattle approach maturity and growth rate declines, as was found in several earlier experiments (Huuskonen 2009b, Keane 2010). Restricting feed intake could represent a method to improve FCR (Sainz et al. 1995, Rossi et al. 2001, Schmidt et al. 2005).

3.3.1. Effects of continuous energy restriction

Growth rate. A decrease in LWG during the late part of the growing period was observed (I, II, III) when energy intake was steady and silage or TMR intake was *ad libitum* (Figure 2). The decrease in LWG was 6–27% compared with LWG during the early part of the growing period. The result of decreased LWG as animals grow older and were fed evenly during the growing period is in accordance with many results reported previously (Cummins et al. 2007, Huuskonen et. al 2007, Huuskonen 2009b, Keane 2010).

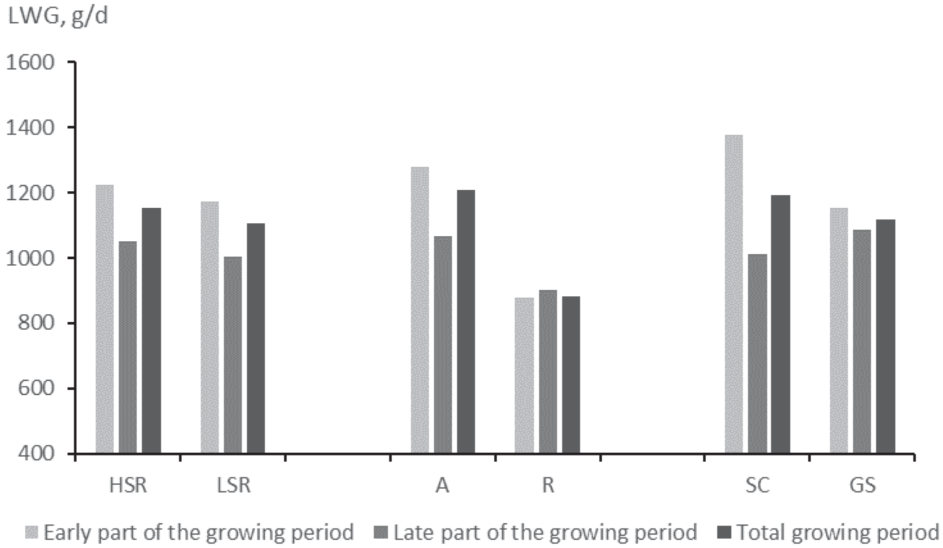

Figure 2. Live weight gain (LWG; g/d) during early and late part of the growing period and over the total growing period (data in I-III). HSR = high steady energy intake and LSR = low steady energy intake (I), A = steady energy intake and R = restricted steady energy intake (II), SC = steady energy intake and GS = restricted steady energy intake (III).

When grass silage was provided as the sole feed, LWG decreased by only 6% during the late part of the growing period, which was substantially less than in steady barley fed treatments (III). When both barley and grass silage intake were restricted during the whole growing period, LWG remained even until the end of the growing period (II). This indicated that decrease in LWG was inhibited by severe restriction of energy intake.

Increasing barley proportion in the diet increased MEI and consequently there was a trend of improved LWG (Figure 3). It is well established that increasing concentrate allowance increases MEI and LWG increases as a consequence (Scollan et al. 2003, Keane et al. 2006, Huuskonen et al. 2014b, Huuskonen & Huhtanen 2015), which is supported by the results reported in this thesis.

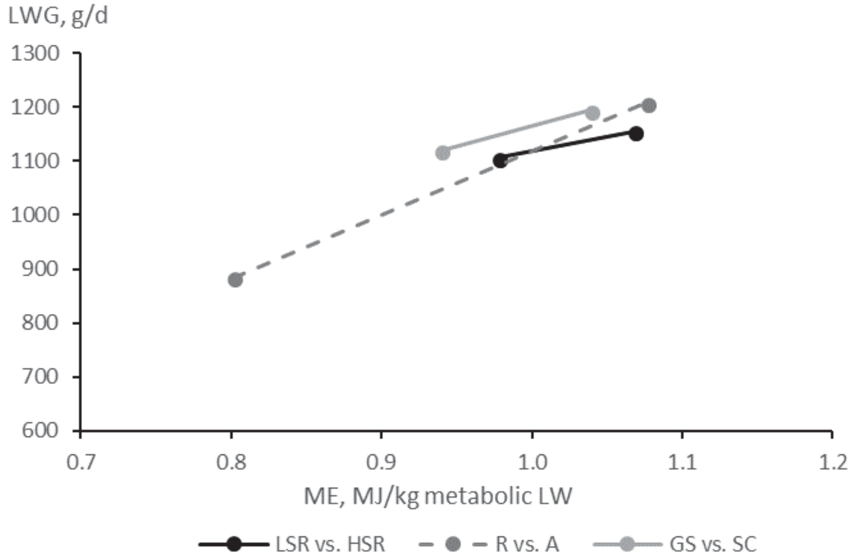

Figure 3. Effect of energy intake (metabolizable energy (ME), MJ/kg metabolic live weight (LW)) on the live weight gain (LWG; g/d) (data in I-III). LSR vs. HSR = low steady energy intake vs. high steady energy intake (I), R vs. A = restricted steady energy intake vs. steady energy intake (II), GS vs. SC = restricted steady energy intake vs. steady energy intake (III).

With good quality silage, a reasonable LWG can be achieved even when the silage is given alone (Randby et al. 2010, III). When highly digestible grass silage (III: D-value 703 g/kg DM) was used, as high or almost as high LWG was achieved as with lower digestible grass silage (I: D-value 677 g/kg DM) supplemented with steady concentrate proportion at 0.23 or 0.43 of DM (III, I). Although good quality silage can support relatively high growth capacity, increasing the allowance of concentrate improved growth rate and decreased days until slaughter (Scollan et al. 2003, Randby et al. 2010). When highly digestible grass silage was supplemented with moderate amounts of barley (0.30 of DM), LWG increased by 7% compared with when grass silage was provided as a sole feed (III: SC vs. GS). The difference (75 g/d) was not statistically significant but was numerically substantial.

Increase in growth rate was 34 and 30 g LWG per kg increased concentrate DM, when concentrate proportion of DM increased from 0.23 to 0.43 (I: LSR vs. HSR) and from 0 to 0.30 (III: GS vs. SC), respectively. Although digestibility of grass silage differed between these two experiments, differences in LWG response were minor. This is in contrast with the hypothesis that when using silage of high digestibility, the growth response to increased concentrate intake is generally lower, which can be derived from the results reported by Randby et al. (2010). The differences in intake remain marginal due to high SR, showing that responses to concentrate feeding can be limited. In addition, according to Keane et al. (2006) and Huuskonen et al. (2007), the response to supplementary concentrates decreases with increasing level of concentrates used. The data in this thesis were consistent with those of Huuskonen et al. (2007, 2014b), where increase in LWG was 33 and 25 g per kg increased concentrate DM, respectively. The proportion of DM concentrates increased from 0.30 to 0.50 and from 0.33 to 0.66, respectively.

Feed efficiency. Based on these data, FCR (MJ ME/kg LWG) decreased during the late part of the growing period with increased LW (Figure 4), similarly as reported earlier (Huuskonen 2009b, Keane 2010). As a consequence, beef production efficiency decreases as the animals get older and biologically it is not efficient to raise bulls to heavy carcass weights. However, raising bulls to heavy carcass weights could be economically profitable if the pricing system of slaughterhouses were to encourage it, as in Finland.

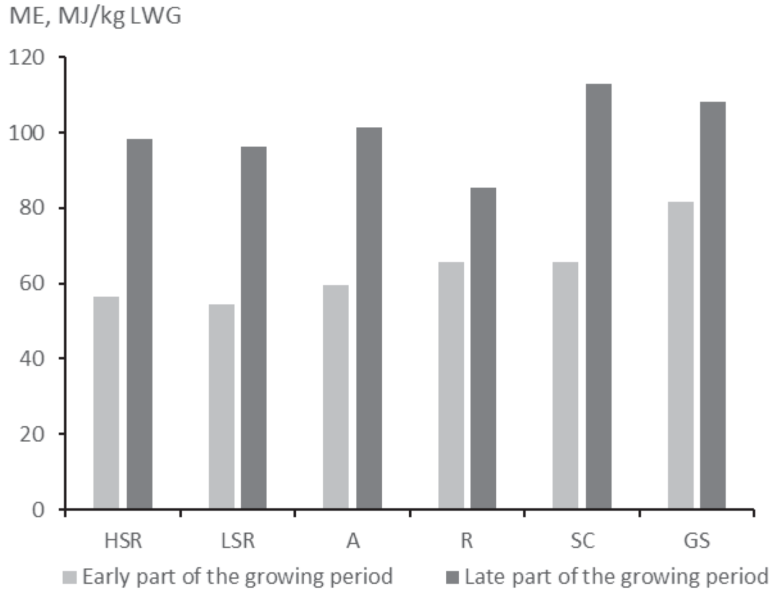

Figure 4. Effect of increased live weight during the late part of the growing period on feed conversion rate (metabolizable energy (ME) MJ/kg live weight gain (LWG)) (data in I–-III). HSR = high steady energy intake and LSR = low steady energy intake (I), A = steady energy intake and R = restricted steady energy intake (II), SC = steady energy intake and GS = restricted steady energy intake (III).

Increased barley intake did not improve FCR, contrary to results from some earlier experiments (Huuskonen et al. 2007, Randby et al. 2010, Pesonen et al. 2013) (I, III). However, when grass silage was supplemented with barley and compared with grass silage as a sole feed, FCR clearly improved numerically over the whole growing period (III: SC vs. GS).

In contrast to results from some earlier experiments (Hicks et al. 1990, Murphy & Loerch 1994; exp. 2, Schmidt et al. 2005), restricted DMI did not improve DM conversion rate over the whole growing period (II: R vs. A). During the early part of the growing period it even impaired FCR, whereas during the late part of the growing period FCR clearly improved numerically. In two experiments of Keane & Fallon (2001), efficiency of conversion of ME to LW and carcass weight tended to be better for higher than for lower feeding levels during the early part of the growing period but tended to be poorer during the late phase. A similar trend was also apparent in these data (II A vs. R; III SC vs. GS). This may partly result from the differences in LWG, which were greater during the early part of the growing period than during the late part. Based on the literature, suggested reasons for improved FCR as a consequence of restricted feed intake are increased diet digestibility and reductions in feed waste, animal activity and size of viscera, which reduce energy requirements for maintenance (Hicks et al. 1990). These factors may have affected the observed changes in FCR.

Benefits. The benefits of restricted energy intake depend particularly on the price of feeds, feed efficiency, effects on carcass classification and weight and also the number of slaughter animals per unit time. Based on the results reported in this thesis, restricting DMI did not bring benefits for beef production: growing days increased without improved feed efficiency. Consequently, the rotation time of beef production will slow down and lead, *inter alia*, to increasing fixed costs per animal and decreasing revenues.

3.3.2. Effects of periodic energy restriction

Growth rate. If the growth rate is manipulated by altering the amount and/or quality of feeds offered during growing and finishing periods, growth curves are affected (Carstens 1995, Knoblich et al. 1997, Hornick et al. 2000) similarly as shown in Figure 5 (I, II, III).

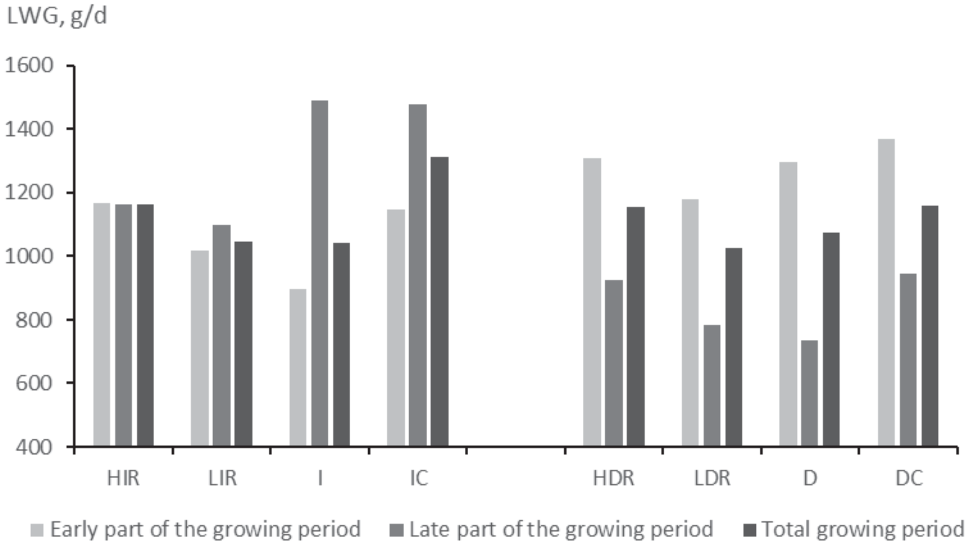

Figure 5. Live weight gain (LWG; g/d) during early and late part of the growing period and during the total growing period (data in I-III). HIR = high increased energy intake and LIR = low increased energy intake (I), I = increased energy intake (II), IC = increased energy intake (III), HDR = high decreased energy intake and LDR = low decreased energy intake (I), D = decreased energy intake (II), DC = decreased energy intake (III).

The effects of periodic energy restriction on average LWG over the whole growing period and the number of growing days differed between experiments. When energy restriction was not too severe, periodic energy restriction did not affect average LWG over the whole growing period or number of growing days (I). When restricted energy intake was more severe, periodic energy intake decreased average LWG over the whole growing period and increased the duration to reach the target slaughter weight (II). When energy intake increased during the late part of the growing period and the total barley intake was highest, it resulted, numerically, in the highest average LWG over the whole growing period (III).

Compensatory growth – Increased energy intake. During the compensatory growth LWG typically increases when feed or nutrient intake increases after a restriction period, even to the extent that it enables animals to reach the weight of those animals whose growth was not reduced (Hornick et al. 2000). However, restrictively fed animals rarely compensate totally and consequently require more time to reach the target slaughter weight (Hornick et al. 2000, Keane 2010), as was also found in these data (II). The increase in growing days to achieve the target slaughter weight was 87 d (II: I vs. A), but also full recovery was recorded (I, III). The extent of compensatory growth can be demonstrated using a compensatory index, which generally lies between 50% and 100% of recovery (Figure 6) (Hornick et al. 2000). A value of 100% indicates full recovery. Compensatory index was only 4% at that point when steadily energy fed animals achieved the target slaughter weight (II: I vs. A). It was the result of a long restriction period and short realimentation period, which lasted only 28 days until steadily energy fed bulls were slaughtered.

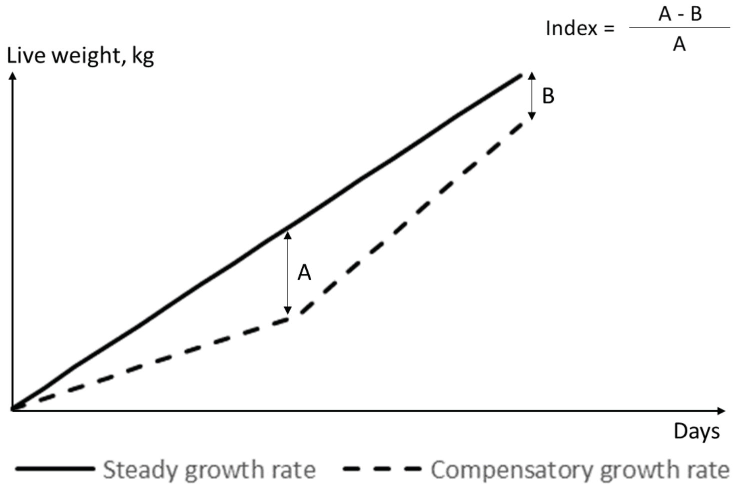

Figure 6. The compensatory index to measure recovery of restricted growth (according to Hornick et al. 2000).

The factor that inhibited full growth compensation probably resulted from the substantially decreased LWG during restriction and the quite long period of restricted feeding (II: 349 d) before realimentation and rather moderate increase in energy intake during realimentation. Typically, after realimentation, the compensatory growth increases during about one month and the maximal growth lasts, on average, for another month and is then followed by decreasing growth (Hornick et al. 2000). However, in these data (I, II) the growth rate continued at a high level during the whole compensatory growth period, which lasted 179 (I: L), 156 (I: H) and 115 days (II).

When both silage and barley intake were restricted during the early part of the growing period (II), restriction was more severe than when only barley intake was restricted (I). As a consequence, growth rates were considerably lower during the restricted period (II: 898 g/d vs. I: 1016 (L) and 1166 (H) g/d). During realimentation, LWG increased substantially more when restriction was more severe (II: 593 g/d vs. I: 81 (L) and -1 (H) g/d). Coleman & Evans (1986) reported a negative correlation in LWG between growing and finishing periods (during finishing from day 60 to 120). Also, Block et al. (2001) concluded that higher LWG during the early part of the growing period resulted in lower LWG during the finishing period. These results support these findings.

When highly digestible grass silage was used as a sole feed during the restriction LWG was quite high, 1149 g/d (III). However, during the realimentation, when barley was included in the diet (0.58 of diet DM), animals had substantial capacity to increase LWG, which increased to 330 g/d and was 468 g/d higher compared with the steady energy intake treatment (barley proportion 0.30 of diet DM). Also, Cummins et al. (2007) observed that finishing steers that were offered first silage only and then fed concentrate *ad libitum* (proportion 0.73 of diet DM, restricted silage intake) expressed compensatory growth and they gained 480 g/d more when moved to *ad libitum* concentrate than the animals that were fed at a flat rate with concentrate at 0.44 of diet DM.

Based on the literature, it has been assumed that factors contributing to compensatory growth are increased DMI and gut fill weight or improved FCR (Carstens 1995). However, Sainz et al. (1995) concluded that gut fill was not involved in the compensatory growth but an altered maintenance energy requirement may have been a major factor in compensatory magnitude.

Growth - Decreased energy intake. When energy intake was restricted during the late part of the growing period, LWG decreased (I, II, III) (Figure 5). The decrease in LWG from early growing period to the late phase ranged between 29–43%. When decreased energy intake treatments are compared with steady energy intake treatments during the late part of the growing period, LWG was 221 (I: L), 128 (I: H) and 64 (III) g/d lower. When both grass silage and barley intake were restricted, the restricting period was more severe (II). Consequently, the reduction was greater, 329 g/d (D vs. A). When restriction in energy intake was moderate, it did not affect the number of growing days (I) statistically significantly, but more severe restriction increased growing days (II).

Feed efficiency – Increased energy intake. Periodically restricted energy intake affected FCR in different ways (Figure 7). When energy intake was restricted during the early part of the growing period, FCR declined (II: I vs. A significantly, III: IC vs. SC numerically) or was not affected (I) when compared with unrestricted treatments. During realimentation, a numerical trend of improved FCR was established (I, II, III). When DMI was restricted during the whole growing period, a trend of first impaired and then improved FCR was also evident (II: R vs. A). The improvement in FCR during the realimentation period may partly be a consequence of compensatory growth, which has been reported to improve FCR (Sainz et al. 1995, Keogh et al. 2015). Possible explanation for improved FCR may be reduced size of viscera resulting from the restricted period and consequent reduced maintenance requirements. Over the whole growing period, no differences in FCR between increased or steady energy intake treatments were found. The result was similar to that of Cummins et al. (2007), but contrary to that of Moloney et al. (2008b) and Keane (2010) where FCR over the whole growing period was improved.

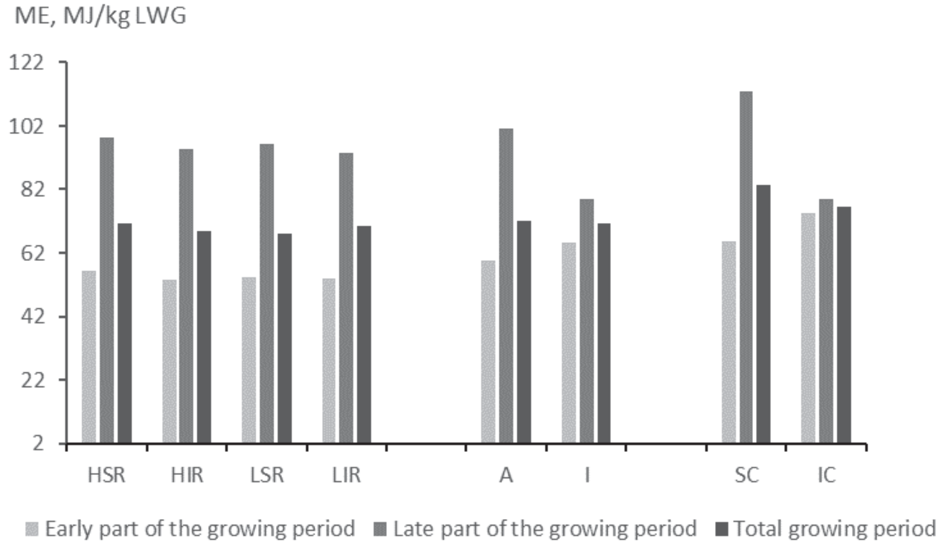

Figure 7. Feed conversion rate (metabolizable energy (ME) MJ/kg live weight gain (LWG)) in steady and increased energy intake during early and late part of the growing period and over the total growing period (data I–III). HSR = high steady energy intake, HIR = high increased energy intake, LSR = low steady energy intake and LIR = low increased energy intake (I), A = steady energy intake and I = increased energy intake (II), SC = steady energy intake and IC = increased energy intake (III).

Feed efficiency – Decreased energy intake. Decreased energy intake did not improve FCR during the late part of the growing period when compared with steady energy feeding groups, nor did it affect FCR over the whole growing period (Figure 8). Restricted DMI during the late part of the growing period even impaired FCR significantly compared with restricted DMI during the whole growing period (II: D vs. R). When the late phase was observed, restricted DMI during the late part of the growing period impaired FCR significantly compared with restricted DMI during the whole growing period (II: D vs. R). This may partly be a consequence of higher maintenance requirement and significantly lower LWG. The higher maintenance requirement, in turn, could be a consequence of larger size of viscera resulting from higher feed intake during the early part of the growing period. It seems likely that no benefits in terms of FCR can be expected from restricting DMI during the late part of the growing period.

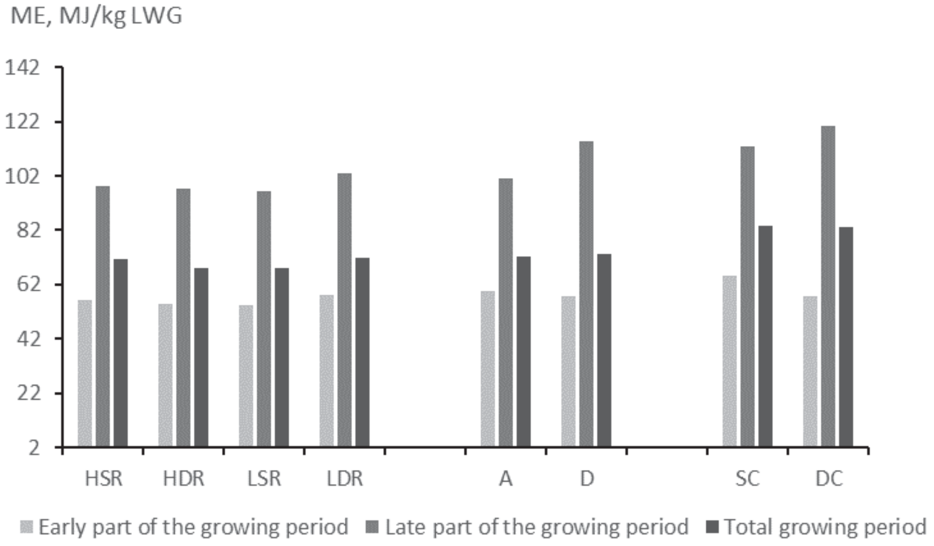

Figure 8. Feed conversion rate (metabolizable energy (ME) MJ/kg live weight gain (LWG)) in steady and decreased energy intake during early and late part of the growing period and over the total growing period (data in I-III). HSR = high steady energy intake, HDR = high decreased energy intake, LSR = low steady energy intake and LDR = low decreased energy intake (I), A = steady energy intake and D = decreased energy intake (II), SC = steady energy intake and DC = decreased energy intake (III).

3.4. Carcass characteristics

Carcass characteristics are affected by numerous factors, including feeding, LWG, LW, carcass weight, age, genetic background and breed. During normal development, initially deposited tissue growth is mostly muscles followed by increased deposition of fat (Hornick et al. 2000). The relative rates at which lean muscle and fat are deposited in the carcass depend on the maturity of the animal. Mature weight is considered to be the stage at which muscle mass reaches its maximum (Owens et al. 1993). If carcass characteristics are manipulated by changing energy intake, the severity and length of the restricted and realimented period may cause variation in the effects.

In the feeding experiments, it is not possible to standardise all factors that affect carcass characteristics. Therefore, interpretation of the results and comparing them with other experiments is challenging. In addition, in single experiments, differences between treatments may be numerically high, but not statistically significant, as was evident from these data. Reasons for this could include a low number of animals and/or highly dispersed data.

3.4.1. Effects of continuous energy restriction

Including concentrate in the diet (0 vs. 0.30 of DM) did not affect carcass weight (III). This may be consequence of highly digestible grass silage and good LWG. Contrary to this, Keane & Fallon (2001; exp. 1) reported that increased concentrate proportion (from start to day 179: concentrate 0.33, 0.59 and 0.89 of diet DM and from day 179 to day 272: concentrate 0.27, 0.48 and 0.92 of diet DM, DM digestibility of silage 688 g/kg) increased carcass weight when the length of finishing period was similar. Also, Keane et al. (2006) and Murphy et al. (2017) found that animals finished on high concentrate diets had greater carcass weight at the same slaughter age. These results are highly dependent on management choices, whether the end point of the experiment is set at constant weight of animals or length of growing period. In later comparisons of dressing proportion and carcass quality, it is crucial whether comparisons are made according to similar or varying carcass weights between treatments because carcass weight and age of the animals may have independent effects on the carcass and meat quality.

Barley proportion or restricted DMI during the whole growing period did not affect dressing proportion (I, II, III). This is in contrast with earlier experiments, where increased energy intake increased dressing proportion (Keane & Fallon 2001, Keane et al. 2006, Pesonen et al. 2013, Huuskonen et al. 2014b, Nogalski et al. 2014). In the meta-analysis of Huuskonen & Huhtanen (2015), increased MEI and LWG increased dressing proportion. They concluded that it resulted from the lower gut fill as forages typically increase gut fill compared with concentrates. Rinne et al. (1997) reported a positive relationship between diet NDF concentration and gut fill. However, when the data from this thesis were considered numerically, there was a tendency for higher barley proportion increasing dressing proportion (I: HSR vs. LSR, III: SC vs. GS). When DMI was restricted during the whole growing period, dressing proportion was numerically higher (II: R vs. A). This could result from the differences in concentrate proportion (I, III) and in DM and NDF intakes.

Neither barley proportion nor restricted DMI during the whole growing period affected carcass conformation (I, II, III). In earlier experiments, the responses to increased concentrate and energy intake on carcass conformation varied. In some experiments increasing the allowance of concentrate and MEI did not affect carcass conformation (Keane & Fallon 2001; exp. 2, Huuskonen et al. 2007, Huuskonen et al. 2014b) but in others it improved (Aronen et al. 1994, Keane & Fallon 2001; exp. 1, Caplis et al. 2005, Keane et al. 2006, Nogalski et al. 2014, Murphy et al. 2017). Based on the meta-analysis of feeding experiment data for growing cattle, Huuskonen & Huhtanen (2015) found that increased MEI improved carcass conformation.

It is generally agreed that increased energy intake of growing cattle increases carcass fatness (Martinsson & Olsson 1993, Keane et al. 2006, Nogalski et al. 2014, Huuskonen & Huhtanen 2015, Murphy et al. 2017). When decrease in MEI was only 9% it did not affect carcass fat scores (I: LSR vs. HSR). When average daily DMI and MEI were restricted by 27%, carcass fat score decreased by 29% (II: R vs. A). The result is similar to that of Steen & Kilpatrick (1995), where restricted DMI (20% of *ad libitum* DM intake) decreased carcass fat score of bulls by 11% at a carcass weight of 317 kg. Murphy & Loerch (1994; exp. 1) reported decreased carcass fat thickness when DMI was restricted to 90% or 80% of *ad libitum* DMI. Contrary to earlier results, a restriction of DMI to 80% resulting in an 18% decrease in energy intake did not affect carcass fat score (Steen & Kilpatrick 2000).

Keane et al. (2006) reported that beef steers finished on silage only had lower fat scores than steers finished on a diet containing 0.42 concentrate of DMI or more and receiving at least 65% more energy. This kind of trend was not established in the work reported here (III), similarly as for Randby et al. (2010), which may be the result of smaller differences in MEI. Also differences in carcass weights may have had an effect. In Keane et al. (2006) the number of growing days was similar among treatments and as a consequence of higher LWG of concentrate-fed animals, carcass weights were higher.

When looking at the data included in the present thesis it seems that increased MEI due to higher concentrate allowance improved growth rate and simultaneously increased fatness of the carcasses (Figure 9a, b), although the differences in the individual experiments did not show this clearly. A similar trend was found in the meta-analysis of Huuskonen & Huhtanen (2015) and in many other experiments (Keane et al. 2006, Huuskonen et al. 2007, Pesonen et al. 2013, Murphy et al. 2017). However, the results vary, as in Randby et al. (2010) and Huuskonen et al. (2014b), where increased concentrate allowance did not affect carcass fat scores. In the above-mentioned single experiments, the amount of concentrate was, on average, lower when fatness was not increased. However, Manninen et al. (2010) observed that *ad libitum* concentrate feeding three months pre-slaughter did not affect carcass fat score compared with restricted concentrate allowance. Steen & Kilpatrick (2000) concluded that reducing slaughter weight might be a more effective strategy for controlling carcass fatness than reducing energy intake either by diet restriction or reducing concentrate proportion.

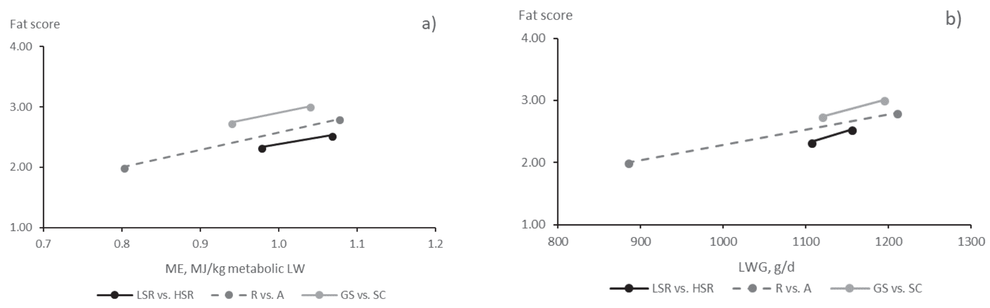

Figure 9. The effects of average energy intake (ME; MJ/kg metabolic live weight (LW)) (a) and average live weight gain (LWG; g/d) (b) on carcass fat scores (data in I–III). LSR vs. HSR = low steady energy intake vs. high steady energy intake (I), R vs. A = restricted steady energy intake vs. steady energy intake (II), GS vs. SC = restricted steady energy intake vs. steady energy intake (III).

Typically, carcass fatness increases when animals grow older (Kirkland et al. 2007). However, this was not apparent in these data, although restrictively fed bulls were substantially older (approx. 4 mo.) than the steady energy feeding group at slaughter (II). The age effect was probably overridden by the effect of reduced MEI.

3.4.2. Effects of periodic energy restriction

Periodic energy restriction did not affect carcass weight when comparing treatments with similar barley allowances (III: DC vs. SC). In two experiments of Moloney et al. (2008a), during a restricted period steers were offered grass silage as a sole feed and during realimentation grass silage and concentrate were fed *ad libitum*. Control treatments were silage *ad libitum* and supplemented with concentrate (average 6 kg/d). Treatments within both experiments comprised the same total amount of concentrate. When the restricted period was short (35 d; Exp. 1), days to slaughter were the same for steady and periodic feeding treatments and no differences in carcass weights were found. When the restricted period was longer (112 d; Exp. 2), periodic feeding increased the number of days to slaughter but slaughter weight also increased. These results indicated that carcass weight might be affected by both feeding and length of the growing period.

When the total barley allowance between the treatments varied, effects of periodic energy intake on carcass characteristics were not clearly discernible (III: IC vs. SC). However, resulting from the greatest barley intake, also possibly a consequence of compensatory growth, carcass weight increased compared with the effects of other treatments. Statistically it differed from the treatment where grass silage was used as a sole feed.

Dressing proportion was not affected by periodic energy intake (I, II, III). The result is similar to that of Cummins et al. (2007), where concentrate intake was steady or increased and the amount of concentrate among the treatments was similar. Forages generally promote a greater gut fill compared with concentrates (Owens et al. 1995), which decreases dressing proportion, but this was not evident from these data, although concentrate proportions differed between the treatments during the late part of the growing period. However, numerically, decreased DMI during the late part of the growing period increased dressing proportion (II: D vs. A and I), which may have resulted from smaller gut fill.

Increased energy intake during the late part of the growing period did not affect carcass conformation scores when compared with steady energy intake treatments. The result is similar to that of earlier experiments (Steen & Kilpatrick 2000, Rossi et al. 2001, Cummins et al. 2007, Keady et al. 2017), but contrary to others where conformation increased (Carstens et al. 1991) or decreased (Keane 2010; at LW 560 kg, Keogh et al. 2015) (Table 4). In the experiment of Keane (2010), when LW increased from 560 to 620 kg, differences in conformation were no longer evident. In the experiment of Keogh et al. (2015), carcass weight of periodically fed bulls was lower compared with that for steady feeding and it may have contributed to decreased conformation.

Table 4. The effects of periodic energy intake, first restricted and then realimented, on dressing proportion and carcass classification in growing and finishing steers and bulls.

	Live weight, kg				Duration of growth, d		Effects on carcass performance, periodic growth compared to continuous growth		
	Continuous		Periodic		Continuous	Periodic			
Reference	Initial	Final	Initial	Final	Total	Rest.[1]/total	Dressing proportion	Fat score	Conformation
Cummins et al. (2007)	458	590	460	580	164	79/164	NS[2]	NS	NS
Keady et al. (2017)	296	669	298	630	299	99/299	NR[3]	Tended to decrease	NS
Keane (2010)	433	560	429	563	91	84/127	Decreased	NS	Decreased
	432	619	434	626	155	84/180			
Keane & Moloney (2010)	415	555	420	627	94	94/192	NS	Increased	NS
Keogh et al. (2015)	370	678	372	594	180	125/180	Decreased	Decreased	Decreased
Moloney et al. (2008a; exp. 1)	568	659	566	666	126	35/126	NR	NS	NR
Moloney et al. (2008a; exp. 2)	491	640	491	672	154	112/196	NR	Increased	NR
Rossi et al. (2001; exp. 1)	309	604	309	589	186	137/186	Decreased	Decreased (back fat)	NS (longissimus area)
Rossi et al. (2001; exp. 2)	309	569	308	573	149	129/158	NS	NS (back fat)	NS (longissimus area)
			308	572		116/149			
Steen & Kilpatrick (2000)	NR	~560	NR	~560	247	until 510 kg /247 d	NS	Decreased	NS (longissimus area)
I	93	558	95	554	424	261/440	NS	NS	NS
	94	558	95	565	404	253/409			
II	124	578	122	604	377	349/464	NS	NS	NS
III	222	659	231	712	366	183/366	NS	NS	NS

[1] Restricted.

[2] Not significant difference.

[3] Not reported.

Decreased energy intake during the late part of the growing period did not affect carcass conformation (I, II, III). The result is similar to that of Moloney et al. (2008b).

Periodically restricted energy intake decreased carcass fat score (I: IR and DR vs. SR) or did not affect it when compared with steady energy intake, which contained barley and silage or TMR intake was *ad libitum* (I: L and H; IR or DR vs. SR, II: I or D vs. A, III: IC or DC vs. SC).

The effects of decreased energy intake prior to slaughter on carcass fatness varied in earlier experiments. Steen & Kilpatrick (1995) reared cattle in a high-forage system and reducing feed intake during the finishing period by 20% reduced carcass fat content and increased lean meat content. In the experiment of Moloney et al. (2008b) no differences were found.

Effects of compensatory growth on carcass fatness varied in earlier experiments (Table 4), which may partly be due to differences in slaughter weight, but not invariably. In some experiments carcass fatness decreased (Steen & Kilpatrick 2000, Keogh et al. 2015) and in others it increased (Moloney et al. 2008a; exp. 2, Keane & Moloney 2010) or no effect was evident (Cummins et al. 2007, Moloney et al. 2008a; exp. 1, Moloney et al. 2008b, Keane 2010) when animals exhibited compensatory growth. In previous experiments, a positive relationship between increased carcass weight and carcass fat score was found, which indicates that carcass weight could have affected fatness more than compensatory growth. When carcass fatness was not affected, animals were slaughtered at the same weight. However, Steen & Kilpatrick (2000) observed that when carcass weight was similar between the treatments of steady and periodic energy intake, fatness nevertheless decreased when energy intake increased during the late part of the growing period.

According to Wright & Russel (1991) and Hornick et al. (2000), during compensatory growth, initial deposition of lean tissue is substantial and lasts for some weeks. Thereafter, high feed intake leads to increased fat deposition and protein synthesis decreases. Thus, the length of the finishing period may also affect compensatory growth effects on carcass fatness, as was reported by Hessle et al. (2007). However, according to these data, although the length of the realimentation was relatively long (115-183 d), carcass fatness did not increase (I, II, III).

Regarding energy intake over the whole growing period, there was a tendency for increased energy intake to increase carcass fatness (Figure 10) (I, II, III). However, energy intake during the late part of the growing period tended to have different effects: increased energy intake tended to decrease carcass fatness (Figure 11) (I, II). This indicates that increased energy intake during realimentation does not necessarily increase carcass fatness if the animals exhibit compensatory growth.

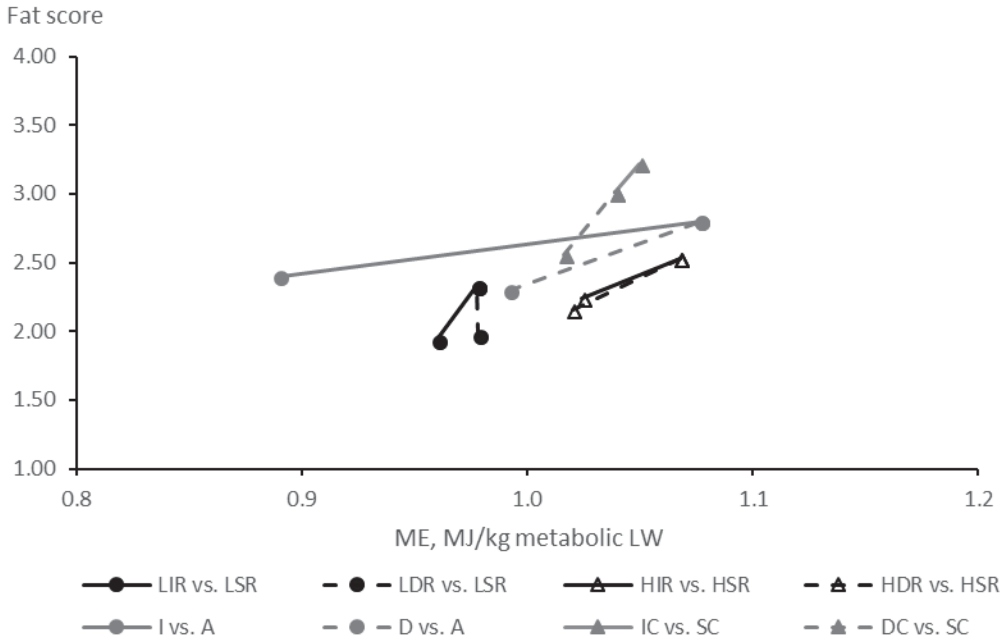

Figure 10. The effects of average energy intake (ME; MJ/kg metabolic live weight (LW)) on carcass fat scores (data in I–III). LIR vs. LSR = low increased energy intake vs. low steady energy intake, LDR vs. LSR = low decreased energy intake vs. low steady energy intake, HIR vs. HSR = high increased energy intake vs. high steady energy intake, HDR vs. HSR = high decreased energy intake vs. high steady energy intake (I), I = increased energy intake vs. A = steady energy intake, D = decreased energy intake vs. A = steady energy intake and (II) and IC = increased energy intake vs. SC = steady energy intake, DC = decreased energy intake vs. SC = steady energy intake (III).

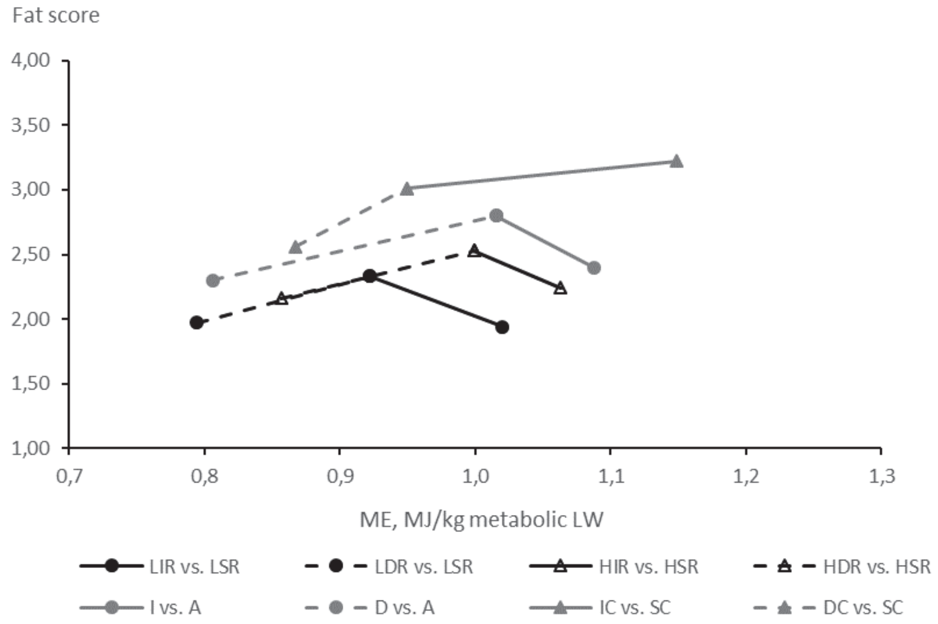

Figure 11. The effects of energy intake (ME; MJ/kg metabolic live weight (LW)) during the late part of the growing period on carcass fat scores (data in I–III). LIR vs. LSR = low increased energy intake vs. low steady energy intake, LDR vs. LSR = low decreased energy intake vs. low steady energy intake, HIR vs. HSR = high increased energy intake vs. high steady energy intake, HDR vs. HSR = high decreased energy intake vs. high steady energy intake (I), I = increased energy intake vs. A = steady energy intake, D = decreased energy intake vs. A = steady energy intake and (II) (II) and IC = increased energy intake vs. SC = steady energy intake, DC = decreased energy intake vs. SC = steady energy intake (III).

Overall, effects of compensatory growth on carcass classification are variable. The conflicting results may originate partly from differences in severity and duration of the growth restriction, duration of realimentation and genetic background of the animals (Hornick et al. 2000). Steen & Kilpatrick (2000) concluded that reducing slaughter weight is the most effective strategy for reducing carcass fatness. The data included in this thesis support this viewpoint because the highest fat scores were associated with the highest carcass weights (III). Periodic energy intake was not very effective, but represented, however, a potential strategy to decrease fat scores.

3.5. Effects of energy intake on meat quality

Feeding strategy is a management option that is used to influence an animal's performance and meat quality. The challenge is that many factors, including breed, sex, feeds, energy intake, growth rate, duration of growing and finishing period, age and carcass fatness and conformation, are able to affect meat quality (Matthews 2011). In the feeding experiments it is not possible to standardise all factors that affect meat quality.

Therefore, interpretation of the results and comparing them with those from other experiments can be complex (Priolo et al. 2001).

Based on the literature, it is challenging to influence meat quality through modifying diets. Sinclair et al. (2001) suggested that there are limited possibilities to improve beef eating quality by increasing growth rate through dietary means, by developing practical diets. Keady et al. (2017) found that when the realimentation period after restricted feeding lasted 200 days, it had no effects on most meat quality characteristics, in accordance with results reported in this thesis (IV). Results in this thesis also demonstrate the ability of growing bulls to adapt to different feeding regimes without major effects on meat quality, but it is simultaneously highlighted that it is a challenge to alter beef quality by feeding alternative diets (IV).

3.5.1. Effects of energy intake on meat tenderness

Tenderness is generally considered to be the single most important quality characteristic of beef. Effects of energy intake on meat quality vary (Table 5). Based on the data reported in this thesis, feeding intensity did not affect meat tenderness when it was measured objectively by shear force (IV: L vs. H). When tenderness was assessed through sensory analysis, higher energy intake improved tenderness. According to Keady et al. (2017), based on the moderate negative association between objectively measured shear force and subjectively measured sensory analysing, shear force may not always be a reliable indicator of tenderness as perceived by the consumer.

Table 5. The effects of energy intake on meat quality in growing and finishing steers and bulls.

		Energy intake strategy		Total duration of exp.	Restricted/total duration of exp.	Age at slaughter		Carcass weight, kg		Carcass fatness	Meat fat content	Shear force	Sarcomere length	Lean colour	Meat tenderness	Meat juiciness	Meat flavour
Reference	Gender	Steady vs. increased	Lower vs. higher	Steady/lower energy intake	Increased/higher energy intake	Steady/lower energy intake	Increased/higher energy intake	Steady/lower energy intake	Increased/higher energy intake	Increased/higher energy intake compared to steady/lower energy intake							
Aberle et al. (1981)	Steers	X		210 d	77/217 d	455 d	458 d	287	287	NS[1]	NR[2]	+4% NS	-1% NS	NS	-2% NS	+1% NS	+3% NS
Aberle et al. (1981)	Steers	X		210 d	153/223 d	455 d	467 d	287	245	Decreased	NR	+10% NS	0% NS	NS	-10% NS	-2% NS	-2% NS
Aberle et al. (1981)	Steers		X	230 d	210 d	471 d	455 d	199	287	Increased	NR	-36%	2% NS	NS	+82%	+9% NS	+14%
Fishell et al. (1985)	Steers		X (treatments T-1 vs. T-2)	120 d	120 d	NR	NR	158	242	Increased	NR	-14% NS	+4% NS	NR	+10%	+5% NS	NR
Keady et al. (2017)	Steers	X		299 d	99/200 d	NR	NR	373	350	Tended to decrease	-12% NS	+31%	NR	a[3] -5%	-9% NS	-1% NS	-1% NS
Moloney et al. (2008a) (exp. 1)	Steers	X		126 d	35/91 d	NR	NR	356	364	NS	-28% NS	Day 2: 0% NS	-1% NS	NS	Day 2: -9% NS	Day 2: -9%	Day 2: -2% NS
Moloney et al. (2008a) (exp. 2)	Steers	X (treatments control vs. CD112)		154 d	112/84 d	NR	NR	335	357	Increased	-9% NS	Day 2: +28%	-1% NS	Day 2: a -7%	NR	NR	NR
Moloney et al. (2008a) (exp. 2)	Steers		X (treatments control vs. CD0)	154 d		NR	NR	335	326	Increased	-2% NS	Day 2: +50%	-5%	Day 2: a -8%, b[4] -10%	NR	NR	NR
Moloney et al. (2008b)	Steers	X		17 w	8 /1 w transition/8 w	22.5 mo	22.5 mo	300	303	NS	-15% NS	Day 2: +22% NS	+1% NS	Day 2: NS	Day 2: -2% NS	Day 2: -11% NS	Day 2: -2% NS
Nuernberg et al. (2005)	Bulls		X (treatments German Holstein)	NR	NR	732 d	594 d	NR (slaughtered at LW[5] 620 kg)	NR (slaughtered at LW 620 kg)	NR	+16% (marbling)	Day 12: -23%	NR	L[6] +13%	+19% NS	+2% NS	-4% NS
Pesonen et al. (2013)	Bulls		X (treatments no rapeseed meal, Charolais)	336 d	306 d	NR	NR	406	438	Tended to increase	+22% NS	-3% NS	NR	Day 14: L +3%	+5% NS	+4% NS	-4% NS
Sami et al. (2004)	Bulls		X	100 d	100 d	18 mo	18 mo	324	358	Increased	+33%	+9% NS	+1% NS	NS	-13% NS	-4% NS	-1% NS
Sami et al. (2004)	Bulls		X	138 d	138 d	19 mo	19 mo	351	385	Increased	+75%	+7% NS	-2% NS	NS	+9% NS	+3% NS	+11% NS
Sinclair et al. (2001)	Steers	X		20 w	10 /10 w	19 mo	19 mo	286	310	NS	NR	-1% NS	NR	NR	+1% NS	+5%	+1% NS
Sinclair et al. (2001)	Steers		X	20 w	20 w	19 mo	19 mo	286	320	NS	NR	-11% NS	NR	NR	+5% NS	+5%	+2% NS
Therkildsen et al. (2008)	Bulls	X		132 d	91/41 d	302 d	304 d	208	157	NR	-42% NS	Day 2: -2% NS	NR	NS	Day 7: -21%	NR	NR
IV	Bulls		X	434 d	405 d	515 d	487 d	285	295	Tended to increase	+22%	0% NS	-7% NS	NS	+8%	+1% NS	+1% NS
Mean											**5**	**4**	**-1**	**NR**	**5**	**1**	**1**
Standard deviation											±33	±21	±3	NR	±24	±6	±5

[1] Not significant difference; [2] Not reported; [3] Redness; [4] Yellowness; [5] Live weight, [6] Lightness.

Generally, it is assumed that high energy intake and high growth rate during the finishing period improve meat quality, especially tenderness (Aberle et al. 1981, Fishell et al. 1985, Purchas et al. 2002, Therkildsen et al. 2002, Nuernberg et al. 2005). It is hypothesized that there is a relationship between the growth rate and protein synthesis and degradation (protein turnover) and it affects meat tenderness, as reviewed by Andersen et al. (2005). Protein degradation in the living muscle is associated with the activity of proteolytic enzymes and the same enzymes are involved in the development of meat tenderness post mortem (Koohmaraie et al. 2002, Therkildsen 2005). This seems to be the link between feeding strategy and tenderness within specific muscles (Therkildsen et al. 2008). However, there is also evidence that increased energy intake and LWG pre-slaughter did not affect meat tenderness (Sinclair et al. 2001, Sami et al. 2004, Juniper et al. 2005, Moloney et al. 2008a; exp. 1) or even decreased it (Keady et al. 2017). The differences may partly result from the differences in LWG pre-slaughter, age at slaughter and carcass fatness between various experiments.

Greater intramuscular fat content, but also higher LWG, may have affected improved meat tenderness (IV). It is generally agreed that increased intramuscular fat influences meat quality positively, particularly flavour, juiciness, tenderness and overall acceptability (Hocquette et al. 2010). In the experiment of Nian et al. (2017) intramuscular fat was positively correlated with initial tenderness assessed using sensory analysis. Intramuscular fat content may also improve tenderness by decreasing resistance to shear force (Wood et al. 1999). Keady et al. (2017) reported a negative correlation between intramuscular fat and shear force. The lack of effects on shear force may be a consequence of relatively small differences in LWG (L 1059 vs. H 1158 g/d) and fat content (L 43 vs. H 53 g/kg) of LL (IV). Neither feeding intensity nor periodic energy intake had an effect on sarcomere length, consistent with results from other experiments (French et al. 2001, Purchas et al. 2002, Sami et al. 2004), which may partly explain why no differences in shear force were found. Muscles of longer sarcomere length have lower shear force (Weaver et al. 2008) and meat tenderness increases (Koohmaraie 1996).

Increasing energy intake decreased slaughter age but did not affect shear force (IV), contrary to the typical hypothesis that increased slaughter age decreases meat tenderness (Shorthose & Harris 1990, Dransfield et al. 2003, Czyżak-Runowska et al. 2017). However, lower slaughter age may have contributed to the improved tenderness assessed by the taste panel. Nonetheless, Bureš & Bartoň (2012) reported that meat tenderness was positively influenced by age (14 vs. 18 months) at slaughter when assessed by a sensory panel. They concluded that it was at least partly attributable to differences in intramuscular fat, which increased with age and may have overridden the effect of age as such. In the data included in this thesis, increased fat content of LL reflected feeding intensity rather than age (IV).

Periodically restricted energy intake decreased tenderness when it was assessed by a taste panel and compared with steady energy intake (IV: IR and DR vs. SR). The reason for this is unclear and the result does not support the hypothesis that compensatory growth increases the tenderness of beef. Decreased tenderness may partly result from the lower carcass fatness. A positive correlation between carcass fatness and muscle tenderness was found in earlier studies (Dolezal et al. 1982, May et al. 1992) and a negative correlation between carcass fat score and shear force in the data of this thesis support this (IV). Sufficient fat cover insulates the carcass and slows post-mortem chilling, in which case cold-induced muscle shortening decreases and muscle tenderness improves (Wood et al. 1999, Fiems et al. 2000, French et al. 2001). The results reported in this thesis (IV) are in partial agreement with those of Moloney et al. (2008b), who concluded that an increase in pre-slaughter growth rate does not increase tenderness. In the experiment of Keady et al. (2017), the meat of compensatory growth steers had higher shear force values and lower tenderness assessed using sensory analysis when compared with that of continuously grown steers. However, they concluded that it is unlikely that an untrained consumer would detect decreased tenderness resulting from compensatory growth.

High ultimate pH may decrease beef tenderness (Purchas 1990) and it is related to the level of glycogen in the muscles at slaughter. Feeding intensity did not affect ultimate pH of meat although energy intake differed significantly (IV: L vs. H). Immonen et al. (2000) reported that in the repleted state, muscle glycogen concentration was not markedly affected by dietary energy density. This indicates that energy intake was probably high enough in all treatments to decrease pH adequately (IV).

3.5.2. Effects of energy intake on meat juiciness, flavour and colour

It is generally accepted that juiciness and flavour are positively related to intramuscular fat content: very low levels of intramuscular fat resulting in dry and less-tasty beef (Hocquette et al. 2010). According to the review of Muir et al. (1998), when grass-fed and concentrate-fed animals were compared at similar weights and/or fat cover, in most cases feed type had no effects on juiciness.

For beef the minimum amount of intramuscular fat needed is about 3-4% to meet acceptable consumer requirements (Savell & Cross 1986). This was in line with the data reported in this thesis for all treatments (IV). However, although feeding intensity increased intramuscular fat content, it did not affect juiciness or flavour (IV: L vs. H). This may be explained by the relatively small difference in carcass and meat fat content, in agreement with French et al. (2001) and Keady et al. (2017). According to Hocquette et al. (2010), a significant relationship between intramuscular fat and sensory quality traits is often evident only when there is substantial variation in intramuscular fat content.

It is well established that muscle colour is generally darker (low L* and a* values) in forage-fed than in concentrate-fed animals (Priolo et al. 2001, Caplis et al. 2005, Nuernberg et al. 2005). However, forage-intensive feeding did not increase darkness of the meat and the explanation for this is unclear (IV: L vs. H and DR vs. IR). Some earlier experiments also reported similar results (French et al. 2000, 2001, Sami et al. 2004).

Typically, concentration of myoglobin increases with age and beef becomes darker (Muir et al. 1998, Priolo et al. 2001). Increased subcutaneous fat and intramuscular fat may improve lean meat colour (Muir et al. 1988). However, Priolo et al. (2001) concluded that the effect of carcass fatness seems not to be extremely important for meat colour. The lack of the difference in colour values L* and a* may result from not only the rather small differences in age of the animals (IV: L vs. H 29 d) but also from low carcass fat scores and meat fat contents.

It seems that within the range of diets tested during the work reported in this thesis, significant effects on juiciness, flavour and meat colour are unlikely.

4. Conclusions and practical applications of the results

4.1. Concluding remarks

1. Growing dairy bulls can achieve moderate to good performance when highly digestible grass silage is used as a sole feed. Increasing energy intake by increasing concentrate allowance is a method to improve growth rate further and decrease the length of the growing and finishing period of dairy bulls resulting in improved efficiency of beef production, but simultaneously carcass fatness increases.
2. Restricted DMI during the whole growing period did not improve feed conversion rate.
3. Restricted energy intake during the entire growing period may decrease LWG and carcass fatness and reduce meat tenderness.
4. Increased or decreased energy intake during the late part of the growing period resulted in different growth patterns but average growth rates did not differ significantly over the entire growing period.
5. Periodic energy intake strategies demonstrated the great ability of growing bulls to adapt to different feeding regimes without major effects on their overall productive performance. Reduction in carcass fatness may be possible.
6. Compensatory growth could be demonstrated when energy intake was increased after a period of restricted energy intake.
7. During compensatory growth LWG increased and there was a tendency of improved feed conversion rate. However, over the whole growing period, compensatory growth did not improve beef production parameters or meat quality when compared with steady energy intake.
8. Different energy intake strategies demonstrated the ability of growing bulls to adapt to different feeding regimes without detrimental effects on meat quality. On the other hand, there seem to be limited possibilities for influencing beef quality of animals on *ad libitum* grass silage based diets supplemented with barley at practically feasible levels.
9. Based on the results reported in this thesis, higher slaughter weight and increased energy intake produced higher fat scores and indicated that it is challenging to produce heavy low-fat carcasses without impairing the eating quality of beef.
10. At the farm level, if there is a temporary lack in the amount and/or quality of feeds offered, or feed prices fluctuate, manipulated growth altering the amount and/or quality of feeds offered may be used successfully. A prerequisite for this is that during part of the growing period energy intake increases so that the animals have a possibility to compensate for the growth. The usefulness of this kind of feeding strategy may be limited to situations where annual feed supply or prices of feeds vary substantially. The results can be used in evaluating novel beef production methods to improve the profitability under variable conditions.

4.2. Further research

1. The optimum carcass weight varies depending on set priorities. Typically, LWG and feed efficiency decrease and carcass fatness increases by increasing carcass weight. Biologically it would be efficient to slaughter animals at low carcass weight. High LWG, short growing time and slaughtering before LWG decreases substantially are beneficial from an environmental point of view. When targeting high slaughter weight, the environmental load increases. However, if the pricing system of slaughterhouses favours heavy carcasses, it may be more profitable to rear animals to high carcass weights. Further research is required to optimize carcass weight from biological, environmental and economic points of view, and in the case of e.g. Finland, also consider the amount of beef produced domestically.
2. Duration of restricted feeding and realimentation period may affect performance of growing animals. In the experiments reported in this thesis, duration of restricted feeding and realimentation period were rather long and further studies are needed to assess the effects of shorter restriction (approx. 3 mo) and realimentation (approx. 4 mo) periods on performance of dairy bulls.
3. The total number of the bulls was 118 in the three experiments of this thesis. This dataset, comprising all three experiments, could be used for modelling the effects of duration and severity of restriction of LWG on carcass fatness.
4. There is lack of domestic beef in Finland and new methods should be established to increase beef production. One method would be to increase and improve growing of dairy heifers for beef. The challenge is that beef production efficiency of growing heifers is not as high as that of bulls. The easily increased fatness of carcasses is a challenge and consequently heifers must be slaughtered at rather low slaughter weights. Restricted or periodic energy intake could be an option to decrease fatness of heifers and enable growing them to higher carcass weights. This method could also be utilized when heifers are reared for milk production.
5. To improve economic profitability of beef production, it is important to take into account the economic effects of different feeding strategies. The economics of restricted energy intake and periodic growth depend on many factors, the most important being feed prices, total feed intake and animal performance. Economic evaluation of continuously or periodically restricted energy intake strategies should be conducted.

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