HELSINGIN YLIOPISTON KOTIELÄINTIETEEN LAITOKSEN JULKAISUJA
UNIVERSITY OF HELSINKI, DEPT. OF ANIMAL SCIENCE, PUBLICATIONS
60

Effect of feeding before puberty and during gestation on milk production potential and body development of dairy replacement heifers

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Academic dissertation

To be presented, with the permission of
the Faculty of Agriculture and Forestry of the University of Helsinki,
for public criticism in Auditorium B2, Viikki,
on June 8th 2001, at 12 o'clock noon

Helsinki 2001

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ISBN 952-10-0027-9(nid.)
ISBN 952-10-0028-7 (PDF)
ISSN 1236-9837
Helsinki 2001
Yliopistopaino

Mäntysaari, P. 2001.
Effect of feeding before puberty and during gestation on milk production potential and body development of dairy replacement heifers. University of Helsinki, Department of Animal Science. Publications 60. 44p. + 5 encl.

ABSTRACT

This thesis consists of studies concerning the effect of feeding before puberty and during gestation on pre-pubertal mammary growth, subsequent milk yield and body development of replacement heifers. Publications I and II investigated the effect of high (daily gain 850 g) or low (daily gain 650 g) levels of feeding with urea or rapeseed meal as protein supplements on growth and mammary development of pre-pubertal Finnish Ayrshire heifers. It was shown that heifers on the high feeding level had less mammary parenchymal tissue compared with heifers fed lower levels of feeding. The amount of mammary parenchymal tissue was positively correlated with plasma growth hormone (GH), but not plasma IGF-I concentrations. Furthermore, no correlation existed between plasma GH and IGF-I concentrations. On a high feeding level Finnish Ayrshire heifers under 220 kg live weight had a higher growth rate when rapeseed meal rather than urea was used as protein supplement on a hay-barley based diet. For pre-pubertal slaughter heifers it appears that urea is not suitable source of supplementary nitrogen for hay and barley based diets. Instead, protein source had no effect on pre-pubertal mammogenesis at either feeding level.

The effect of feeding intensity during gestation on subsequent milk yield was investigated in publication IV. It was shown that during the first six months of gestation daily gains of 800 g, or higher, had no effect on subsequent milk yield but resulted in greater fat deposition and reduced postpartum intake potential. On the other hand, during the last trimester a high level of feeding (live weight change over 800 g/d) was advantageous in attaining maximal milk production.

The effect of feeding on body development of pre-pubertal (publications I and III) and pregnant heifers (publication IV) was examined. It was observed that pre-pubertal heifers fed on a low level of feeding had higher wither heights at puberty than heifers fed more intensively. Results suggest that pre-pubertal wither height is determined more by age than live weight. Heart girth was shown to be a good predictor of pre-pubertal live weight. During pregnancy high (gain 800 g/d) compared with moderate (gain 650 g/d) planes of nutrition had no effect on body size (wither height, body length) but increased heart girth, hip width and body condition score of primiparous cows at parturition.

Live weight at parturition and daily gain before and after breeding had positive genetic correlations with first lactation milk yield within field data reported in publication V. Therefore, it appears that genetic selection for higher milk production will gradually lead to higher genetic growth potential. Such changes need to be taken into account in future recommendations of daily gain acceptable for pre-pubertal dairy replacement heifers.

Based on the current studies it was suggested that for pre-pubertal Finnish Ayrshire heifers daily gains above 650 to 700 g have detrimental effects on pre-pubertal mammogenesis. Dietary protein source has no effect on mammary growth. During the first six months of gestation a moderate feeding level is recommended to avoid excessive fat deposition and ensure maximal postpartum intake. However, during the last trimester intensive feeding is necessary in attaining maximal milk production.

ACKNOWLEDGEMENTS

Experiments documented in this thesis were conducted at MTT Agrifood Research Finland in Jokioinen. I want to extend my sincere thanks to the former and present Heads of the Animal Nutrition, Professor Vappu Kossila and Professor Tuomo Varvikko, for providing the opportunity to conduct this research within the department.

I wish to express my unreserved gratitude to Professor Liisa Syrjälä-Qvist at the Department of Animal Science, University of Helsinki for her unfailing encouragement and guidance, particularly during the last stages of this work. My special thanks go to Professor Pekka Huhtanen for his endless support, inspiring discussions and valuable comments on individual articles and thesis text. I also wish to thank Dr. Hannele Khalili for her support and pertinent comments concerning this thesis manuscript.

I sincerely wish to express my deepest thanks to Dr. K. Lønne Ingvartsen and Dr. Kris Sejrsen for their helpful guidance on heifer and mammary research. Our collaboration has been invaluable and highly encouraging.

I am indebted to the referees appointed by the Faculty, Professor Timo Soveri and Docent Ilmo Aronen for their comments and useful suggestions for improving the manuscript.

To the staff of Lintupaju experimental farms I extended my deepest appreciation for skilled care of experimental animals. Acknowledgements are also extended to Lic.Phil. Vesa Toivonen, as well as the entire laboratory staff in Animal Nutrition. I also wish to thank all my colleagues and staff in Animal Nutrition for their help and support during these years. I express my thanks to Dr. Kevin Shingfield for thesis linguistic revision.

For financial support during various stages of this research I would like to thank the Academy of Finland, the Agricultural Research Foundation of August Johannes and Aino Tiura, and the Finnish Cultural Foundation.

Finally, I want to express my warmest thanks to my husband Esa, for creative discussions, valuable advice and loving support. I am also grateful to him for taking full responsibility of house keeping during the last months of this work. Special thanks go to my lovely children Juho, Mari, and Lauri, for their patience and warm hugs during these years. I am also grateful to my parents for their encouragement to start a career in Animal Science.

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original publications subsequently referred to in the text by their Roman numerals:

I Mäntysaari, P. 1993. The effects of feeding level and protein source of the diet on growth and development at slaughter of pre-pubertal heifers. *Acta Agriculturæ Scandinavica, Section A, Animal Science. 43: 44-51.*

II Mäntysaari, P., Ingvartsen, K.L., Toivonen, V., and Sejrsen, K. 1995. The effects of feeding level and nitrogen source of the diet on mammary development and plasma hormone concentrations of pre-pubertal heifers. *Acta Agriculturæ Scandinavica, Section A, Animal Science. 45: 236-244.*

III Mäntysaari, P. 1996. Predicting body weight from body measurements of pre-pubertal Ayrshire heifers. *Agricultural and Food Science in Finland. 5: 17-23.*

IV Mäntysaari, P., Ingvartsen, K.L., and Toivonen, V. 1999. Feeding intensity of pregnant heifers. Effect of feeding intensity during gestation on performance and plasma parameters of primiparous Ayrshire cows. *Livestock Production Science. 62: 29-41.*

V Mäntysaari, P., Ojala, M., and Mäntysaari, E. 2001. Measures of before and after breeding daily gains of dairy replacement heifers and their relationships with first lactation milk production traits. *Submitted to Livestock Production Science.*

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The first experiment (I and II) was carried out during 1990-91, and the second experiment (IV) during 1994-96 at MTT, Agrifood Research Finland. Publication III was based on growth data collected from heifers in experiments I and II during 1990-94. Publication V was based on field data collected during 1994-95.

The author was responsible for planning and conducting the experiments in addition to the collection of data and experimental samples. Dr. K.L. Ingvartsen and Lic.Phil. V. Toivonen were responsible for chemical analysis of collected samples. The author was responsible, with the assistance of co-authors, for the analysis of data reported in I, II, III, and IV and participated in the analysis of data in V. All manuscripts were prepared by the author and revised according to the comments and suggestions of respective co-authors.

ABBREVIATIONS

AAT	amino acids absorbed from the small intestine
ADF	acid detergent fibre
AI	artificial insemination
Ay	Ayrshire
BCS	body condition score
BHBA	ß-hydroxybutyrate
CP	crude protein
DFFT	dry fat free tissue
DM	dry matter
FFA	free fatty acids
Fr	Friesian
GH	growth hormone
IGF-I	insulin like growth factor-I
k_l	efficiency of utilisation of metabolisable energy for milk production
LW	live weight
NDF	neutral detergent fibre
NE	net energy
ME	metabolisable energy
PBV	protein balance in the rumen
RDM	Red Danish Milk Breed
RSM	rapeseed meal
SDM	Danish Black and White

CONTENTS

1. INTRODUCTION

The goal of heifer rearing is to produce healthy animal with high milk production potential at minimum cost. The genetic capacity of the animal sets the platform for subsequent performance. The extent to which this potential is realised, depends on the feeding and management regimen during rearing. Replacement costs can be decreased by reducing the duration of rearing. This is equivalent to more intensive feeding in an attempt to achieve the puberty at an earlier age. However, this can lead to decreased performance due to detrimental effects on mammary development.

The effect of heifers feeding on subsequent performance as primiparous cows was reported as early as 1915 by Eckles who noticed that intensively fed heifers produced somewhat less than the moderately fed heifers (ref. Schultz 1969). In 1946 Herman and Ragsdale (1946), measured lower than expected milk yields on the first, second and third lactations for rapidly reared heifers. In the summary of Hansson (1956) milk yield of primiparous Swedish Red cows reared at 40, 60, 80, 100, 120, or 140% of Swedish feeding standards declined progressively from 3328 kg fat-corrected milk for the 60% group to 2635 kg for the 140% group. Swanson (1960) used seven pairs of identical dairy twins and noted, that intensively fed animals produced 15% less milk during the first lactation than those fed slightly below recommended levels. The production differences also persisted through the second lactation. In contrast, no effect of plane of nutrition on milk yield of Holstein heifers fed 65, 100 or 120 % of Morrison’s TDN standards was observed in the Cornell data (Reid et al. 1957).

Swanson (1960) suggested that the reduction in milk production potential of intensively fed heifers was due to an abnormal udder structure with some areas lacking developed secretory tissue. Since milk production is primarily determined by the number of secretory cells in the mammary gland (Knight et al. 1984, Tucker 1987, Sorensen et al. 1998), it is evident that abnormal development of secretory tissue will negatively affect milk yield. Therefore, in studies where the effect of plane of nutrition during rearing on subsequent milk yield has been investigated, mammary growth and development during rearing have also been used as determinants of milk production potential.

It has been shown that there are different phases in the growth and development of the mammary gland (Sinha and Tucker 1969). Phases are related to the stage of heifer maturity. Effect of nutrition on mammary development varies between phases. This was noticed in the study of Swanson (1960), where the heifers gaining extra fat during early stage of growth had less developed udders than animals depositing fat around one year of age. Later studies have also shown that the pre-pubertal period is central for nutritional manipulations of mammary growth (Sejrsen et al. 1982).

Most studies examining the effect of nutrition during the pre-pubertal phase have documented the effect of feeding level (energy intake) on milk production. In Finland, heifers typically receive grass silage supplemented with cereal concentrates. Consequently the majority of dietary protein is rapidly and extensively degraded in the rumen. At the time when the present studies were conducted little attention had been focused on the quality of dietary protein. However, there was some evidence in rats that dietary protein intake may influence mammary development (Park et al. 1987). During recent years the effects of protein intake and protein quality on mammary growth has received greater attention (Van Amburgh et al. 1998b, Whitlock et al. 1999, Dobos et al. 2000, Radcliff et al. 2000).

Feeding during gestation can affect subsequent milk production potential of heifers by influencing mammary growth, live weight (LW) at parturition, body size and postpartum feed intake. Heifers fed a high plane of nutrition during gestation have a higher LW which has been shown to be positively correlated with milk production during the first lactation (Ingvartsen et al. 1988, Foldager and Sejrsen 1991). However, excessive nutrition prepartum can reduce postpartum dry matter (DM) intake (Grummer et al. 1995). Both the extent and duration of intensive feeding and the plane of nutrition before gestation have an influence. Changes in feeding intensity during gestation may also affect first lactation milk production (Park et al. 1989, Choi et al. 1997). However, the effects of alternating feeding intensity during gestation have not been extensively studied.

With respect to milk production potential of primiparous cows the optimum plane of nutrition during rearing (pre-puberty, post-puberty and gestation) is dependent on breed, and probably the genetic potential within breed. Most of the rearing studies examining the effect of feeding on pre-pubertal mammary development or subsequent milk yield have been conducted with Holstein heifers as experimental animals. No studies conducted with Ayrshire heifers have been reported in the literature. It is also notable that animal genetics and management regimens change over the time, such that contemporary studies are required. Prior to the current research, no studies concerning the effect of feeding during rearing on mammary development and subsequent milk production of Finnish primiparous cows had been conducted.

The objectives of the experiments documented in the current thesis were to examine the effect of feeding level (pre-pubertal after 3 months of age and during gestation) and dietary protein quality (pre-pubertal) on growth, body measurements, mammary growth and subsequent milk production of Finnish Ayrshire heifers. In addition, relationships between pre-pubertal body measurements and LW were assessed with the aim of developing a prediction model to be used for monitoring LW and growth. The ultimate goal of these studies was establishing the fundamental principles necessary for attaining maximal production potential of dairy replacement heifers.

2. MATERIAL AND METHODS

2.1. Animals and experimental periods

Finnish Ayrshire heifers were used in all studies except V, which also included data collected from Friesian heifers (Table 1). In the first experiment (I, II and partly III), the average age and LW of heifers at the beginning of the experiment was 88 days and 86 kg, respectively. All the heifers were slaughtered at approximately 220 kg live weight, at an average age of 293 and 249 days, for low and high feeding levels, respectively (I).

Data used in publication III originated from two sources. IIIa consisted measurements of body characteristics from heifers in experiment I, and IIIb from 51 Ayrshire heifers, 40 of which were used in a subsequent gestation study (IV). Data for IIIb was collected during pre-pubertal period from 3 months of age and 98 kg LW to 9.5 months of age and 225 kg LW. In the experiment IV, 40 pregnant Ayrshire heifers were blocked by expected calving date (three blocks) and assigned randomly to one of four treatments during the fourth week of gestation.

Table 1. Experimental animals and treatments for studies I – V.

Publ.	**Animals**	**N**	**Experimental period**	**Feeds**	**Feeding procedure**
I	Ayrshire heifers	24	Live weight: 86 – 220 kg	Hay, barley, minerals, vitamins and RSM[1] or urea	Low (650 g/d gain) or high (850 g/d gain) feeding intensity with RSM or urea as a protein supplement.
II	Ayrshire heifers	24	See I	See I	See I
III	Ayrshire heifers	IIIa 24 IIIb 51	IIIa See I; IIIb Live weight: 98 – 225 kg	IIIa See I; IIIb Grass silage, hay, barley (LW[2] <200 kg), RSM (LW < 130 kg), and minerals and vitamins.	IIIa See I; IIIb Reared to gain 650 g/d.
IV	Ayrshire heifers/ Primiparous cows	40	Rearing: 2 month of gestation – 2 weeks prepartum. Lactation: Parturition - 160 d of lactation	Rearing: Grass silage, barley, minerals and vitamins. Lactation: Grass silage and a concentrate mixture of barley, oats, RSM, molassed sugar beet pulp and minerals and vitamins.	Rearing: Treatments[3] MM, MH, HM and HH. Lactation: Concentrate mixture 7.5 kg/d and silage fed *ad libitum.*
V	Ayrshire and Friesian Heifers / primiparous cows	Ay 2194, Fr 738, Relatives 7215	Rearing: Birth – parturition Lactation: First lactation	Field study, feeds varied across herds	Varied across herds.

[1] RSM= rapeseed meal, [2] LW = live weight, [3] M= expected daily gain 650 g/d; H= expected daily gain 850 g/d; period1=2-6 months of gestation; period 2= 7-9 months of gestation.

Publication V was based on data collected from 2194 Ayrshire and 738 Friesian heifers and of their 7215 relatives. Body measurement data was collected by 31 artificial insemination (AI) technicians from 6 AI co-operatives. Thus, experimental measurements closely reflect the heifer population in Finland.

2.2. Experimental procedures and treatments

Experiment I was designed to study the effect of feeding level (L=low and H=high) and dietary protein source, rapeseed meal (RSM) or urea on heifer pre-pubertal growth and development. Experimental treatments were applied according to a 2x2 factorial design. Diets were based on hay and barley supplemented with RSM or urea. For L diets hay intake was limited to 3.0 – 3.5 kg/d, whereas heifers fed H diets were offered hay *ad libitum.* Based on the assumption that animals would consume 3 kg hay a day, concentrate intake was adjusted to satisfy energy requirements for daily gains of 550 or 850 g. Diets were reformulated every four weeks according to LW. A dietary crude protein (CP) content of 130 g/kg DM was targeted. For RSM and urea supplemented diet approximately 0.30 and 0.20 of total CP intake was derived directly from protein supplements, respectively.

Paper II was based on mammary and hormone data collected from the heifers in experiment I. The aim of study II was to evaluate the effect of feeding level (L or H) and dietary protein source (RSM or urea) on mammary development of pre-pubertal heifers. In addition, the influence of pre-pubertal feeding on plasma hormone concentrations and their relationship with mammary growth was also assessed.

Study III was conducted to investigate the value of body measurements for the prediction of LW of pre-pubertal Finnish Ayrshire heifers. Prediction of LW was based on data collected from IIIb which consisted of measurements of pre-pubertal heifers reared to gain 650 g/d. Feeding of heifers was based on grass silage and hay (about 0.5 kg/d). When heifer LW was below 200 kg, the diet included barley. For heifers below 130 kg LW, RSM was also included in the diet. Diets had an average CP content of 133 g/kg DM. The effect of plane of nutrition on the prediction of LW was evaluated using data of IIIa.

In study IV the effect of feeding intensity at different stages of pregnancy on the performance of primiparous Ayrshire cows was investigated. Gestation was divided into two periods:

months 2 to 6 (days 29 – 182 of gestation; period 1) and months 7 to 9 of pregnancy (days 183 – 266 of gestation; period 2). During period 1, half the heifers received a medium (M) and the other half a high (H) plane of nutrition. For period 2, half the heifers fed on both planes of nutrition were changed to the other plane giving four experimental treatments MM, MH, HM and HH. During gestation heifers were fed restricted amounts of grass silage, barley and a mineral and vitamin supplement to meet requirements for 650 and 850 g daily gain for M and H, respectively. Diets contained 136 g CP/kg DM. During the last two weeks before expected calving date all heifers received the same diet. Concentrates during transition were fed at increasing amounts reaching 5 kg/d at parturition. After calving concentrate feeding was gradually increased to 7.5 kg/d and remained constant until 160 days in lactation. From two weeks before parturition to the end of the experimental period animals were offered grass silage *ad libitum*.

Study V was based on data collected from 2932 herds. Data included body measurements and milk recording data alone, since no information of feeds and feeding practices were available. Data reported in V was used to estimate environmental and genetic relationships between average daily gain before and after breeding, LW at parturition, age at calving and milk production traits of Ayrshire and Friesian heifers.

More detailed descriptions of the experimental procedures used are outlined in articles I-V.

2.3. Data recording and sampling

In feeding trials daily feed intakes were measured through out the experiments (Table 2). Both LW and body measurements presented in I, III and IV (gestation) were recorded every four weeks. During lactation (IV) cows were weighed once a week and body condition scores were assessed at the end of the experiment. In study V, growth was assessed through heart girth measurements. Heart girth was measured on the day of insemination by AI technicians and at parturition within the national milk recording scheme. Daily gains before and after breeding were calculated by difference using estimates of LW at insemination and calving. Birth and calving dates were obtained from the national milk recording scheme and birth weights were based on breed averages.

During the slaughter of experimental heifers in study II mammary glands were separated from the abdominal wall and divided into left and right halves. The right half was trimmed of skin, teats and lymph nodes and stored at –20 °C until analysed.

Plasma samples for the determination of urea and hormone concentrations in studies I and II were collected at 150 kg (I) and 210 kg (I and II) LW using catheters placed in a jugular vein a day before sampling. Blood samples were collected at 30 min intervals over a 6 h period (2 h before and 4 h after feeding). In study IV blood samples were taken 5 h after feeding from the coccygeal vein of each animal at 35, 28, 21, 16, 12, 8 and 4 days before due date and 0, 1, 3, 7, 14, 21, 28, 35, 42, 56, 84 and 112 days postpartum. Plasma and precipitated blood (for BHBA-analysis) samples were frozen and stored at –20 °C prior to chemical analysis.

In study IV milk yields were recorded daily and milk protein, fat, and lactose were analysed once a week. For study V, the milk yield and composition was derived from national milk recording data.

Table 2. Variables measured in studies I – V.

Publication	Variable measured
I	Feed intake, growth, body measurements, carcass quality, plasma urea concentration
II	Mammary growth and composition, plasma hormone concentrations
III	Body measurements, growth
IV	Feed intake, growth, body measurements, body condition scores, milk yield, milk composition, plasma hormone and metabolite concentrations
V	Growth (based on heart girth measurements), milk yield[1] and composition[1], LW[1] at calving, and age[1] at calving

[1] From national milk recording data.

2.4. Feed, mammary and blood analysis

Daily samples of feeds were pooled to give a composite 4-wk sample for proximate (I, IV), NDF (I, IV), ADF (I) and amino acid (RSM and barley, I) analysis. In study I, apparent *in vivo* digestibility of hay was determined by total faecal collection using wethers. Digestibility coefficients of other feeds were obtained from feed tables (Salo et al. 1990, Tuori et al. 1996). Feed metabolisable energy (ME) content (I and IV) was calculated according to Ministry of Agriculture Fisheries and Food (MAFF 1975) and net energy (NE) content (I and III) was based on starch equivalents according to Salo et al. (1990). Rumen degradability of feeds (I) was measured by the nylon bag technique (Vanhatalo et al., 1992) and effective protein degradability was calculated according to Ørskov and McDonald (1979). Amino acids absorbed from the small intestine (AAT) and protein balance in the rumen (PBV) were calculated according to Madsen (1985).

In II, frozen mammary glands were cut into 1 cm slices and divided into parenchymal and extra-parenchymal tissues based on colour. Parenchymal tissue was minced, and parenchymal dry fat-free tissue (DFFT) submitted for DNA and RNA analysis was prepared according to Anderson (1975). DNA and RNA concentrations were assessed using the methods of Martin et al. (1972) and Martin and Hodgson (1973), respectively.

In study I, plasma urea content was calculated as the difference in ammonia N concentrations in non-hydrolysed and urease hydrolysed samples. Ammonia N was determined as described by McCullough (1967) while BHBA was measured according to Hansen and Freier (1978). In study IV glucose and free fatty acids (FFA) were analysed using respective commercial kits (Peridochrom GOD-PAP/glucose; Boehringer Mannheim GmbH, and Waco Pure Chemical Industries, Ltd.). Plasma concentrations of GH, prolactin and insulin in studies II and IV and IGF-I in study II were measured by a double antibody radioimmunoassay. Concentrations of GH and IGF-I were determined according to Ingvartsen et al. (1995a). Prolactin was measured using a procedure similar to that used for GH. Insulin was measured with a Phaseseph Insulin RIA (Pharmacia Diagnostics, Uppsala, Sweden).

Detailed information of analytical procedures used is described in respective papers I-V.

3. RESULTS AND GENERAL DISCUSSION

3.1. Feeding during rearing and milk production potential of replacement heifers

3.1.1. Measuring milk production potential

In studies assessing the effect of plane of nutrition during rearing on subsequent milk production, milk production potential has been estimated either directly or indirectly based on measurements of mammary growth. The amount of mammary parenchyma and total DNA (an indirect measurement of cell number) and RNA (an index of metabolic activity) in parenchyma have been used, since milk yield is determined largely by the number of milk synthesising cells and their secretory activity (Knight et al 1984, Knight and Wilde 1987, Tucker 1987). Although cell number and cell activity contribute to lactation potential, cell number is ultimately the limiting factor (Knight et al. 1984, Tucker 1987, Sorensen et al. 1998). Development of the mammary ductal network during the pre-pubertal period is essential in attaining maximised milk production potential, since this provides an adequate framework for future development of ductal side branches at puberty and alveolar structure during gestation.

Mammary parenchyma only constitutes a small proportion of the total mammary gland in pre-pubertal heifers and is therefore difficult to measure in live animals. In most studies, experimental animals have been killed and the mammary glands have been removed and separated from the body for dissection and analysis (e.g. II, Sejrsen et al. 1982, Harrison et al. 1983, Capuco et al. 1995, Radcliff et al. 1997). Computer tomography-scanning for excited udders of heifers has also been used to estimate the amount of parenchyma (Sørensen et al. 1987). In some studies mammary gland development in pre-pubertal heifers has been measured in live animals by udder palpation, teat length and distance (e.g. around gland) measurements and with tissue biopsies (Swett et al. 1956, Stelwagen and Grieve 1990, Lammer et al. 1999). However, it has been shown that only a weak correlation exists between these measurements and the true amount of mammary parenchymal tissue in pre-pubertal heifers (Stelwagen and Grieve 1990, Withlock et al. 1999). In mature animals measurements of udder volume have provided a reasonable estimate of milk production potential (Linzell 1966, Fowler et al. 1990, Dewhurst et al. 1993). Fowler et al. (1990) used magnetic resonance imaging while Linzell (1966) used water subtracting and a plaster casting method to measure the udder volume of adult goats. Dewhurst et al. (1993) used a quick-setting polyurethane foam technique to measure the udder volume of dairy cows.

In study II, milk production potential of heifers was estimated by measurements of mammary tissue growth. In the current study the mammary gland was divided into parenchyma and extra-parenchyma tissue by dissection based on tissue colour, and concentrations of DNA and RNA in parenchymal tissue were subsequently determined. In studies IV and V, milk production potential was measured directly.

3.1.2. Overview of mammary growth and development

The growth and development of mammary glands occurs during several distinct phases. At birth, the mammary glands of the heifer calves consist of a restricted immature duct system and stroma (Tucker 1987). Before puberty, the mammary fat pad grows rapidly and ducts branch into the fat pad. During the first weeks of life mammary glands grow isometrically. At 2 to 3 months of age the glands start to grow at a faster rate than the rest of the body (Sinha and Tucker 1969). During allometric mammary growth DNA content of mammary tissue in Holstein heifers increases 3.5 times faster (3 to 9 months of age) than LW (Sinha and Tucker 1969). Between 10 and 12 months of age, the increase declines to 1.5 times that of LW. Allometric growth phase ends at the onset of puberty or shortly thereafter (Sinha and Tucker 1969).

After puberty mammary glands grow isometrically. Within the oestrus cycle most of the increase in mammary development occurs at oestrus while mammary development is generally lower during the luteal phase (Sinha and Tucker 1969). During gestation mammary growth is allometric. The growth of mammary parenchymal tissue increases exponentially throughout gestation. According to Swanson and Poffenbarger (1979) the rate of growth was approximately 25 % per month for parenchyma weight. During early gestation mammary growth involves enlargement and branching of ducts while the formation of alveoli does not start until mid-gestation (Swanson and Poffenbarger 1979). The final proliferation and differentiation of alveolar secretory cells occurs during the last trimester of gestation (Hollman 1974, Knight and Wilde 1993).

Mammary growth and development occurs under the influence of ovarian and pituitary hormones. Ovariectomy at an early age either abolishes or markedly reduces mammary development (Wallace 1953, Purup et al. 1993a). The role of oestrogen and GH has also been shown in studies where exogenous GH stimulated peripubertal mammary growth in intact heifers (Sejrsen et al. 1986), but has only minor effects in the absence of a functioning ovary (Purup et al. 1993a). In the classic studies of Lyons et al. (1958) oestrogen and GH increased duct growth, whereas progestins and prolactin stimulated lobulo-alveolar development in ovariectomized- adrenalectomized – hypophysectomized rats. Maximal mammary development was achieved using a combination of these four hormones and glucocorticoids (Lyons et al. 1958).

Despite exogenous GH is shown to increase milk production and mammary development in pre-pubertal ruminants (Sejrsen et al. 1986, Stelwagen et al. 1992, Stelwagen et al. 1993, Radcliff et al. 2000), there is little evidence that GH has a direct effect on the mammary gland (Woodward et al. 1994, Purup et al. 1999). It is thought that GH acts indirectly on pre-pubertal mammary gland, probably via IGF-I (Purup et al. 1993b, Purup et al. 1995). However, other factors are also involved. Recent studies have introduced the effects of both systemic and mammary specific production of growth factors that potentially mediate many of the effects of ovarian and pituitary hormones. Among these are insulin-like growth factors (IGF-I and IGF-II) and their binding proteins, transforming growth factors (TGFα and TGFβ) and epidermal growth factors (EGF) (Plaut 1993, Forsyth 1996, Weber et al. 2000).

3.1.3. Effect of plane of nutrition on mammary growth

3.1.3.1. Pre-pubertal plane of nutrition

In study II the effect of feeding level on mammary growth of pre-pubertal Ayrshire heifers was examined. The negative effect of a high plane of nutrition was demonstrated by a significant decrease in the total amount of mammary parenchyma when daily gain increased from 674 to 848 g a day. This is consistent with studies reported in the literature (Figures 1 and 2). In Figure 1 mammary growth is assessed by the total amount of dissected mammary parenchyma and in Figure 2 by the amount of total DNA in parenchyma. Based on Figures 1 and 2 it can be concluded that in most studies there is a clear tendency towards reduced total mammary parenchyma and total DNA in parenchyma with increases in feeding level (Sejrsen et al. 1982, Harrison et al. 1983, Petitclerc et al. 1984, Sejrsen et al. 1998, II). However, in some cases the reduction has not been significant (Capuco et al. 1995).

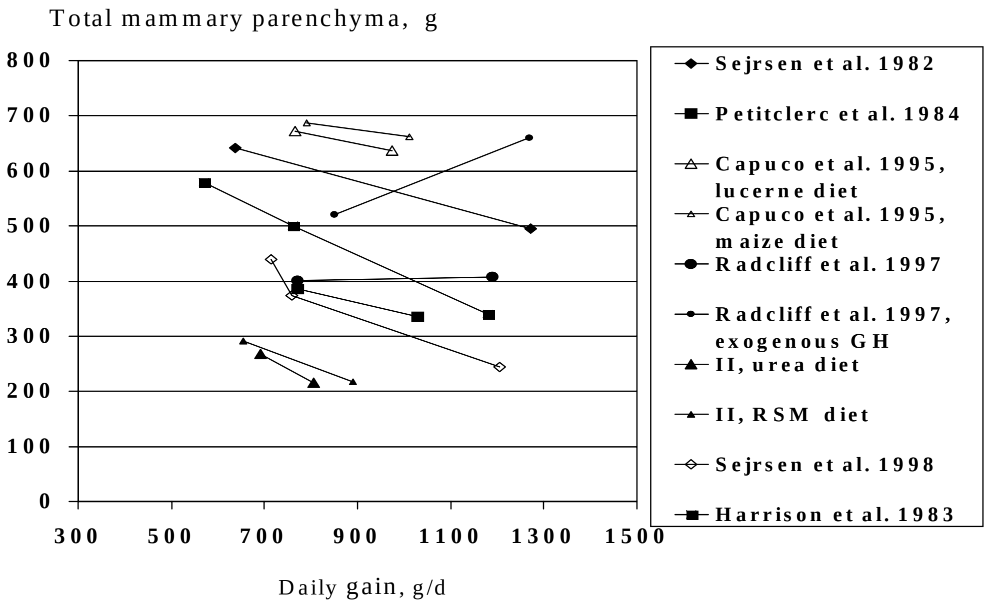


Figure 1. Relationship of pre-pubertal daily gain (g/d) and total mammary parenchyma (g) reported in the literature.

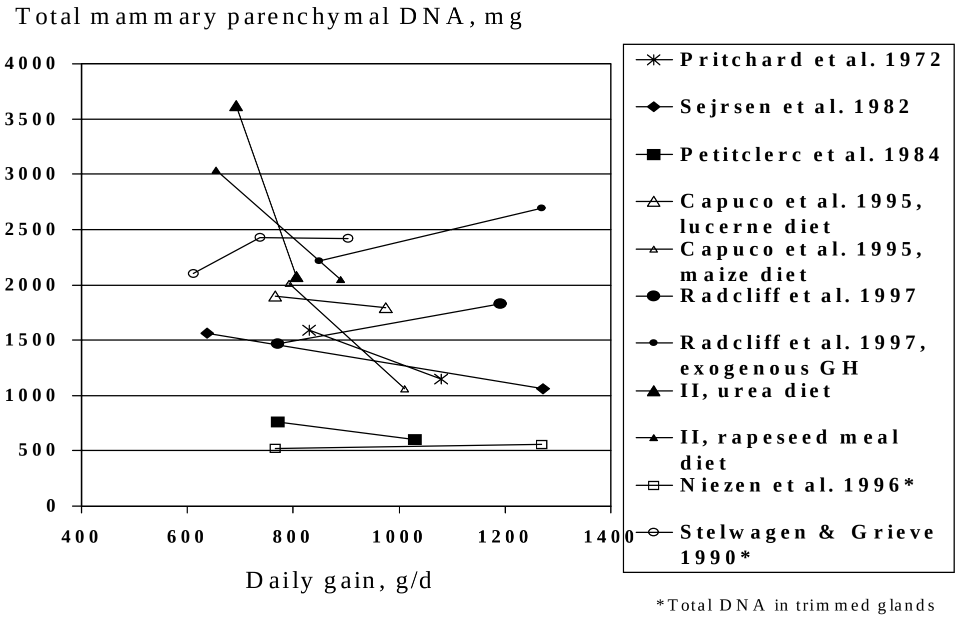


Figure 2. Relationship of pre-pubertal daily gain (g/d) and total mammary parenchymal DNA (mg) reported in literature.

In the study of Harrison et al. (1983) heifers were reared on three different feeding levels corresponding to daily gains of 570, 760 and 1180 g. Based on their findings, the relationship between daily gain and total mammary parenchyma appears to be linear (Figure 1). However, milk production studies (Foldager and Sejrsen 1991, Sejrsen and Purup 1997) tend to suggest that there is a certain upper limit after which feeding level has a negative effect. A scatter plot of the relationship between total mammary parenchyma and pre-pubertal daily gain observed in study II is shown in Figure 3. If the existence of an upper limit in daily gain is assumed, it can be speculated that daily gains approaching 700 g have no detrimental effects on pre-pubertal mammogenesis.

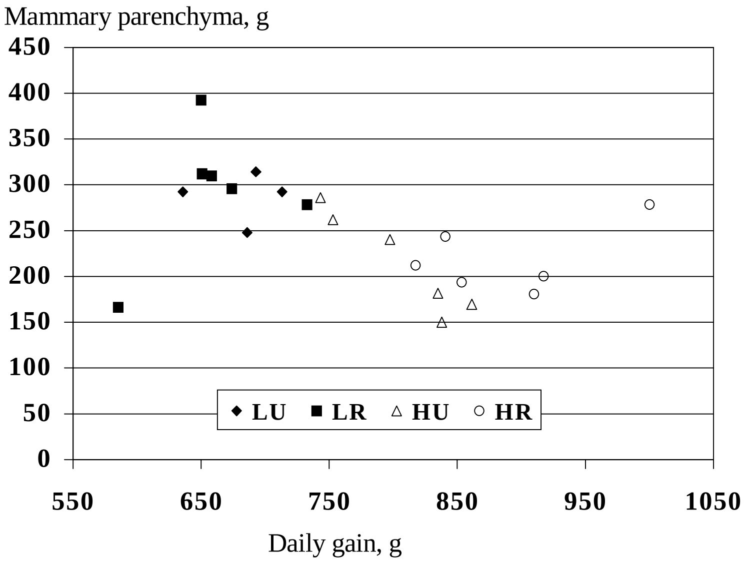


Figure 3. A scatter plot of the relationship between total mammary parenchyma (g) and pre-pubertal daily gain (g) of Ayrshire heifers on a low (L) or high (H) plane of nutrition based on diets containing urea (U) or rapeseed meal (R) in study II.

Either no, or positive effects of pre-pubertal feeding level on mammary growth have been observed in the studies of Stelwagen and Grieve (1990), Niezen et al. (1996) and Radcliff et al. (1997). The lack of a negative effect may be related to the age and body size of heifers at the beginning of these studies. In study II the experiment started at about 90 kg LW and 3 months of age. In most studies where the effect of pre-pubertal feeding on mammary development has been examined heifers have entered the study well in advance of puberty. However, in the studies of Stelwagen and Grieve (1990) and Capuco et al. (1995) the heifers were already 6-8 months old at the beginning of the study and in the study of Stelwagen and Grieve (1990), 5 out of 41 heifers were already cycling. Slaughter LW in the study of Stelwagen and Grieve (1990) was 400 kg, whereas in other studies with Holstein heifers LW at slaughter has been around 300 kg. In studies with smaller breeds such as the Ayrshire (II), LW at slaughter has been below this level. The absence of an effect of feeding intensity on total mammary DNA in the studies of Stelwagen and Grieve (1990) and Niezen et al. (1996) may also be related to the fact that the total mammary DNA was measured instead of total parenchymal DNA.

In the study of Radcliff et al. (1997) intensive feeding either increased or had no effects on mammogenesis. In their study half the heifers were reared to attain daily gains of 800 g while the other half were fed a diet formulated for a daily gain of 1200 g between 4 and 10 months of age. Half of the heifers on both feeding levels were injected daily with GH. In the absence of GH, plane of nutrition had no effect on mammogenesis, but in the presence of GH the high plane of nutrition significantly increased total parenchyma or total parenchymal DNA. It was concluded that exogenous GH increased mammogenesis and that in the absence of exogenous GH a high dietary CP content prevented the negative effects of high feeding intensity.

In study II the high daily gain groups (HU and HR) had total parenchymal tissue mass of 216 g compared with 280 g for the low gain groups (LR and LU). Compared to other studies the total amount of parenchyma was relatively low (Figure 1). This can be related to the fact that heifers were smaller at slaughter than those in many other studies. The magnitude of the difference decreased when the mass of parenchyma was expressed as a function of LW (Figure 4). It is also notable that heifers in study II were less mature, since only 3 out of 24 were cycling at slaughter. In other studies all heifers had already experienced 2 (Petitclerc et al. 1984, Capuco et al. 1995) or more (Sejrsen et al. 1982, Niezen et al. 1996, Radcliff et al. 1997) cycles. Differences may also arise due to variations between breeds. Furthermore, it is important to recognise that separation of mammary parencymal tissue from extraparenchymal tissue on the basis of colour is somewhat subjective.

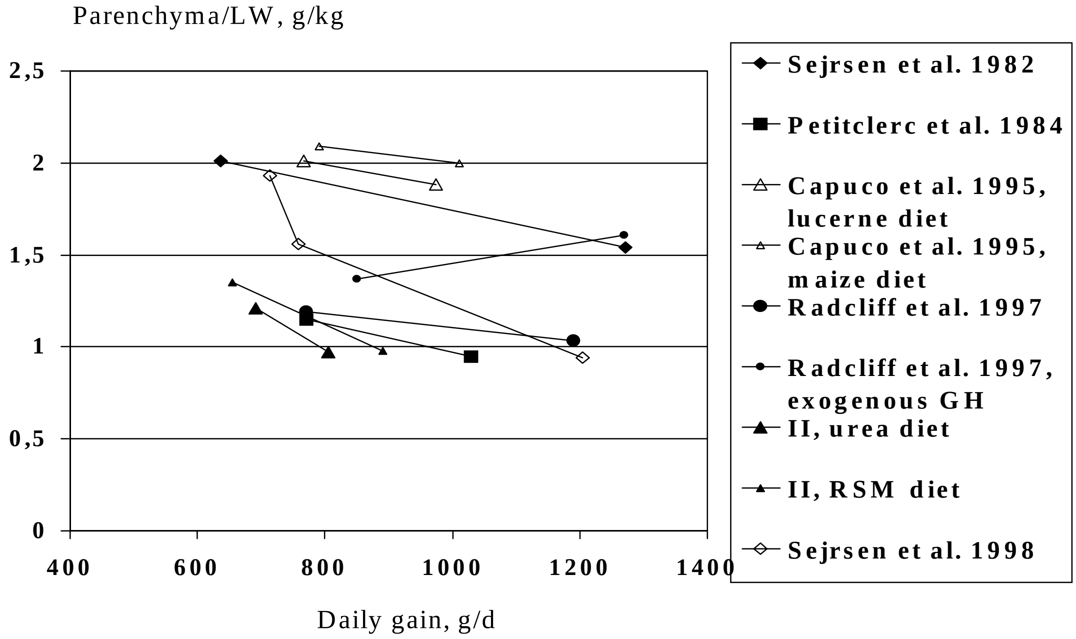


Figure 4. Effect of pre-pubertal daily gain (g/d) on pre-pubertal mammary parenchymal tissue expressed as a function of LW reported in the literature.

It has been suggested that the negative effect of intensive feeding on mammogenesis before puberty is caused by decreased GH secretion commonly observed in animals fed at a high plane of nutrition (Sejrsen et al. 1983, Stelwagen and Grieve 1992, Capuco et al. 1995). In study II intensive feeding had a significant negative effect on mammary growth, but had no effects on plasma GH concentrations. This apparent contradiction was related to the blood sampling protocol used since the peak in GH concentration prior to feeding confounded subsequent interpretation of the data. It was concluded that use of longer sampling period would allow difference in plasma GH concentrations between heifers fed at a low and high plane of nutrition to be measured.

Consistent with previous studies (Sejrsen et al. 1983, Johnsson et al. 1986) a positive across treatments correlation (r = 0.44, $P < 0.05$) between plasma GH concentration and the amount of mammary parenchyma was identified (II). Although exogenous GH increases mammary development of pre-pubertal heifers, mammary tissue does not bind GH (Purup et al. 1999) and GH does not stimulate mammary cell growth in vitro (Woodward et al. 1994, Purup et al. 1995). It has been suggested that the effects of GH are mediated through IGF-I, since IGF-I secretion is increased by GH administration (Purup et al. 1993a, Stelwagen et al. 1993, Weber et al. 2000) and IGF-I stimulates mammary cell proliferation in vitro (Purup et al. 1993b).

However, under restricted feeding, plasma IGF-I concentrations are usually decreased but GH levels increased which is in contrast with the proposed role of IGF-I in enhanced mammogenesis of pre-pubertal heifers with restricted energy intakes. In study II the plasma IGF-I concentration was not affected by the feeding level and no significant correlation between plasma GH and IGF-I concentrations was found. Furthermore, specific binding of IGF-I to mammary membranes from heifers in study II was unaffected by feeding level (Purup et al. 1999). This suggests that the negative effect of high feeding intensity on mammary growth in study II was not mediated via circulating levels of IGF-I or changes in IGF-I receptor capacity. Based on recent findings it has been suggested that the effect of feeding level on the pre-pubertal mammary gland is mediated in part by alterations in local production of IGF-I and IGF-I binding proteins (Weber et al. 2000).

3.1.2.2. Plane of nutrition during post-pubertal period and gestation

The effect of nutrition during the unbred post-pubertal period or gestation on mammary growth has not been widely studied. It appears that the effect of nutrition on post-pubertal mammary growth is less important compared with the effects during the pre-pubertal period. Sejrsen et al. (1982) found no effect of feeding level on mammogenesis in post-pubertal unbred heifers. Correspondingly, mammary growth of pregnant heifers has been shown to be unaffected by the plane of nutrition (Valentine et al. 1987). In contrast, Foldager and Sejrsen (1991) reported an increase mammary parenchyma in RDM/SDM heifers when daily gain from 325 kg LW up to the seventh month of gestation increased from 363 to 657 g. However, further increases in daily gain from 657 to 908 g had no effect. In the study of Harrison et al. (1983) parenchyma mass was highest for Holstein heifers reared at a moderate (580 g/d) plane of nutrition in the first year and higher (840 g/d) plane of nutrition during pregnancy. In both studies increased mammogenesis was related to higher milk production (Little and Harrison 1981, Foldager and Sejrsen 1991).

In study IV high feeding level during the period of rapid mammary growth, the last trimester of gestation, increased milk production of primiparous cows. It has been suggested that GH, prolactin and insulin have mammogenic effects during gestation (Tucker 1981, Akers 1985, Stelwagen et al. 1993). However, prepartum GH concentrations in study IV were not related to milk yield. In addition, milk production was not correlated with prepartum plasma prolactin or insulin concentrations. It appears that the increased milk yield associated with high feeding level during the last trimester was not strongly related to changes in prepartum mammary development due to endocrine factors. It was suggested that, the higher production was due to changes in calving LW, mobilisable body reserves and postpartum feed intake.

3.1.4. Effect of plane of nutrition on milk production

Initial studies concerning the effect of feeding level during rearing on subsequent milk yield were published at the beginning of the last century. However, the current discussion considers data obtained from more recent studies (Tables 3 and 4) since data obtained in early studies do not reflect the growth and milk production potential of contemporary animals. Only milk production during the first lactation has been evaluated. In some experiments the effect of nutrition on multiple lactations has been presented. In general, effects in subsequent lactations have been broadly similar to those reported for animal performance during the first lactation (Gardner et al. 1977, Little and Kay 1979, Gaynor et al. 1995). However, interpretation of data reported in later lactation is confounded due to culling of experimental animals.

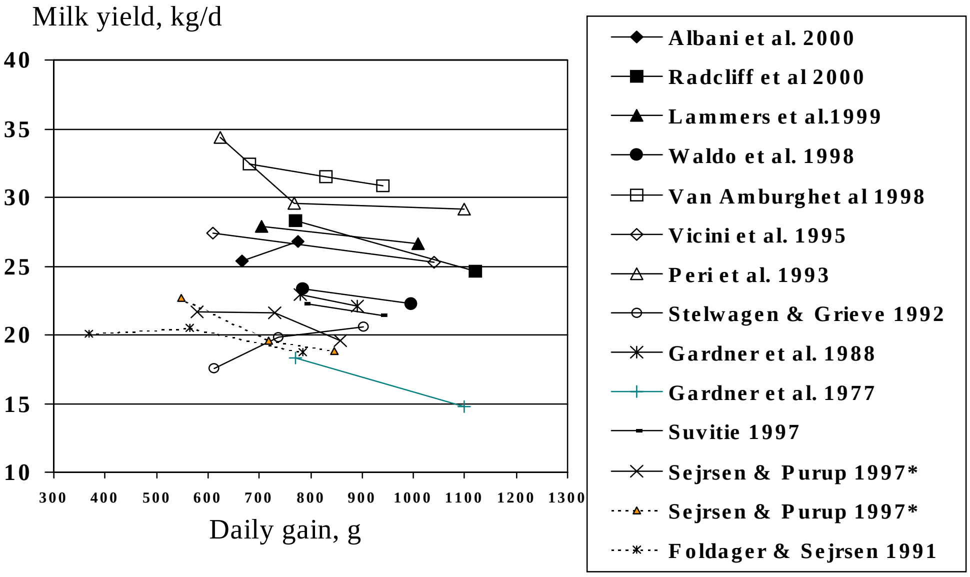
3.1.4.1. Pre-pubertal plane of nutrition

The effect of pre-pubertal daily gain on milk production during the first lactation reported in the literature is documented in Table 3 and Figure 5. There is a trend towards reduced milk production with increased pre-pubertal daily gain in most but not all (Stelwagen and Grieve 1992, Albani et al. 2000) studies. Based on Figure 5 and Table 3 it can be suggested that in cases where growth rates of Holstein and Friesian heifers have exceeded 800 g/d negative effects on milk production have been observed in all reported cases with one notable exception (Stelwagen and Grieve 1992). However, when the growth rate has been below 800 g/d the effects of increasing feeding intensity on milk production has been more variable (Figure 5).

Table 3. Effect of pre-pubertal daily gain (g/d) on milk yield (kg/d) reported in the literature.

Reference	N	Breed	Daily gain, g	Experimental period	Milk yield, kg/d[1]	LW after calving, kg	Calving age, month
Albani et al. 2000	17	Holstein	667	160 – 305 kg LW	25.4	559	28.7
		-Fr	775		26.8	540	28.6
Radcliff et al.	70	Holstein	770	135 kg LW -	28.3^{a}	539	23.6
2000			1120	conception	24.6^{b}	515	20.7
Lammers et al.	68	Holstein	705	133 – 273 d	27.9^{a}	547	22.9
1999			1009	of age	26.6^{b}	538	22.8
Waldo et al. 1998	75	Holstein	793 lucerne	175 - 325 kg LW	22.8	535	23.9
			992 lucerne		21.6	520	23.2
			776 maize		24.0	521	24.4
			997 maize		22.9	531	23.2
Van Amburgh	273	Holstein	680	90 – 320 kg LW	32.4^{a}	550	24.5
et al. 1998b			830		31.5^{ab}	529	22.0
			940		30.8^{b}	520	21.3
Vicini et al. 1995	12	Holstein	610	Prior puberty	27.4		23.5
	pens		1040		25.3		21.6
Peri et al. 1993	15	Holstein	625/1162	6-10 months/	34.4^{a}	463**	
			768/705	10-12 months	29.6^{b}	478**	
			1100/797	of age	29.2^{b}	482**	
Stelwagen and	47	Holstein	611	6 – 16 months	17.6^{a}	520	26.2
Grieve 1992			737	of age	19.8^{b}	477	26.2
			903		20.6^{c}	492	26.4
Gardner et al.	433	Holstein	780	6 weeks of age –	22.9		24.6
1988			890	breeding (340kg)	22.1		22.2
Gardner et al.	48	Holstein	770	91 kg LW–	18.3^{a}	538	26.9
1977			1100	conception	14.8^{b}	506	19.7
Suvitie 1997	16	Fr	789	106 – 300 kg LW	22.3	551*	25.0
			939		21.4	568*	24.9
Sejrsen and Purup	161	Fr	579	6 wk - puberty	21.7$^{\#}$	513	29
1997;			731		21.6$^{\#}$	500	26
From data of			858		19.6$^{\#}$	498	23
Hohenboken et al.	155	RDM	549	6 wk - puberty	22.7$^{\#}$	530	29
1995			718		19.6$^{\#}$	525	26
			845		18.8$^{\#}$	490	23
	129	Danish	362	6 wk - puberty	20.5$^{\#}$	341	29
		Jersey	487		19.0$^{\#}$	353	26
			557		16.5$^{\#}$	329	23
Foldager and	180	RDM	369	90 – 325 kg LW	20.1^{a}	481	32.4
Sejrsen 1991		SDM	565		20.5^{a}	484	27.3
			785		18.7^{b}	489	24.8
Ingvartsen et al.	84	Jersey	438/365	65-140 kg LW/	16.5^{a}	342	28.5
1988			443/508	140 – 230 kg LW	16.2^{a}	341	26.4
			554/501		14.5^{b}	326	25.3
Valentine et al.	90	Holstein	180	110 kg LW →	17.2	461	26.5
1987		-Fr	620	15 weeks	15.2	467	24.0
			1090		13.1	473	22.0
Little and	71	Fr	580		10.2$^{\#}$	465*	
Harrison 1981			670	3 - 11.5 months	10.9$^{\#}$	476*	
			760	of age	11.2$^{\#}$	468*	
			800		11.0$^{\#}$	480*	
			1040		9.6$^{\#}$	508*	
Little and Kay		Fr	570	13 wk –	12.8$^{\#a}$	487	27.3
1979		FrxAy	776	conception	7.9$^{\#b}$	453	27.9
			1090		6.1$^{\#c}$	430	19.0

[1] Treatment means with different subscripts differ significantly ($P<0.05$). ***** LW before calving. ** LW 4 weeks after calving. # Fat corrected milk. Fr = Friesian; Ay = Ayrshire; RDM = Red Danish Milk Breed



*Data of Hohenboken et al. 1995

Figure 5. Effect of pre-pubertal daily gain (g/d) on milk production (kg/d) of primiparous Holstein-Friesian (—) or RDM (----) cows reported in the literature.

Results from the study of Peri et al. (1993) are inconsistent with other studies. In the former study the heifers were fed to gain either 625 g/d (A), 708 g/d (B), or 1100 g/d (C) from 6 to 10 months of age. Heifers on treatment A had significantly higher milk yields than heifers on treatment B, but further decreases in milk yield with increasing gains (treatment C) were not observed. It could be that exposure to treatments was too short before the puberty to elicit negative effects. The significantly higher milk yield of the heifers on treatment A than treatments B or C can also be related to *ad libitum* feeding of heifers on treatment A during 10 to 12 months of age. In the studies of Park et al. (1998) and Choi et al. (1997) use of stair-step feeding where restricted and *ad libitum* feeding regimens were alternated, increased milk production by 6 and 9%, respectively. However, Barash et al. (1994) observed no effect on milk production when six-months old heifers were fed 4 months with low-energy diet followed by 2 months with a high-energy and high-protein diet that led to compensatory growth.

In the study of Stelwagen and Grieve (1992) milk yields tended to increase when daily gains increased from 737 to 903 g. This is in agreement with study V based on field data (Friesian and Ayrshire), which indicated a positive environmental correlation between 305-d milk yield and daily gain before insemination. However, it was speculated (V) that the measured rearing period from birth to breeding did not represent the critical period with respect mammary development. Another reason for the positive correlation was due to between herd differences in feeding management (forage quality etc.). In herds with good quality feeds, heifers are more likely to attain good growth during the pre-pubertal period but also during the post-pubertal period. Therefore in such herds heifers are larger at calving than their counterparts fed low quality feeds. In addition, in herds with good quality feeds, it is also likely that feeding management during the first lactation is more efficient allowing higher production.

Effect of pre-pubertal plane of nutrition on milk production of Red Danish (RDM) has been investigated by Hohenboken et al. (1995). Based on the data of Hohenboken et al. (1995) Sejrsen and Purup (1997) reported a 14% drop in milk yield of RDM when daily gains increased from 549 to 718 g. Correspondingly, age at calving decreased from 29 to 26 months. Sejrsen and Purup (1997) recommended a 600 g daily gain for RDM. Finnish Ayrshires are about the same size as RDM cows. Based on data from study II it can be inferred that a pre-pubertal daily gain up to 700 g can, with respect to mammary growth be tolerated for Finnish Ayrshire heifers. In study V daily gain before and after insemination had a positive genetic correlation with first lactation milk yield. Thus, it seems that genetic selection for higher milk yield will lead to higher genetic growth potential. This change in genetic potential should be considered in future recommendations of daily gains acceptable for pre-pubertal dairy replacement heifers.

3.1.4.2. Plane of nutrition during post-pubertal period and gestation

The effect of growth rate during post-pubertal period and gestation on first lactation milk yield reported in the literature is presented in Table 4. The duration of experimental periods varies greatly between studies. In some it only included a part of gestation and in some it included also the unbred post-pubertal period. In most cited experiments, feeding during transition, which varied from 10 to 38 d before calving, has been equal for heifers within experiments.

Table 4. Effect of daily gain (g/d) during post-pubertal period and gestation on milk production reported in the literature.

Reference	N	Breed	Exp. Period prepar., d (trans. per.)[1]	Daily gain, g/d	Calving LW, kg	Calving Age, Months	Lactation Period,d	Milk yield, kg/d[2]	DM intake, kg/d
Albani et al. 2000	22	Holstein - Fr	300 kg LW→ 7 months[3]	748	579	29.3	305	27.0	
				824	551	27.8		26.3	
IV, 1999	40	Ay	154+98(14)	638/ 710	462	24.4	160	20.4a	15.6
				638/1042	498	24.5		22.8b	16.2
				844/ 636	480	24.5		20.2a	15.1
				844/ 874	499	24.8		22.3b	14.9
Hoffman et al. 1996	70	Holstein	10 months of age -> 280(10)	778	591	24.6	305	26.9	
				933	569	21.7		25.5	
Grummer et al. 1995	67	Holstein	170(10)	1000	580		161	28.0	19.6
				1120	618			28.1	18.6
Ingvartsen et al. 1995b	27	SDM	84	721	493		168	25.4	16.6
				1300	514			25.3	15.9
Ingvartsen et al. 1995d	35		168	837	484		168	24.8	14.0[4]
				1251	539			23.7	13.3
				1473	564			22.7	12.8
Lacasse et al. 1993	59		12 months of age->3 months of gestation + 180(14)	840/ 660	553	24.8	287	22.4	16.5
				720/ 730	559	25.1		23.5	16.5
				840/ 840	584	24.9		23.1	16.5
				720/ 950	593	24.5		24.5	16.9
Foldager and Sejrsen 1991	180	RDM SDM	325kg→ 280(91)	363	439	30.4	250	18.2a	
				657	478	27.3		19.9b	
				908	513	26.8		20.3b	
Valentine et al. 1987	90	Holstein - Fr	143(38)	220	419	24.4	252-274	11.0	
				590	467	24.0		11.4	
				1060	493	24.1		12.8	
Ducker et al. 1985	100	Fr	70	682			245	16.6	
				1027				16.4	
Little and Harrison 1981	29	Fr	12 months-> 280 (30)	720	465		305	10.2	
				840	496			11.6	

[1] Experimental period (d) before parturition including the transition period. Duration of transition period in parentheses (d).
[2] Treatment means with different subscripts differ significantly ($P<0.05$).
[3] Half the heifers were inseminated at first observed oestrus above 370 kg and half above 420 kg live weight.
[4] Dietary energy concentration differs between treatments.
Fr = Friesian; Ay = Ayrshire; RDM = Red Danish Milk Breed; SDM = Danish Black and White; LW = live weight.

Post-pubertal period: Feeding intensity of unbred post-pubertal heifers had no significant effect on milk production of dairy cows in the experiments of Lacasse et al. (1993) and Albani et al. (2000). Similar effect have also been observed in beef cattle (Johnsson and Obst 1984). This agrees with the findings of Sejrsen et al. (1982) that high feeding level had no effects on mammary development in post-pubertal heifers. In the study of Foldager and Sejrsen (1991) the experimental period included the post-pubertal period prior to insemination and gestation up to the seventh month. They demonstrated that milk yield and mammary development were enhanced with increasing daily gains from 363 to 657 g, but further increases to 908 g had no effect on milk production. In this study LW at parturition increased with higher growth rates. Hoffman et al. (1996) noticed a tendency for decreased milk yield with accelerated daily gain (933 g/d) compared to moderate gain (778 g/d) during the post-pubertal and gestation periods. However, accelerated growth was combined with early insemination and lower LW after calving which could account for lower yields. The influence of LW at parturition on the milk production potential of primiparous cows is discussed in more detailed in chapter 3.3.

Gestation: In study IV the effect of feeding level at two stages of gestation on milk yield of primiparous cows was evaluated. Stages investigated were 2-6 (period 1) and 7-9 months of gestation (period 2). Feeding during the two week transition period was equal for all treatments. The high feeding level (LW change over 800 g/d) during period 2 increased milk yield by 11%. In contrast, feeding level during period 1 had no effect on milk production. In most gestation studies where the prepartum experimental period has been longer than 2 to 4 weeks before calving, no significant effect of feeding level on first lactation yield has been reported (Table 4). However, consistent with results from IV milk yield tended to increase with increasing prepartum feeding level in the study of Valentine et al. (1987). For the field study (V) a positive environmental correlation was estimated between daily gain after insemination and milk production. As was discussed previously this effect can to a certain extent be explained by between-herd differences.

In study IV, as well as in many previous studies (Valentine et al. 1987, Lacasse et al. 1993, Grummer et al. 1995, Hoffman et al. 1996,) feeding level during gestation had no effect on milk protein and fat content *per se*. However, in some studies (IV, Grummer et al. 1995, Ingvartsen et al. 1995d, Hoffman et al. 1996) a significant interaction between treatment and stage of lactation existed for milk fat content. During the first weeks of lactation, milk fat content was higher for cows fed on a high plane of nutrition throughout gestation (HH) than for cows fed the other prepartum treatments. Presumably this is caused by greater mobilisation of body fat reserves as indicated by higher plasma FFA concentrations in cows fed a high prepartum plane of nutrition (IV). Prepartum plane of feeding does not usually affect first lactation milk protein content (Lacasse et al. 1993, Foldager and Ingvartsen 1995, Grummer et al. 1995). However, in study IV, a lower milk protein content was observed for heifers fed high plane of nutrition during the last trimester of gestation. Milk protein content was the lowest for treatment HH which may be related to lower postpartum feed intakes associated with a decrease in the supply of amino acids available for absorption.

A comparison of different studies is difficult, since the breed of the heifers and the duration of treatment periods during gestation varies. Also the shift from low to high feeding levels and subsequent compensatory growth can affect experimental findings (Park et al. 1989, Choi et al. 1997, Park et al. 1998, IV). Furthermore, rearing during the pre-pubertal period varies between studies and in some cases between animals within a study which can also confound a clear interpretation. In study IV heifers were reared equally from birth to the beginning of the experiment to minimise the effects of pre-pubertal management.

In study IV the increased milk yield of the cows fed intensively during the last trimester of gestation was speculated to be due to differences in the calving LW, feed intake capacity and the amount of body reserves available for mobilisation. It is known that the milk yield of primiparous cows is correlated with LW at parturition (Clark and Touchberry 1962, Ingvartsen et al. 1988, V). In study IV a high plane of nutrition during the last trimester (treatments HH and MH) significantly increased postpartum LW. However, there was a difference in LW change and feed intake during lactation between heifers fed HH and MH treatments. For treatment HH the mobilisation of body reserves during the first few weeks of lactation was high (total mobilisation 28.4 kg) and DM intake was low (11.9 kg/d, weeks 0-5), whereas mobilisation of body reserves was lower (11.6 kg), and DM intake was higher (13.7 kg /d, weeks 0-5) for heifers fed treatment MH.

Thus, a high feeding level during period 1 significantly decreased postpartum intake and resulted in greater mobilisation of body reserves, as indicated by higher plasma FFA and BHBA concentrations (IV). On HH treatment the BHBA values during the first weeks of lactation approached to levels indicative of an increased risk of ketosis. The high apparent efficiency of ME utilisation for milk production (k_l = [Milk energy/(ME intake – ME maintenance)] at the beginning of lactation in heifers fed treatment HH is consistent with extensive mobilisation of body reserves (Figure 6). On MM treatment k_l values were relatively low even at the onset of lactation indicating that these cows were not in negative energy balance. In agreement with these results Ingvartsen et al. (1995c) suggested that intensive prepartum feeding and a high body condition score at calving will cause a lower initial intake and delay the time taken to achieve the maximal intake. Based on these findings it can be suggested that for Finnish Ayrshire heifers a daily gain of 800 g or higher during the first two trimesters of gestation can result in greater deposition of fat stores and diminished intake potential. Instead, intensive feeding during the last trimester to attain LW changes above 800 g is desirable for achieving maximal milk production.

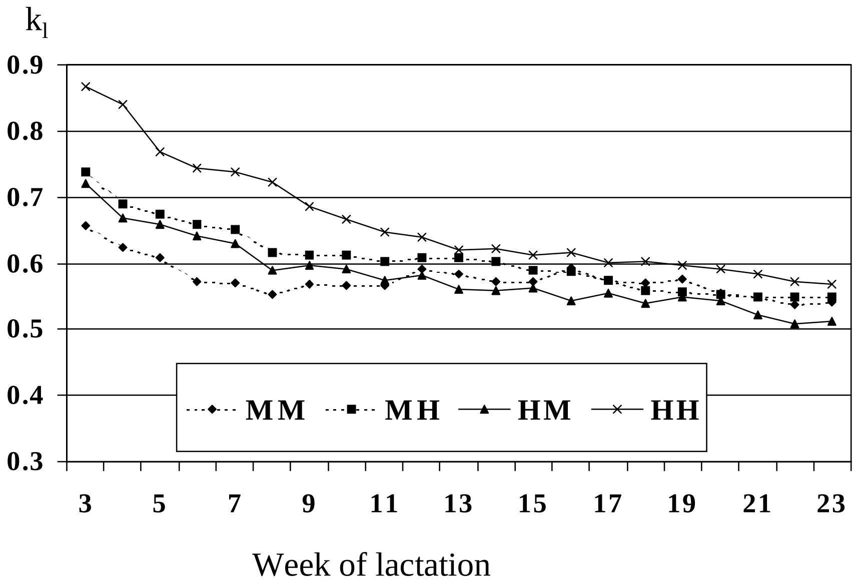


Figure 6. Variations in the apparent efficiency of ME utilisation for milk production (k_l) during the first lactation of cows fed at different feeding intensities (M=medium and H=high) during the first two trimesters (period 1) and the last trimester of gestation (period 2) observed in study IV.

3.1.5. Effect of protein intake and diet composition

Protein source. The effect of dietary protein quality on mammary development was studied in experiment II, where half of the heifers on both feeding levels received either urea or RSM as protein supplements. On urea and RSM treatments 260 and 390 g/ kg CP was rumen undegraded CP, respectively. It was calculated that for both feeding levels total AAT supply was higher for RSM than urea supplemented diets (I). On high feeding level heifers fed RSM grew faster than those receiving urea, whereas on low feeding level protein source had no significant effects on growth (I). It was suggested that urea was not an adequate nitrogen source for heifers gaining 800 g/d on a barley-hay diet. Even if protein source had a significant effect on growth at the high feeding level, no effect of protein source on mammary development was detected (II). This finding is consistent with those of Van Amburgh et al. (1998b) who observed no effect of protein source (plant protein + urea; rumen undegraded CP 290 g / kg CP versus plant protein + animal protein; rumen undegraded CP 420 g / kg CP) on subsequent milk yields of primiparous cows. On the other hand, Dobos et al. (2000) reported a tendency for decreased mammogenesis in heifers fed diets (180 g CP/kg DM) containing rumen undegraded protein 270 g/ kg CP compared with 130 g/kg CP. However, milk yield was not affected by protein source. Thus, based on these studies it appears that pre-pubertal dietary protein source has no effects on pre-pubertal mammary development or subsequent milk production.

Dietary protein content. It has been suggested by Radcliff et al. (1997) that high protein intake in heifers fed on a high plane of nutrition will decrease mammary fat deposition and prevent the negative effects of high energy intake on pre-pubertal mammary parenchymal growth (Figure 1). In their study dietary CP content of the low and high feeding levels was 163 and 197 g/kg DM, respectively. In agreement with Radcliff et al. (1997), Capuco et al. (1995) found no negative effect of 925 g compared with 725 g daily gains on pre-pubertal mammary growth of Holstein heifers fed a lucerne silage based diet (220 g CP/kg DM). However, on maize silage based diets (150 g CP/kg DM) the high feeding level significantly decreased total DNA in mammary parenchyma (Figure 1); but had no effect on milk yield (Waldo et al. 1998). In study II the diet CP content was 132 and 144 g/kg DM on low and high feeding levels, respectively. This difference was caused by a lower than expected intake of hay at the high level of feeding. The small difference in dietary CP content was unable to prevent the negative effects of high feeding intensity. On the other hand, even bigger differences in the dietary CP content between treatments (150 vs. 200, 140 vs. 190 and 140 vs. 180 g CP/kg DM) in the studies of Zhang et al. (1995), Whitlock et al. (1999) and Dobos et al. (2000) have not been able to influence pre-pubertal mammary development in fast growing animals. Moreover, Radcliff et al. (2000) reported 14% reduction in milk yield of heifers gaining 1200 g/d fed a diet containing 197 g CP/kg DM compared with heifers gaining 800 g/d receiving diet in which CP content was 175 g/kg DM. Overall there appears to be little evidence to support the hypothesis that extra dietary protein can overcome detrimental effects of a high plane of nutrition on pre-pubertal mammary development. Intake of CP above requirements for target daily gain during the pre-pubertal period appears unnecessary.

The effect of dietary protein intake and quality during gestation on mammary development in heifers has not been extensively studied. In Finland, feeding of heifers during gestation is usually based on grass silage or grass silage and small (0.5-1.5 kg) amounts of cereal supplements. Protein in grass silage is extensively degraded in the rumen, such that for these diets, the amount of protein escaping ruminal degradation is relatively low. However, since protein requirements during the first two trimesters of gestation are low, it is obvious that an adequate supply of rumen degraded carbohydrates to ensure efficient microbial protein synthesis can satisfy protein requirements of pregnant heifers fed grass silage diet during the first stages of gestation.

The effect of dietary CP content during the last trimester of gestation on subsequent milk yield of primiparous cows has been investigated in some studies (Figure 7). In the study of Hook et al. (1989) CP content of the diets fed to pregnant heifers (last 70 d prepartum) was increased from 100 to 130 g/kg DM and in the study of Santos et al. (2001) from 127 to 147 g/kg DM (last 32 d prepartum). In both studies milk production was increased. In the study of Mäntysaari (1999b) pregnant heifers fed grass silage and barley diet were offered RSM supplements during the last 84 or 42 days prepartum. The supplemental RSM increased dietary CP content from 140 to 165 g/kg DM and the intake of AAT from 658 to 719 g/d, but had no effect on milk yield. During the last 3 weeks prepartum all heifers received the same diet. In contrast, Tesfa et al. (1999) reported an increase in milk yield with increased RSM supplementation (0.3 kg/d vs 1.5 kg/d) during the last 42 days prepartum. The average CP content of the diet was calculated to be 128 and 158 g/kg DM (including the diet of both primi- and multiparous cows), but in their other study no effects were observed when dietary CP content of the diet (28 days prepartum) was increased from 156 to 191 g/kg DM with RSM supplementation (Tesfa et al. 1998). Van Saun et al. (1993) found no difference in milk production when the dietary CP content (last 21 d prepartum) was increased from 124 to 153 g/kg DM. To make conclusions from studies reported in the literature is difficult due to variation in the duration of experimental periods. It appears that during the last trimester of gestation feeding diets containing CP concentrations below 130 g/kg DM can potentially lead to depressed milk production, but feeding diets containing 150 g/kg DM do not improve animal performance.

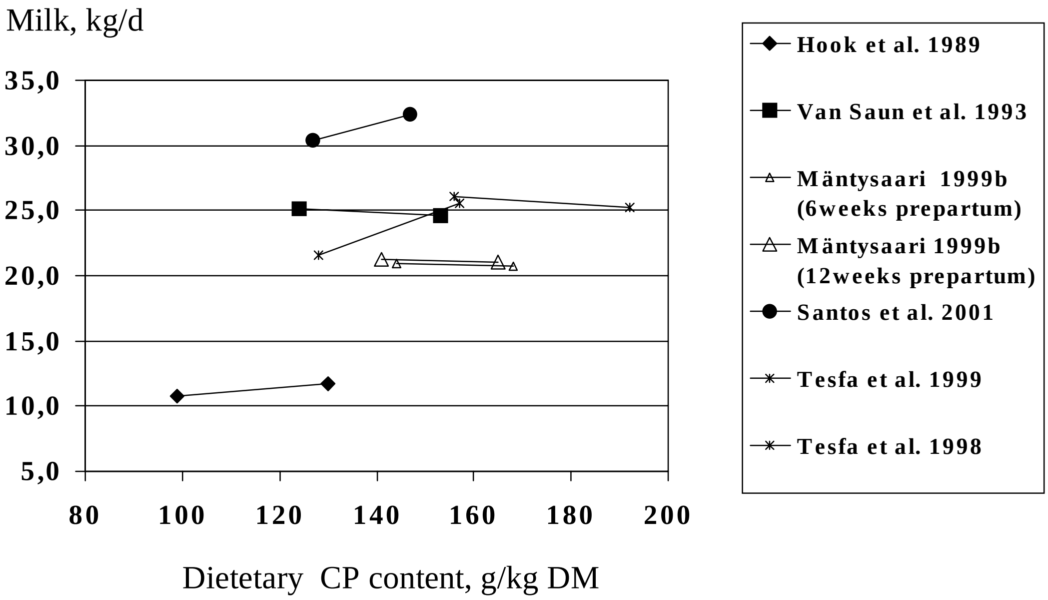


Figure 7. Effect of prepartum (3-12 weeks) dietary crude protein content on milk production of primiparous cows reported in literature.

Diet energy content. The effect of diet energy concentration on pre-pubertal mammogenesis and subsequent milk production has been studied by Strudsholm et al. (1985) and Sejrsen and Foldager (1992). In both studies the experimental period started at 90 kg LW and continued until parturition. In both studies pre-pubertal mammary development and subsequent milk yields were the same for heifers fed either a bulky diet or an energy dense ration. However, Strudsholm et al. (1985) noticed that cows fed the bulky diet from 90 kg LW to 12 weeks prepartum and an energy dense diet during the last 12 weeks prepartum resulted in higher milk production. The higher milk yield was attributed to large mobilisation of body reserves and lower growth rates during lactation (Strudsholm et al. 1985).

3.2. Nutrition and body development of replacement heifers

Since most farmers do not have access to weighing facilities, heifers LW is routinely predicted from measurements of body characteristics. In Finland, estimation of LW from heart girth is based on the studies of Kenttämies and Vehmaan-Kreula (1978). However, the prediction excluded heifers younger than 6 months. Therefore, in study III prediction of pre-pubertal heifer LW was developed based on data from Ayrshire heifers gaining 650 g a day. From all available measurements heart girth was found to be the best predictor of LW, consistent with many previous studies (Johansson and Hildeman 1954, Nelson et al. 1985, Heinrichs et al. 1992). The recommended equation (III) for the prediction of live weight of restrictively fed pre-pubertal Ayrshire heifer from measurement of heart girth was:

$LW = \exp[1.0453 + 0.04196(\text{heart girth}) - 0.00007713(\text{heart girth})^2]$.

The prediction equation was tested using data from study I. It was found that the equation underestimated the LW of intensively fed heifers, while dietary protein source had no effect on goodness of fit. In agreement with our results, Hvidsten (1940) and Johansson and Hildeman (1954) reported that at a given heart girth, an increase in condition score increased LW. In contrast, the effect of feeding level for RDM heifers was found to be reversed such that at given heart girth LW was greater in animals fed at a lower plane of nutrition (Sørensen and Foldager 1991).

For replacement dairy heifers skeletal growth is important. It is usually measured by heart girth, wither height, body length, hip width and hip height. Heinrichs and Hargrove (1994) have assessed the optimal body size criteria for replacement heifers. They recorded heart girth and wither height. Wither height of a cow is considered to be important because tall animals have longer bodies and therefore more body capacity. Tall cows also have udders higher off the ground which is important for injury prevention and ease of milking. In addition in the study of Heinrichs and Hargrove (1987) there was a positive correlation between average herd milk production and estimated mean heifer wither height at 24 months of age.

In studies I, III and IV body development of experimental heifers was determined using measurements of wither height (I, III, IV), body length (III, IV) and hip width (IV). It was concluded that wither height and body length represented more animal frame size. Instead, hip width was found to be more closely correlated with body fat and body condition score in study IV.

Feeding intensity had a significant effect on wither height of pre-purbertal heifers in study I. Wither height was higher ($P<0.001$) for heifers fed low compared with high levels of feeding at 220 kg LW (Figure 8). Stelwagen and Grieve (1990) and Radcliff et al. (2000) also observed higher wither height at puberty (290 kg LW) and at breeding, respectively, for heifers fed on low compared with high feeding levels. Thus, it seems that at the same LW restrictively fed heifers are taller than intensively reared heifers. Instead, if we compared the body measurements of heifers fed on different levels of feeding at the same age but different LW, a positive correlation between wither height, heart girth, body length and feeding level was observed in the studies of Daccrett et al. (1993) and Albani et al. (2000), but not in I. Our results suggest that the pubertal wither height is more related to the age of the heifers than with animals LW (Figure 8).

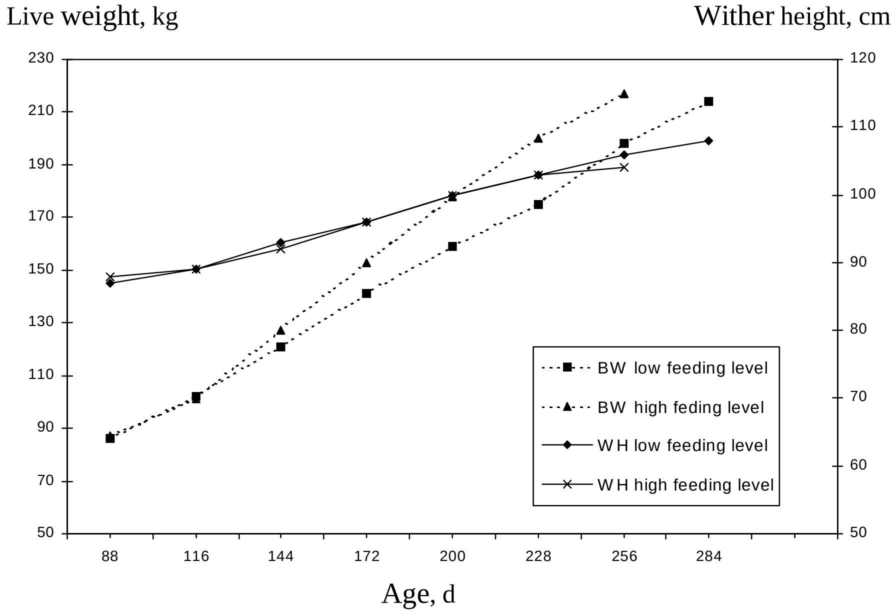


Figure 8. Increase in live weight and wither height of Finnish Ayrshire heifers fed to gain 650 or 850 g/d (I).

In paper IV the effect of nutrition on body measurements of pregnant heifers was studied. Prepartum plane of nutrition had no effect on wither height or body length of heifers at parturition. In agreement, Lacasse et al. (1993) found no difference in wither height of heifers reared under different planes of nutrition prepartum. However, in study IV, the high feeding level during gestation, especially during the first six months, increased heart girth, hip width and BCS. These results indicate that a high compared to moderate plane of nutrition during pregnancy has no effect on body size (wither height, body length) of primiparous cows, but increases body fat deposition as indicated by increase in heart girth, hip width and BCS.

The effect of protein source on body development of pre-pubertal heifers was examined in study I. Although on a high feeding level, heifers fed RSM grew significantly faster than heifers fed urea supplements, no effect of protein source on body measurements at either level was found. Steen et al. (1992) and Daccarett et al. (1993) found no difference in the body length, wither height or heart girth of heifers fed diets containing different amounts of rumen degradable protein. In these studies the protein source had no effect on the daily gain either. However, Van Amburgh et al. (1998a) identified small but significant increases in wither height for heifers fed animal compared with vegetable protein supplements.

In the experiment of Lammers and Heinrichs (2000) increases in the ratio of CP to energy increased linearly hip width, hip height, wither height and heart girth of pubertal heifers. They concluded that higher CP intakes and increases in dietary CP (g) to ME (MJ) ratio (11:1, 13:1, 14.5:1 g/MJ) enhanced lean tissue and structural growth. In this study dietary protein content was 118, 138 or 156 g/kg DM and the corresponding daily gains of the heifers were 1010 g, 1030 g and 1106 g. Whitlock et al. (1999) reported no differences in wither height of rapidly growing pre-pubertal heifers (1200 g/d) attained with diets containing 140, 160 or 190 g CP/kg DM, corresponding to dietary CP to ME ratio of 12:1, 13:1 and 16:1 g/MJ, respectively. In study I the ratio of CP to ME was 13:1 for both feeding levels but AAT intake was increased for RSM compared with urea supplemented diets. However, no differences in structural growth or carcass fat grade were observed between protein sources indicating that structural growth was not improved by increases in AAT intake.

3.3. Effect of live weight and age at calving on first lactation milk production

3.3.1. Live weight at parturition

From field data positive genetic (+0.26±0.13) and environmental (+0.16±0.04) correlations were estimated between LW at parturition and milk yield of primiparous cows (V). A positive genetic correlation has also been reported in previous studies (Miller and McGillard 1959, Wilk et al. 1963, Lin et al. 1985, Van Elzakker and Van Arendonk 1993). This indicates that genetically large cows are also better milk producers. Correspondingly, a positive phenotypic relationship between these traits has often been observed in feeding studies (e.g. IV, Ingvartsen et al. 1988, Foldager and Sejrsen 1991).

In study V it was suggested that the positive environmental correlation can be due to the combined effects of reduced energy requirements for growth during the first lactation and greater mobilisable body reserves in larger cows. The effect of mobilisable body reserves is supported by the fact that the phenotypic correlation changes from positive to negative when live weight is measured after three months postpartum (Miller et al. 1973, Van Elzakker and Van Arendonk 1993). One reason for the positive phenotypic correlation between milk yield and LW at parturition is the increased feed intake capacity of primiparous cows heavier at calving (Roseler et al. 1997). In the study of Roseler et al. (1997) the phenotypic correlation between DM intake and calving LW of primiparous cows was +0.38. In field data the positive environmental correlation also reflects differences in feeding management between herds. The herds with more efficient feeding management regimes tend to have larger cows and higher milk yields than the herds with poor feeding management.

LW at parturition is linked with growth rate (before puberty, post-puberty and during gestation) and to the duration of the rearing period (calving age). Based on the field data it is apparent that a high LW is necessary for attaining maximal milk production potential. On the other hand, excessive feeding before puberty can have a detrimental effect on milk production potential of primiparous cows (see 3.1.4.1.). In most studies where the effects of pre-pubertal feeding level on milk production has been investigated, heifers fed on high feeding level before puberty have lower daily gains during the post-pubertal period and gestation, or have been inseminated at an earlier age and hence have had a lower LW at parturition. Van Amburgh et al. (1998b) suggested that after adjustment for calving LW no difference exists between pre-pubertal rearing groups with respect to milk yields. However, Lammers et al. (1999) reported a negative effect of intensive feeding on milk production and the results were unaffected by LW adjustment. Similarly, Radcliff et al. (2000) reported that LW at parturition had no significant effects on subsequent milk yield.

Furthermore, if differences in calving LW are levelled by post-pubertal compensatory growth of the heifers fed restricted before puberty, then there is no reason for LW adjustment. Compensatory growth during gestation has been demonstrated in the study of Radcliff et al. (2000) where post-pubertal growth of the heifers restrictively fed before puberty was 930 g/d and growth of the heifers fed on high plane of nutrition before puberty was 680 g/d. Post-pubertal diet was equal for all heifers. Correspondingly, in study V a negative phenotypic and environmental correlations were observed between daily gains before and after insemination. Besides LW at parturition, compensatory growth can influence the milk production potential by affecting mammary differentiation and functional activity as reported by Park et al. (1989) and Choi et al. (1997).

A period of compensatory growth during the last trimester of gestation was also noticed in study IV. Heifers fed on moderate plane of nutrition during the first two trimesters of gestation but then moved to higher feeding level during the last trimester (MH) grew significantly faster during the last trimester than the heifers who had received high feeding level throughout gestation (HH). Furthermore, calving LW, wither height and body length were not different between groups. It appears that if heifers are fed on a high plane of nutrition during the last trimester feeding intensity during the first part of gestation can be moderate without having a negative impact on LW at parturition.

3.3.2. Age at calving

Age at calving depends on management decisions and the inherent fertility of heifers. It is also dependent on feeding intensity since puberty is not reached until heifers attain a certain LW. To decrease age at calving accelerated growth coupled with early breeding is required. In study V the average calving age for Finnish Ayrshire and Friesian heifers was 25.5 months. Within this data phenotypic (+0.03) and environmental (+0.07) correlations between age at calving and milk yield were relatively low compared with estimates reported previously (Lee 1976, Lin et al. 1987, Moore et al. 1991). Danell (1982) reported a 50 kg increase in lactation milk yield when the age at calving increased one month between 24-34 months of age. The corresponding regression in field data of study V was a 32 kg increase in 305 day milk yield for a month increase in calving age between 19- 34 months of age.

The positive relationship between calving age and milk production is presumable mediated through LW. Older heifers are also heavier at calving, which will on average result in higher production. However, Clark and Touchberry (1962) and Fisher et al. (1983) concluded that age affected the first lactation milk yield independent of LW. According to Clark and Touchberry (1962) its influence was approximately fourfold less than that of LW.

4. GENERAL CONCLUSIONS

Based on the current studies (I-V) and data reported in the literature the following remarks can be summarised.

1. High feeding level during the pre-pubertal period (3-12 months of age) can have a negative effect on mammary growth. The level of feeding (expressed as daily gain) that elicits negative effects depends on the breed of the heifer. Based on mammary growth measurements it was suggested that for Finnish Ayrshire heifers a daily gain higher than 650 – 700 g is detrimental for pre-pubertal mammogenesis. For published studies, it was shown that for Holstein - Friesian heifers pre-pubertal daily gains higher than 750 - 800 g decreased subsequent milk yield.

2. Pre-pubertal dietary protein source (RSM vs urea) had no effect on mammary growth of pre-pubertal heifers. The effect of dietary CP content on pre-pubertal mammogenesis and subsequent milk yield have been variable, but based on data reported in the literature, it seems unlikely that CP intakes above those required for targeted pre-pubertal daily gain are necessary.

3. Heifers reared on a low plane of nutrition during pre-puberty had a greater wither height at puberty (at the same LW) than heifers fed more intensively. Thus, wither height seems to be determined more by age than LW. Dietary protein source had no effect on heifers wither height during pre-pubertal period.

4. Heart girth was shown to be a good predictor of LW. The prediction equation for estimation of LW of restrictively fed pre-pubertal Ayrshire heifers from heart girth was given as:

   $$LW = \exp[1.0453+0.04196(\text{heart girth})- 0.00007713(\text{heart girth})^2].$$

5. On a high feeding level (daily gain over 800 g/d) Finnish Ayrshire heifers under 220 kg LW had higher growth rates when RSM rather than urea was used as a protein supplement for hay and barley diets. On lower levels of feeding (daily gain 650 g/d) protein source had no effect on growth.

6. For Finnish Ayrshire heifers daily gains of 800 g or higher during the first six months of gestation had no effect on subsequent milk yield but resulted in greater fat deposition and reduced postpartum intake capacity. Instead, intensive feeding during the last trimester of gestation (LW change over 800 g/d) was advantageous in attaining maximal milk production.

7. The plane of nutrition during pregnancy had no effect on body size (wither height, body length) but a high plane of nutrition particularly during the first six months of gestation increased heart girth, hip width and body condition score of primiparous cows.

8. LW at parturition and daily gain before and after insemination had a positive genetic correlation with first lactation milk yield. Thus, it seems that genetic selection for higher milk yield will gradually lead to higher genetic growth potential. This change needs to be taken into account in future recommendations of daily gains acceptable for pre-pubertal dairy replacement heifers.

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