COMPENSATORY GROWTH IN DOUBLE MUSCLED BULLS

Different Periods of Feed Restriction Before Compensatory Growth in Belgian Blue Bulls: I. Animal Performance, Nitrogen Balance, Meat Characteristics and Fat Composition[1]

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[1] The IRSIA (Institut pour l'Encouragement de la Recherche dans l'Industrie et l'Agriculture, Brussels, Belgium) is gratefully acknowledged for financial help.

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ABSTRACT: Thirty double-muscled Belgian Blue bulls were maintained at a rate of gain of .5 kg/d during four length of time, 4 (G2), 8 (G3) or 14 (G4) mo (low growth period, LGP), before fattening (rapid growth period, RGP). Ten control animals (CG) were fed a high-energy, high-protein diet. The G2, G3, and G4 were fed a low-energy, low-protein diet during LGP and the same diet as CG during RGP. Live weight was recorded biweekly, feed consumption (FC) daily, and nitrogen balance at 3 occasions in each group. At the slaughterhouse, the 7, 8, and 9th ribs were removed to determine carcass composition, meat quality, and meat and fat composition. Compensatory growth reached a maximum 2 mo after refeeding. The G2 and G4 exhibited compensatory growth ($P < .05$) and had higher daily FC ($P < .001$). Feed conversion ratio (FCR) increased sharply after refeeding. Nitrogen balance was higher in compensating groups ($P < .05$). Compensating animals had higher carcass connective and adipose tissue contents ($P < .05$) but lower meat fat content ($P < .05$). Cattle exhibiting compensatory growth had higher redness, yellowness, hue, cooking losses and drip losses, but tended to have lower Warner-Bratzler peak shear force (WBPSF) values. The saturated fatty acid (SFA) content of the fat decreased with the length of the LGP. Compensatory growth in double-muscled bulls at the expense of higher feed intake increased peripheral fat but decreased intramuscular fat deposition.

Key Words: Belgian Blue Bulls, Compensatory Growth, Animal Performance, Carcass, Meat, Fatty Acids

Introduction

Compensatory growth is the ability of an animal to exhibit, after disease (Thomas et al., 1978) or feed restriction (Wilson and Osborn, 1960), larger growth rates than in unaffected animals of the same chronological age. In cattle, compensatory growth is well expressed when feed restriction occurs at a relatively late stage of life (Berge, 1991; Berge et al., 1991). Factors contributing to compensation are increases in feed intake (Baker et al., 1992), increases in gut-fill weight, or higher efficiency of feed utilization (Carstens et al., 1991). The response varies according to the pattern of undernutrition and realimentation, and stage of development of the animal (Wilson and Osborne, 1960). The Belgian Blue breed, double-muscled type, is a large beef breed with early maturity, characterized by high average daily gain, low feed conversion ratio, and high quality of carcass (Clinquart et al., 1991). Currently, there is no published work on compensatory growth in Belgian Blue bulls. Therefore, an experiment was conducted with Belgian Blue bulls in order to study the effects of a restricted growth, lasting for three different durations, on fattening performances. Results are presented in 2 papers. This paper summarizes animal performance, nitrogen balance, and carcass, meat, and fat characteristics.

Materials and Methods

Animals and Management

The Animal Care and Use Council of our institute approved the use and treatment of animals in this study. A total of 40 Belgian Blue bulls, double-muscled type, initial age and weight range of 9.7 mo and 310 ± 38 kg, were divided into four groups of similar live weight. In each group, four animals were randomly penned in individual stalls allowing for collection of urine and feces, and the remaining

six were housed in a stanchion barn with straw as bedding. Each group was randomly assigned to one of the four treatments. The first group (control, CG) was given from the beginning ad libitum access to a fattening diet allowing for rapid growth. The fattening diet was based on sugar beet pulp complemented with cereals, protein from vegetable origin, and a mineral mixture (Table 1). During three periods with different lengths of time, the other groups received a limited quantity of a low-energy, low-protein diet calculated to support an ADG of .5 kg daily gain (LGP, low growth period). The low growth diet was based on pelleted straw complemented with dried lucerne, cereals, protein from vegetable origin, and mineral mixture. The three groups, namely groups 2, 3, and 4 (G2, G3, G4), received the low-growth diet for 115, 239, and 411 d, respectively. Subsequently, G2, G3 and G4 were adapted to the concentrate fattening diet over a 15-d period of transition. The amount of concentrate feed was then progressively increased and animals were allowed to consume their ration on an ad libitum basis for about 1 mo after the beginning of the transition period. The concentrate diet was offered during the rapid growth period (RGP) which lasted until the animals were slaughtered. The animals were fed twice daily at 0600 and 1400 and were slaughtered per group when mean live weight reached at least 600 kg and when the average daily gain (ADG) was lower than 1 kg/d at two consecutive measurements.

Measurements

Feed intake of the bulls was recorded each day and live weight at 15-d intervals. Feed samples were withdrawn at regular intervals for chemical analysis. At the slaughterhouse, abdominal fat was removed from the carcass. Carcass weight was recorded and pH of both Longissimus thoracis muscles were measured (7, 8, 9 ribs) 1, 2, and 4 h postmortem using a Portamess 751 knick pH-meter (Knick

GmbH & Co, Berlin, Germany) with an Ingold "penetration" pH-electrode (Ingold AG, Urdorf, Switzerland).

Two days after slaughter, the 7, 8, and 9th ribs were removed from the carcass. They were dissected in order to separate lean meat, fat and connective tissue, and bones. Regressions of Martin and Torreele (1962) for double muscled cattle were then used to assess the composition of the carcass. Meat quality was determined from one 2.5-cm-thick cut of the longissimus thoracis muscle. Five measurements of the final pH were performed on this cut at 48 h postmortem using the technique described above. At the same time, the HunterLab Labscan II device was used for objectively measuring CIE Lab brightness (L*), redness (a*) and yellowness (b*) on 5 spots 2.5 cm diameter. Hue was estimated by a*/b* ratio. Seven days later, the cut was weighed in order to estimate drip loss, and heated in open plastic bags in a waterbath for 50 min at 75°C. After heating, they were cooled in cold tap water to room temperature, bags were drained, and cuts were mopped gently dry with paper tissue. The difference between raw and heated weights was recorded as cooking loss and expressed as a percentage of the raw weight. Warner-Bratzler shear force was determined with a Lloyd LR5K perpendicular to the fiber direction on 10, 1.25-cm-diameter cores obtained from the heated cuts.

The dry matter, ash, ether extract, and crude protein concentrations of the diets were determined according to official procedures (AOAC, 1975). The lipids from peripheral, intermuscular and intramuscular fat samples were extracted and saponified as described by Ter Meulen et al. (1975). The fatty acid composition of fat samples was determined by gas chromatography.

Statistical Analysis and Mathematical Modelling

Bulls were blocked (n = 10) by group (Figure 1). One-way analysis of variance, using group as a factor of variation, was used to analyze data. Data relative to muscle, connective and adipose tissue,

and bone proportions in the carcasses were compared by analysis of covariance, using group as factor of variation and slaughter weight as factor of covariance. Nitrogen balances either performed during LGP, after the transition period or before slaughter were compared at similar live weight using contemporary weight as factor of covariance. Two-way analysis of variance for a 3 x 4 design using location of fat (subcutaneous, inter- or intramuscular) and group as factors of variation was used to analyze data relative to fatty acid composition of fat (Dagnelie, 1975). Modelled evolution of the ADG over time was presented, assuming a quadratic evolution during the LGP and a cubic evolution during the RGP. The model was chosen from the maximum r^2 value within the expected evolution of the ADG. The evolution of ADG during compensatory growth was also studied by GLM procedure of SAS (SAS, 1990), using group and month after the beginning of the compensatory growth as factors of variation. Predicted maxima and minima were obtained from the model of compensatory growth by derivative of the function obtained from analysis.

Results

Table 2 summarizes the performance of the four groups during both periods.

Initial live weight was similar in the four groups (300 kg). The bulls from the CG gained 330 kg during the fattening period, which lasted for 252 d. Feed conversion ratio (FCR) and ADG were 7.37 kg/kg and 1.3 kg/d, respectively. As expected, the live weight at the end of the low-growth period was different in G2, G3, and G4, with values of 368, 435 and 486 kg, respectively ($P < .001$). The ADG was similar and close to .5 kg/d during LGP although it was slightly higher in G2 and lower in G4 ($P < .05$). Total feed consumption (FC) differed to a large extent because length of the LGP was different. Daily feed intake was close to 6 kg/d in the three groups, although higher in G4 ($P < .1$). The FCR was high and increased with the length of the LGP (10.21, 11.12 and 14.42 kg/kg in G2, G3 and G4 respectively, $P < .001$). Live weight at the beginning of the RGP was 402, 474 and 534 in G2, G3 and G4 ($P < .001$) and the fattening period lasted for 147, 120 and 112 d respectively. During RGP, ADG was higher in all three groups than in CG. G2 and G4, which exhibited the largest compensatory gains, also had the largest daily FC (11.8 and 12.1 vs 9.7 and 10.7 kg/d in control and G3 ($P < .001$). However, on a live weight basis, FC was the highest in G2 ($P < .05$). During RGP, FCR was quite similar in the four groups and close to 7.5 kg/kg; it was, however, slightly higher in G2 and G4. When both periods were considered, ADG decreased with increasing length of the LGP. Final live weight was similar in CG, G2, and G3 (631, 622, and 645 kg) and was quite higher in G4 (705 kg). During the whole experiment, total gain was higher in G4 (402.1 kg) than in CG, G2 and G3 (330.2, 320.0 or 340.5 kg, respectively, $P < .001$). Total feed consumption increased similarly as the total growth duration but daily absolute and relative consumption showed opposite evolutions.

The change with time of live weight gain, modelled evolution of the ADG determined between weight records, and FC are given in figure 2. The animals from G2 gained weight rapidly and reached their slaughter weight almost at the same age as CG. In G3 and G4, cattle were slaughtered 4 and 9 mo later, respectively, in winter and in summer because the length of LGP for cattle in G3 and G4 was much greater. The change over time of ADG during RGP was best fitted by a cubic relationship in G2, G3 and G4 (R^2 values respectively equal to 65, 81, and 81%). The maximum ADG after realimentation was close to 2 kg/d in G2 and decreased rapidly. In G3, the amplitude of compensation was less than G2 (1.5 kg/d) but the period during which animals exhibited ADG higher than 1 kg/d was longer than in G2 (140 d). In G4, the maximum ADG reached values close to those in G2, but it was obtained earlier. Animals from G4 were slaughtered before ADG decreased below 1 kg/d because most of them had leg injuries at the end of RGP. The largest growth rate occurred approximately 2 mo after the beginning of the transition period planned between LGP and fattening period. The best model of compensatory growth throughout the 3 compensating groups was cubic, i.e., ADG = .54 + 1.087 x mo - 0.314 x mo^2 + 0.024092 x mo^3 (R^2 = 0.47), where mo indicates the number of mo after the beginning of the transition period ($P < .001$ for the coefficients). Predicted maxima and minima of ADG, obtained from the derivative function, were 1.67 and .94 kg/d, respectively at 2.38 and 6.31 mo after the beginning of the transition period. Voluntary feed intake increased continuously during RGP and reached values of about 11 kg/d when maximum ADG occurred.

During LGP, N intake was limited to about 100 g N/d in G2, G3, and G4 (Table 3). During compensatory growth, N intake increased to values higher than in CG ($P < .05$), corresponding to compensatory intake. During LGP, apparently digested N, as well as N digestibility, were close to 63 g $N.d^{-1}$/animal and 63% respectively. The corresponding values were higher at 140 g $N.d^{-1}$/animal and 69% in CG. Values increased to 160 g N. d^{-1} /animal and 71% respectively, during compensatory

growth. In the CG, N retention was close to 50 g N/d. In the restricted groups, N balance was slightly over 20 g N/d during the LGP, but it increased to values higher than in CG during RGP ($P < .1$).

Table 4 summarizes the effects of treatment on slaughter characteristics and carcass composition. As the final live weight of animals from G4 was greater than in the other groups, their live weight at the slaughterhouse and carcass weight were higher (447 kg vs almost 400 kg in the other groups, $P < .01$). Dressing percentage was similar for CG, G2 and G4 but G3 was characterized by lower values than CG and G4 ($P < .05$). Animals from G4 yielded more lean meat than the others owing to a higher carcass weight ($P < .01$ or $< .001$), but the CG had a higher muscle proportion, while the lowest value was observed in G3 ($P < .05$). The amount of connective and adipose tissue increased from CG to G4 ($P < .05$) but percentages were, as opposed to muscle proportion, the highest in G3 and the lowest in CG. Bone proportion was lower ($P < .1$) in G4. The ratio between muscle to bone was similar among treatment and close to 6. Higher ratio between connective-adipose tissue and bone was observed in G3 and G4 when compared to CG ($P < .05$ or $P < .1$).

Meat quality characteristics are shown in table 5. Meat temperature decreased more rapidly in CG and more slowly in G4; G2 and G3 had a similar pattern ($P < .001$). By contrast, pH values in meat from G4 were lower 1 h, 2 h, and 4 h postmortem than in the other groups ($P < .01$ or .001). However, the pH observed 48 h postmortem was similar and close to 5.5 in all group. There were no differences in brightness measured 2 d postmortem. Both a* and b* values were higher in groups G2, G3 and G4 than in CG but the differences were only in G3 and G4 ($P < .01$, $P < .1$). Cooking losses were lower in CG than in the others groups ($P < .001$). Similarly, higher drip was observed in G3 and G4 when compared to CG and G2 ($P < .1$). The Warner-Bratzler peak shear force (WBPSF) was lower in G2, G3 and G4 than in CG but only G3 showed a significant difference ($P < .1$).

Chemical analysis of the meat (Table 6) revealed differences in ash, crude protein, ether extract, and cholesterol content ($P < .001$; $P < .01$; $P < .05$; $P < .1$). It was of interest to note that the ether extract value was lower in the groups previously restricted whereas the opposite was found for the connective and adipose tissue of the carcass. No difference in cholesterol content was found between CG, G2 and G3. However, G4 showed a lower cholesterol content than others groups ($P < .01$).

The fatty acid composition of the subcutaneous, intermuscular, and intramuscular fat is shown in Table 7. The major fatty acids were C16:0, C18:0 and C18:1, present in proportions of 30, 20, and 35%, respectively. However, large differences appeared between the three types of fat; intermuscular fat was richer in saturated fatty acids (SFA), with an equal proportion of C16:0 and C18:0, and intramuscular fat contained larger proportions of polyunsaturated fatty acids (PUFA), mainly as C18:2 ($P < .001$). The subcutaneous fat was richer in monounsaturated fatty acids (MUFA). The percentage of saturated fatty acids (SFA) decreased with increasing length of the LGP ($P < .01$). This effect was largely due to increases in MUFA contents and was observed in subcutaneous and intermuscular fat ($P < .01$, $P < .05$), but not in intramuscular fat, explaining that a factor of interaction was found between groups and fat effect ($P < .05$).

Discussion

In G2 and G3, the target live weight gain of .5 kg/d was difficult to achieve, mainly at the beginning of LGP (Figure 2). It was therefore necessary to further reduce feed intake. As a consequence of the experimental setup, the restrained animals had different ages and live weights at the start of the compensatory growth period. Thus, confounding effects between length of the low-growth period, animal age and live weight may have occurred. The significantly higher final live weight in G4 when compared to the other groups is explained by the heavy live weight at the beginning of the RGP, associated with the length of the restriction period, and by a large ADG during the fattening period.

Complete compensatory growth expresses the ability of a restricted animal to reach a weight of a control animal at similar age (Wilson and Osbourn, 1960; Ryan et al., 1993a). Such a growth was not possible in G3 and G4 because animals in these groups started the fattening period after the CG animals were slaughtered. In G2, compensation was partial, the slaughter occurring about 1 mo later than in CG. The lack of complete compensation has been reported many times by others (Abdalla et al;, 1988; Ellenberger et al., 1989; Carstens et al., 1991; Drouillard et al., 1991; Hayden et al., 1993). Ryan et al, (1993a) reported, however, a complete compensation with Hereford steers underfed during 3 mo before realimentation.

Both higher daily FC and FCR observed during RGP of compensating groups suggested that compensation was associated with increasing feed intake, without however achieving better efficiency of feed utilization. When FC was expressed on a weight basis, G2 only showed increased intake over CG, whereas in G3 and G4, higher intakes during fattening were the result of the higher live weight than in CG; there was therefore a compensatory intake in G2. Lopez Saubidet and Verde (1976) discarded compensatory feed intake as explanation for compensatory growth after long periods of

growth restriction. They postulated that compensatory growth was attributed to lower maintenance requirements. There was no evidence to support such a hypothesis in the present work. Neither G2, G3, nor G4 showed improved FCR as compared to CG during the RGP. Moreover, ADG related to live weight did not differ between CG and G2 or G3, and was lower in G4. Our results have to be related to the higher fat percentage in the carcass of compensatory groups animals. The efficiency of fat deposition is lower than that of lean meat deposition because lean meat contains larger proportions of water. The higher feed conversion ratio suggests that although high ADG were observed in compensatory groups when compared to CG, nutrients were directed towards fat rather than meat production. The higher N retention during compensatory growth as compared with the LGP may be ascribed to higher N input but also to higher N quality. The increase of N retention during RGP when compared to values in CG indicates that protein deposition was also increased. Carstens et al. (1991) found, in Hereford X Angus steers, that compensatory growth was associated with higher protein accretion in noncarcass protein. In the present experiment, we did not measure the protein content in noncarcass weight. So, the possibility that a higher noncarcass protein deposition occurred in animals that exhibited compensatory growth cannot be excluded.

The lower profile of compensation in G3 when compared with G2 and G4 may be explained by a seasonal effect, because the G3 animals were fattened during autumn and winter, so energy used for thermoneutral maintenance may have been increased (Scott et al., 1993). The rather similar profile in the response of G2 and G4 animals during RGP may be surprising when considering age difference. However, Drouillard et al. (1991) reported that the duration of a mild growth restriction was less important for compensatory growth than the severity of nutrient restriction. The mechanism of growth was perhaps different in the two groups.

The pattern of the daily gain with respect to time during RGP reached a maximum (cubic effect, Figure 2) at a value close to 1.7 kg/d. During realimentation, feed intake increased. It was likely that the previous restriction modified gut capacity so that changes in gut fill accounted partly for compensatory growth, as reported by Carstens et al. (1991). Moreover, during compensation, net energy requirements for growth decrease, as does energy for maintenance (Carstens et al., 1991). The efficiency of energy deposition increases and repletion of proteins, especially in tissues such as liver or digestive tract, allows for a rapid growth (Wright and Russel, 1991;Ryan et al., 1993b). However, according to Carstens et al. (1987, 1989), this phenomenon would be brief, about 19 d to 1 mo. Afterward, FCR increases, fat/protein deposition ratio enhances, and the ADG decreases. In the present experiment the FCR in compensating groups was never lower than in CG, as opposed to observations made by Ryan et al. (1993a) in Hereford steers. This might suggest that a beef breed with a very high potential for lean meat deposition and a low FCR is not able to improve growth during compensation without increasing feed intake.

At heavier weights, as found during the fattening period in G4, the capacity for fat deposition is enhanced (Rompala et al., 1985; Simon, 1989). In this group, FCR increased rapidly without any consistent decrease in ADG, suggesting increasing fat deposition. Fat proportion in carcasses of animals from G4 was, however, similar to that found in G2 or G3; but it must be remembered that the animals were slaughtered before ADG decreased to sufficiently low values. Higher fat deposition in the regions surrounding the gastrointestinal tract could also not be excluded.

The lower dressing percentage found in G3 (table 4) and a trend for a lower value in G2 compared to CG are in agreement with results from Smith et al. (1977) and Carstens et al. (1991) and suggest that the compensation occurs more in other compartments as carcass.

The ratio between muscle to bone is a good indicator of muscle development because it is independant of the degree of fatness (Berg and Butterfield, 1966). Although this ratio was similar among treatment when slaughter weight was used as factor of covariance, it was greater than values reported in other breeds (Shahin and Berg, 1985; Arthur et al., 1989) confirming the exceptional carcass quality of Belgian Blue bulls, double muscled type (Uytterhaegen et al., 1994). The unfavourable effect of compensatory growth on leanness of the carcass has been reported by some authors (Abdalla et al., 1988; Fumagalli, 1989) but not by others (Greenhalgh, 1986; Carstens et al., 1991; Yambayamba and Price, 1991). In the present experiment, all compensatory growth groups showed a trend for or a significantly higher percentage of connective and adipose tissue in the carcass when compared to CG, suggesting an effect of the treatment or of the age of animals. Nevertheless, the animals from G2 had live weight and age similar to those of animals in CG. It appears thus that in this group the compensatory growth had negative effects on leanness of the carcass. The higher ratio between connective and adipose tissue to bone in G2, G3 and G4 confirmed that compensatory groups deposited proportionnaly more fat than CG.

In this respect, the lower proportion of fat in meat of the realimented groups was rather surprising, because advancing age is known to increase the fat proportion in muscle (Szucs et al., 1987; Grosse et al., 1991; Duckett et al., 1993). However, it could be hypothesized that during compensatory growth a developing muscle induces the production of young and therefore leaner meat, either by muscle fiber hypertrophy or by proliferation and incorporation of satellite cells in preexisting fibers (Swatland, 1977). So, compensatory growth possibly increased the proportion of peripheral fat such as subcutaneous or intermuscular fat but decreased the proportion of fat in muscle tissue. Similar results have been reported by Garcia and Casal (1992) with compensatory growth in Angus steers treated with zeranol implants. The lower fat content in meat from G2, G3 and G4 gave thus a meat more in

agreement with the recommandations of the Dietary Guidelines for Americans (1995). The lower meat cholesterol content in G4 probably is related to the lowest ether extract found in this group.

Assuming that slaughterhouse temperature was quite similar in each group at slaughter, the slower decrease of meat temperature after slaughter in G2, G3, and G4 with respect to CG may be explained by the higher proportion of carcass fat preventing heat escape (Lochner et al., 1980). A slower drop in temperature was associated with a quicker decrease of meat pH because higher meat temperature stimulated enzymatic activity and accelerated the rate of pH decline in muscle (Bush et al., 1967; Dutson, 1983). However, no changes in meat pH occurs 48 h postmortem. Higher a* and b* values in groups that exhibited a compensatory growth may come from the higher meat temperature early postmortem. Bruce and Ball (1990) observed increased redness and decreased blueness of steaks maintained to higher curve of declining temperature when compared to low temperature treatment. Higher values in color parameters may also be related to an age effect, because older animals always have a larger amount of myoglobin in muscle (Barton-Gade et al., 1988). Average daily gain has been reported as a possible factor of influence on meat color (Itoh et al., 1989), a* and b* tending to be negatively and positively correlated, respectively. There were, however, no elements that indicated a relationship between ADG and color parameters in this experiment. The higher cooking losses observed in realimented groups and the increase in drip value observed with the length of the restriction period are in agreement with the lower percentage of fat in the meat of these animals, a low fat content in meat being associated with a high water content (Szucs et al., 1987; Grosse et al., 1991). Alteration in water holding capacity could also be ascribed to changes in post-mortem meat temperature or pH (Honikel et al., 1968). However, several experiments report the lack of relation between these parameters (Bruce and Ball, 1990; Boakye, 1993). The lower shear force index found in G2 and G3 may be explained by the production of a younger meat, therefore poorer in connective

tissue. The postmortem muscle temperature was also higher, enhancing meat tenderness by accelerating the aging process (Yates et al., 1983; Lee, 1986). In G4, a more structured connective tissue related to the older age of the animals might explain lower meat tenderness when compared to G2 and G3. The numerically higher tenderness found in G2, G3 and G4 may also be explained by the higher growth rate before slaughter in these groups. Possibly, these groups contained higher amounts of endogenous proteolytic enzymes before slaughter, as suggested by Aberle et al. (1981) and Van eenaeme et al. (1994).

The prevalence of oleic , stearic, and palmitic acids, which accounted for about 85% of the total fatty acids, was in agreement with values commonly accepted for beef fat (Clinquart et al., 1991; Duckett et al., 1993). The larger concentration of PUFA in intramuscular fat at 13.2 mol/100 mol was probably due to the extraction of a higher proportion of phospholipids from the structural components of muscle cell membranes, which are rich in linoleic acids (Duckett et al., 1993). A significant effect of a period of restriction followed by realimentation appeared on the proportion of saturated fatty acids (SFA) in G3 and G4 when compared to CG and G2. The SFA proportion decreased proportionally with the duration of the low growth period, indicating that the age of the animals may have had stronger effects than compensatory growth.

Implications

The reduction of growth in a growing fattening system with double-muscled bulls may be beneficial under some conditions. An almost complete compensatory growth was observed when the low growth period was relatively short, overcompensation being difficult to obtain. However, growth potential seemed to be maintained until advanced age. Although carcass quality was reduced owing to increased fat proportion, meat was leaner and fat richer in unsaturated fatty acids. Further trials need to be conducted with a large size beef breed in order to locate the period of growth restriction in the pattern of overall growth curves.

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Table 1. Composition of the diets.

Item	Period	
	LGP[a]	RGP[b]
Dry matter, %	87.9	87.2
Ingredient, % DM		
Sugar beet pulp	7.7	38.1
Barley	5	8.1
Maize	-	8.1
Spelt	5.4	8.1
Middlings	5	8.1
Soy bean meal	1.8	11.3
Linseed meal	-	3.6
Molasses	1.4	3.6
Dried lucerne	8	-
Pelleted straw	54.1	-
Straw	9.8	9.8
Mineral mixture	1.6	1.1
Chemical analysis, g/kg of DM		
Organic matter	912.2	924.5
Crude protein	113.7	156.8
Ether extract	18.2	25.7
Acid detergent fiber	392.2	244.8
Ca	9	10.1
P	4.3	4.6

[a] Low growth period.

[b] Rapid growth period.

Table 2. Animal performances during fattening (CG) or during low growth periods (LGP) lasting for 4, 8, or 14 mo (G2, G3, G4) before a fattening period (RGP) in Belgian Blue double muscled bulls.

	Group					
Item	CG	G2	G3	G4	Levels of significance	SEM
Low growth period						
Initial weight, kg		301.9	306.1	302.7	NS	12.88
Final weight, kg		367.7^{a}	434.9^{b}	485.7^{c}	***	12.13
Total gain, kg		65.8^{a}	128.8^{b}	183.1^{c}	***	6.33
Length, d		114.7^{a}	238.6^{b}	411.2^{c}	***	3.42
Average daily gain, kg/d		.57^{a}	.54^{a}	.44^{b}	**	.023
Total feed consumption, kg (1)		672^{a}	1411^{b}	2618^{b}	***	36.18
Mean feed consumption, kg/d		5.9^{a}	5.9^{a}	6.4^{c}	+	.13
Feed conversion ratio, kg/kg (1)		10.21^{a}	11.12^{b}	14.42^{c}	***	.33
Rapid growth period						
Initial weight, kg	300.5^{a}	401.9^{b}	473.6^{c}	533.6^{d}	**	14.46
Final weight, kg	630.7^{a}	621.9^{a}	646.6^{a}	704.8^{b}	*	17.99
Total gain, kg	330.2^{a}	220.0^{b}	172.9^{c}	171.2^{c}	**	10.44
Length, d	252.3^{a}	146.6^{b}	120.2^{c}	111.6^{c}	***	4.57
Average daily gain, kg/d	1.32^{a}	1.51^{b}	1.43^{ab}	1.53^{b}	*	.86
First month, kg/d	1.59^{b}	1.86^{b}	1.14^{a}	1.79^{b}	*	.91
Second month, kg/d	1.49^{a}	1.93^{b}	1.60^{b}	1.62^{b}	+	.90
Third month, kg/d	1.56	1.46	1.47	1.28	NS	.95
Total feed consumption, kg	2424^{a}	1700^{b}	1283^{c}	1355^{c}	***	44.03
Mean feed consumption, kg/d	9.7^{a}	11.8^{c}	10.7^{b}	12.1^{c}	+	.33
Feed conversion ratio, kg/kg	7.37	7.71	7.53	7.92	NS	.16
Both periods						
Initial weight, kg	300.5	301.9	306.1	302.7	NS	13.75
Final weight, kg	630.7^{a}	621.9^{a}	646.6^{a}	704.8^{b}	*	17.99
Total gain, kg	330.2^{a}	320.0^{a}	340.5^{a}	402.1^{b}	***	11.69
Length, d	252.3^{a}	291.2^{b}	389.8^{c}	557.7^{d}	***	5.43
Average daily gain, kg/d	1.32^{a}	1.10^{b}	.87^{c}	.72^{d}	***	.033
Total feed consumption, kg	2425^{a}	2559^{b}	2968^{c}	4270^{d}	***	60.67
Mean feed consumption, kg/d	9.7^{a}	8.8^{b}	7.6^{cd}	7.6^{d}	***	.192
Feed conversion ratio, kg/kg	7.37^{a}	8.00^{b}	8.74^{c}	10.65^{d}	***	.16

^{a,b,c,d} Means within a row with common superscript do not differ at $P < .1$ (+), $P < .05$ (*), $P < .01$ (**) or $P < .001$ (***). NS: not significant ($P > .1$)

(1) reported on the basis of air dry values

Table 3. N intake, N digested, N digestibility and N balance during fattening (CG) or during low growth periods (LGP) lasting for 4, 8, or 14 mo (G2, G3, G4) before a fattening period (RGP) in Belgian Blue double muscled bulls [(1).]

	Group					
Items	CG	G2	G3	G4	Levels of significance	SEM
Low growth period						
N intake ($g.d^{-1}$/animal)		100.57	98.43	98.43	NS	4.67
Digested N ($g.d^{-1}$/animal)		63.09	63.67	62.95	NS	2.93
N digestibility (%)		62.7	64.7	63.9	NS	1.44
N balance ($g.d^{-1}$/animal)		21.28	21.56	23.78	NS	3.28
Rapid growth period						
N intake ($g.d^{-1}$/animal)	202.38^{a}	213.29^{ab}	217.56^{ab}	238.89^{b}	*	6.68
Digested N ($g.d^{-1}$/animal)	140.45^{a}	156.47^{ab}	155.67^{ab}	171.39^{b}	*	6.19
N digestibility (%)	68.79^{a}	72.89^{b}	71.48^{ab}	71.69^{ab}	+	0.90
N balance ($g.d^{-1}$/animal)	53.25^{a}	67.85^{b}	65.32^{ab}	72.52^{b}	+	3.81

[a,b] Means within a row with common superscript do not differ at $P < .1$ (+), $P < .05$ (*), *or* $P < .01$ (**). NS: not significant ($P > .1$)

(1) data compared by analysis of covariance, using contemporary live weight as factor of covariance.

Table 4. Slaughter characteristics and carcass composition in Belgian Blue double muscled bulls slaughtered after fattening (CG) or after a low growth periods (LGP) lasting for 4, 8, or 14 mo (G2, G3, G4) followed by a fattening period (RGP).

	Group					
Items	CG	G2	G3	G4	Levels of significance	SEM
Slaughter characteristics						
Final live weight, kg	630.7[a]	633.3[a]	646.6[a]	704.8[b]	*	17.27
Slaughter weight, kg	620.6[a]	613.4[a]	630.2[a]	693.3[b]	*	17.09
Warm carcass weight, kg	398.9[a]	390.4[a]	396.2[a]	447.0[b]	**	11.52
Dressing percentage, %	64.3[a]	63.6[ab]	62.9[b]	64.5[a]	*	.41
Carcass composition						
Yield, kg						
Muscle	298.5[a]	285.5[a]	285[a]	334.4[b]	**	8.36
Connective-adipose tissue	49.6[a]	53.3[ab]	59.5[bc]	64.0[c]	*	3.00
Bone	51.7	51.6	50.4	54.3	NS	1.65
Proportion, % (1)						
Muscle	74.7[a]	73.1[ab]	72.3[b]	73.9[ab]	*	4.25
Connective and adipose tissue	12.4[a]	13.6[ab]	14.9[b]	14.1[ab]	*	3.58
Bone	12.9	13.3	12.8	12.0	NS	2.49
Muscle/bone ratio	5.84	5.54	5.66	6.11	NS	2.17
Connective-adipose tissue/bone ratio	0.97[a]	1.03[ab]	1.17[b]	1.14[b]	+	0.17

[a,b,c] Means within a row with common superscript do not differ at $P < .1$ (+), $P < .05$ (*), *or* $P < .01$ (**). NS: not significant ($P > .1$)

(1) data compared by analysis of covariance, using slaughter weight as factor of covariance.

Table 5. Meat quality parameters after a period of fattening (CG) or after slow growth lasting for 4, 8, or 14 mo (G2, G3, G4) followed by rapid fattening (RGP), in Belgian Blue double muscled bulls.

	Group					
Items	CG	G2	G3	G4	Levels of significance	SEM
Temperature at 1h, °C	37.6[b]	38.5[a]	38.5[a]	39.4[c]	*	.24
Temperature at 2h, °C	34.7[a]	35.1[a]	36[a]	38.8[b]	**	.56
Temperature at 4h, °C	24.1[b]	27.3[a]	28.2[a]	31.9[c]	**	.72
pH at 1h	6.6[ab]	6.8[a]	6.6[b]	6.3[c]	+	.058
pH at 2h	6.4[a]	6.6[b]	6.4[ab]	6.1[c]	+	.073
pH at 4h	6.1[a]	6.0[a]	6.0[a]	5.6[b]	***	.062
pH at 48h	5.6	5.5	5.5	5.5	NS	.032
Brightness L*, %	42.5	41.2	42.0	42.8	NS	.83
a*	16.2[a]	16.9[a]	18.5[b]	18.4[b]	*	.49
b*	16.0[a]	16.4[ab]	17.2[b]	17.7[c]	+	.44
Hue a*/b*	1.01	1.03	1.08	1.05	NS	.022
Cooking loss, %	19.8[a]	22.1[b]	26.1[b]	25.0[b]	*	.9
Drip loss, %	4.3[ac]	3.5[c]	4.9[ab]	5.2[b]	*	.31
Warner Bratzler peak shear force, N	40.3[bc]	33.6[ab]	29.6[a]	38.0[bc]	+	2.79

[a,b,c] Means within a row with common superscript do not differ at $P < .1$ (+), $P < .05$ (*), $P < .01$ (**) or $P < .001$ (***). NS: not significant ($P > .1$)

Table 6. Chemical composition of Longissimus Thoracis muscle from Belgian Blue double muscled bulls, slaughtered after fattening (CG) or after low growth periods (LGP) lasting for 4, 8, or 14 mo (G2, G3, G4) followed by a fattening period (RGP) in Belgian Blue double muscled bulls.

Item	Group					
	CG	G2	G3	G4	Levels of significance	SEM
Dry matter, %	25.0	25.0	24.2	24.8	NS	.38
Ash, % of DM	4.1[a]	4.3[ab]	4.8[c]	4.5[b]	*	.07
Crude protein, % of DM	85.6[a]	89.0[b]	86.9[a]	89.4[b]	*	.71
Ether extract, % of DM	6.2[a]	4.7[b]	4.7[b]	4.1[b]	+	.56
Cholesterol, % of DM	.23[a]	.23[a]	.24[a]	.15[b]	**	.15

[a,b,c] Means within a row with common superscript do not differ at $P < .1$ (+), $P < .05$ (*), $P < .01$ (**) or $P < .001$ (***). NS: not significant ($P > .1$)

Table 7. Fatty acid composition (mol/100 mol) of subcutaneous, intermuscular and intramuscular fat in Belgian Blue double muscled bulls, slaughtered after fattening (CG) or after low growth periods (LGP) lasting for 4, 8, or 14 mo (G2, G3, G4) followed by a fattening period (RGP).

	Fatty acids									
Item	C14:0	C16:0	C16:1	C18:0	C18:1	C18:2	C18:3	SFA[1]	PUFA[1]	MUFA[1]
Group										
CG	3.2^{a}	29.5^{a}	1.9^{a}	22.1^{ab}	35.3^{a}	6.9^{a}	1.07^{a}	54.9^{ab}	8.0	37.2^{ab}
G2	2.5^{b}	29.1^{a}	1.6^{b}	23.5^{a}	34.4^{a}	7.8^{b}	1.00^{a}	55.2^{a}	8.8	36.0^{a}
G3	3.2^{a}	31.8^{c}	2.2^{a}	18.7^{c}	36.9^{b}	6.2^{a}	1.06^{a}	53.7^{b}	7.3	39.0^{c}
G4	3.0^{a}	27.8^{d}	2.4^{c}	20.9^{b}	37.4^{b}	6.5^{a}	1.68^{b}	52.0^{c}	8.2	39.9^{c}
Levels of significance	**	*	+	*	+	+	***	+	*	*
SEM	.15	.51	.19	.99	.70	.76	.10	.78	.83	.81
Fat										
subcutaneous	3.7^{a}	31.4^{a}	3.2^{a}	18.3^{a}	38.2^{a}	4.2^{a}	1.0^{a}	53.5^{a}	5.2^{a}	41.4^{a}
intermuscular	2.8^{b}	27.8^{b}	1.6^{b}	25.8^{b}	36.3^{b}	4.6^{a}	1.0^{a}	56.6^{b}	5.6^{a}	37.8^{b}
intramuscular	2.4^{c}	29.5^{c}	1.4^{b}	19.6^{a}	33.8^{c}	11.6^{b}	1.6^{b}	51.6^{c}	13.2^{b}	35.1^{c}
SEM	.10	.44	.10	.71	.56	.33	.10	.59	.36	.61
Levels of significance	**	**	***	***	**	***	***	*	***	***
Interaction	NS	NS	NS	.1	.01	.1	NS	.05	NS	.05

[1] SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids

[a,b,c] Means within a row with common superscript do not differ at $P < .1$ (+), $P < .05$ (*), $P < .01$ (**) or $P < .001$ (***). NS: not significant ($P > .1$)

Figure 1. Experimental design. Dates relative to fattening of control group (CG) or low growth periods (LGP) for 4, 8, or 14 mo (G2, G3, G4) before a fattening period (RGP) in Belgian Blue double muscled bulls. Arrows indicate the moment of N balance measurements.

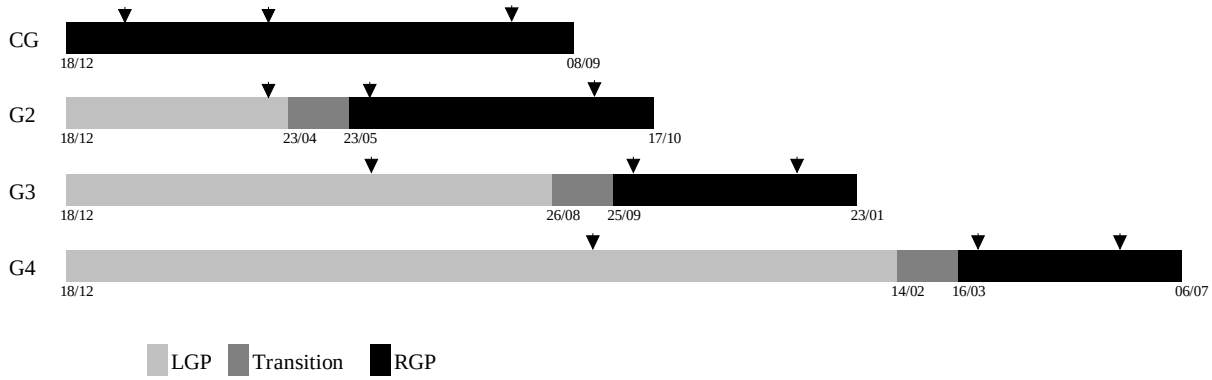
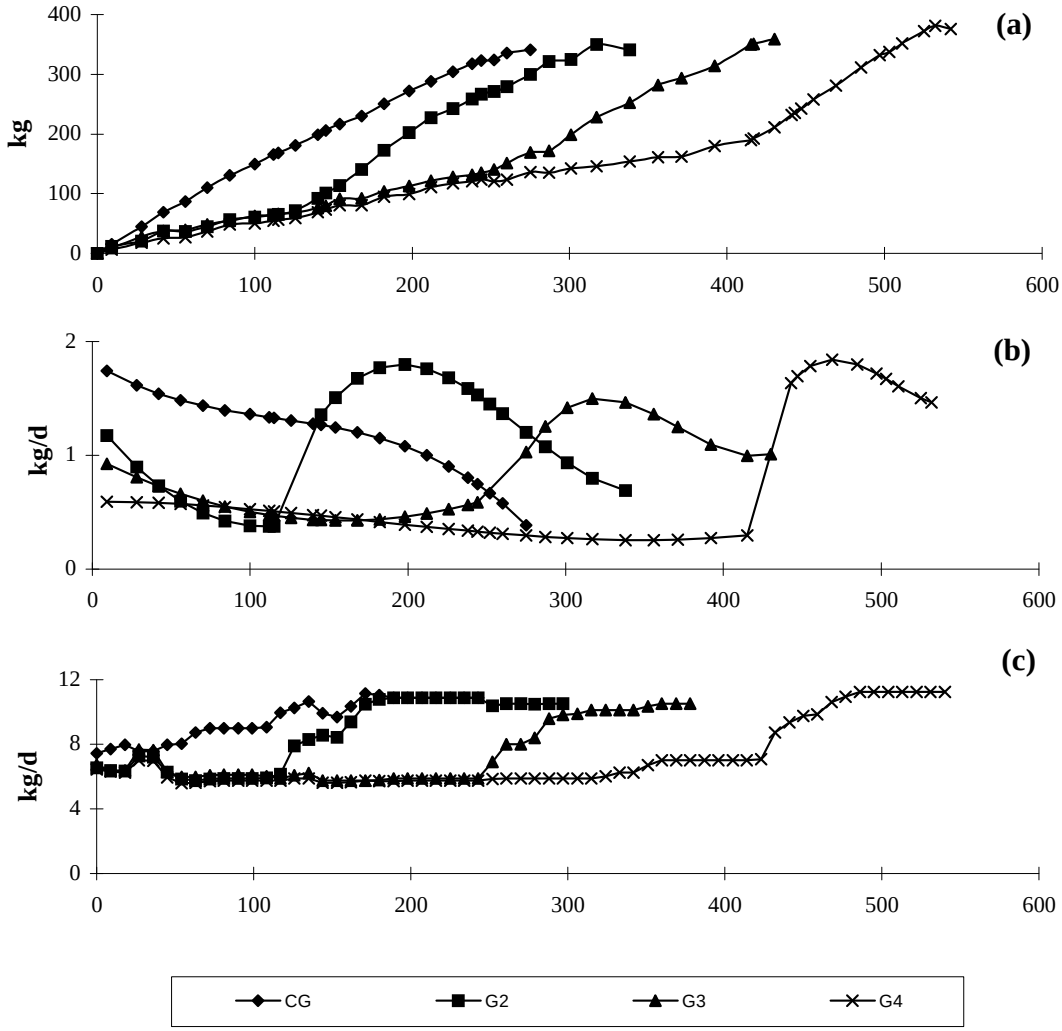

CG
18/12
08/09
G2
18/12
23/04
23/05
17/10
G3
18/12
26/08
25/09
23/01
G4
18/12
14/02
16/03
06/07
LGP
Transition
RGP

Figure 2. Evolution of live weight gains (1a), estimated ADG (1b) and daily feed intake (1c) during fattening (CG) or during low growth periods (LGP) lasting for 4, 8, or 14 mo (G2, G3, G4) before a fattening period (RGP) in Belgian Blue double muscled bulls.


(a)
kg
400
300
200
100
0
0
100
200
300
400
500
600
(b)
kg/d
2
1
0
0
100
200
300
400
500
600
(c)
kg/d
12
8
4
0
0
100
200
300
400
500
600
CG
G2
G3
G4