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**Original article**

# Small intestine growth and morphometry in piglets weaned at 7 days of age. Effects of level of energy intake

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**Abstract** — Two trials involving a total of 56 pigs were conducted to examine the effects of weaning at 7 d of age (trial 1) and of energy intake level and length of post-weaning underfeeding period (trial 2) on small intestinal (SI) development and morphometry. At 3 d after weaning, weight of the SI and mucosa (g/kg body weight) and villous height along SI were reduced by 20, 36 and 41%, respectively, compared to the day of weaning. Intestinal morphometrical changes are dependent on SI site and days post-weaning. Villous atrophy on d 3 and recovery on d 14 post-weaning were greater and occurred earlier in the proximal than in the medial and distal SI. Villous height was dependent on the level of energy intake which explains 56% of the variations in proximal SI villous height in weaned pigs and 73% when data of the sow-reared pigs were included in the analysis. Moreover, after 4 d of refeeding, underfed piglets showed similar villous characteristics to piglets fed a continuously high feeding level after weaning stressing that capacities of intestinal restoration were not affected by the length of the post-weaning underfeeding period. Overall, the present results suggest a spatial and temporal effect of weaning on villous atrophy and recovery, and that the level of energy intake is a major factor accounting for the post-weaning villous height.

**weaning / level of food intake / small intestine / morphometry / piglet**

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## 1. INTRODUCTION

From a nutritional point of view, weaning implies a switch to a complex diet, usually provided in a dry form, at an age when most piglets have little experience with solid feed [33]. As a consequence, weaning results in a growth check caused by a period of low feed intake with the latency to the first feed being variable and up to 2–3 d [2,3]. Successful adaptation to these changes requires profound morphological and enzymatic adjustments of the gastrointestinal tract. In this respect, a consistent feature associated with weaning is a transient shortening of the small intestinal villi and a reduction in the absorptive capacity (for review, see [29, 36]). These alterations are assumed to impair the ability of the small intestine to digest and absorb nutrients and to predispose the weanling piglet to malabsorption and diarrhoea [27, 46]. Although several factors may account for these morphological changes, there is increasing evidence that the level of feed intake is an important factor [27, 34, 47]. However, less is known on the effects of weaning on the spatial and temporal changes in intestinal morphology and on the speed of recovery.

In major pig producing countries, piglets are weaned between 21 and 28 d of age or there about 14 d as a disease-control procedure. However, the development of more prolific genotypes is now successful [24]. As a consequence, in a batch farrowing system, the total number of live born piglets sometimes exceeds the rearing capacity of the batch. A management strategy aiming at saving these supernumerary piglets includes adoption at 24–36 h of age by a foster sow followed by weaning at 6–8 d of age [32]. Therefore, the studies reported herein were aimed at examining the effects of early weaning and the level of feed intake on small intestinal growth and morphological changes in the small intestine of piglets. Moreover, the effect of length of the underfeeding period on intestinal recovery was investigated.

## 2. MATERIALS AND METHODS

### 2.1. General

Treatments and experiments were conducted according to the European Community regulations concerning the protection of experimental animals. In the light of saving piglets in excess of the rearing capacity of the sow, weaning at 6–8 d of age is accepted by the European legislation [38]. Two trials involving a total of 56 crossbred Large White × Landrace piglets of both sex were designed to examine (i) the effects of weaning at 7 d of age on the post-weaning pattern of intestinal morphometry (trial 1) and (ii) the effect of level of food intake on intestinal morphometry (trial 2). Because feed intake in the immediate days following weaning is usually very variable [23], tube feeding was chosen to feed the piglets while enabling a precise measurement of food intake. At weaning, piglets underwent surgery for the insertion of an oesophageal flexible polyvinyl tube (I.D. 3 mm, E.D. 4 mm) (Vygon, Ecouen, France) as previously described [22]. This procedure was usually completed in less than 8 min by which time the piglets regained consciousness. The extremity of the cannula was connected to a swivel located above the piglets' cages thus allowing free mobility of the animal. Previous studies [19, 20] indicated that tube feeding has no detrimental effect on the piglet growth rate or digestive function.

Piglets were fed a complete commercial piglet formula based on dairy products, extruded cereals, fish meal, toasted soybean, soybean and coprah oil and containing levels of vitamins, minerals and trace elements which meet the NRC requirements for piglets [31]. Its chemical composition is given in Table I. Before each feeding, the powdered diet was vigorously mixed with water to a final concentration of 200 $g \cdot L^{-1}$ from d 1 to d 7 post-weaning and 250 $g \cdot L^{-1}$ during the remaining period. The liquid feed was warmed to 37 °C and slowly administered with a syringe via the cannula. The

**Table I**. Gross chemical composition of the diet[1].

| | |
|---|---|
| Dry matter | 92.80 |
| Crude protein (N × 6.25) | 21.70 |
| Lysine | 1.85 |
| Lipids | 11.95 |
| Lactose | 21.00 |
| Starch | 20.60 |
| Ash | 7.55 |
| Crude fiber | 1.65 |
| Metabolisable energy, $kJ \cdot g^{-1}$ [2] | 16.64 |

[1] $g \cdot 100\ g^{-1}$ diet.
[2] Metabolisable energy was determined from the 6 piglets killed at 14 d post-weaning by a 10-d collection of faeces and urine starting on d 4 post-weaning.

piglets were given their calculated feed allocation 6 times daily (at 0700, 1000, 1300, 1600, 1900 and 2300). The actual amount of feed delivered was measured by weighing the syringe before and after feeding. Piglets had no access to additional water. They were housed individually in stainless-steel metabolic cages (40.5 × 40.5 × 50 cm) allowing separate collection of faeces and urine. Room temperature was initially set at 32 °C, progressively decreased to 28 °C on d 7 post-weaning and remained constant thereafter.

### *2.1.1. Trial 1*

Thirty piglets were used in trial 1. Twenty-four piglets from 6 litters were weaned at 7 d of age. They were allotted to the following treatments on the basis of litter origin and body weight (BW) (6 piglets per treatment): killed at weaning, 3, 7 or 14 d post-weaning. Actual ages at killing were 7, 10, 14 and 21 d, respectively. In addition, 6 contemporary piglets were killed at 21 d of age to serve as sow-reared (SR). Both BW at birth and at 7 d of the SR piglets were similar to those of the piglets killed or weaned at 7 d of age. No creep feed was provided during this period, but pigs had access to sow feed. However, examination of the stomach contents at killing revealed that they had not consumed solid feed. Daily amounts of feed administrated to the weaned (W) piglets are presented in Figure 1A. They were calculated in order to mimic what was found in a large number of piglets [32].

### *2.1.2. Trial 2*

Twenty-six piglets were weaned at 7 d of age and assigned to 5 treatment groups (G) according to litter origin and BW. G1 ($n$ = 4, H) and G2 ($n$ = 6, HH) were fed a high level of feed intake and killed at 3 (G1) or 7 d (G2) post-weaning, respectively. G3 ($n$ = 4, L) and G4 ($n$ = 6, LL) were fed a low level of feed intake and killed at 3 (G3) or 7 d (G4) post-weaning, respectively. A fifth group ($n$ = 6, LH) was fed as G3 during the first 3 post-weaning days and was switched to a high level of feed intake during the remaining period and killed at 7 d post-weaning. Daily amounts of feed administered to piglets are presented in Figure 1b.

## 2.2. Slaughter procedure

Both SR and W piglets were killed 2:30 h after their final meal. Piglets were killed by an intra cardiac administration of an overdose of sodium thiopental (Nesdonal, Merial, France, 30 $mg \cdot kg^{-1}$ BW) and were exsanguinated. The stomach, the entire small intestine (SI) from the pyloric sphincter to the ileocoecal junction and the large intestine (LI) were removed. The SI was laid on a sheet of glass placed on crushed ice. The SI was separated from the mesentery, flushed with cold isotonic saline, blotted dry, weighed and its length was determined. It was divided into three segments of equal length (proximal, medial and distal intestine) and was weighed. A small mid-segment was removed from each intestinal segment for histology. Each remaining portion had its length determined and weighed. The mucosa was removed using a glass microscope slide, weighed, homogenized in a container immersed in crushed ice and sampled. Stomach and LI were emptied, flushed with water, blotted dry and weighed.

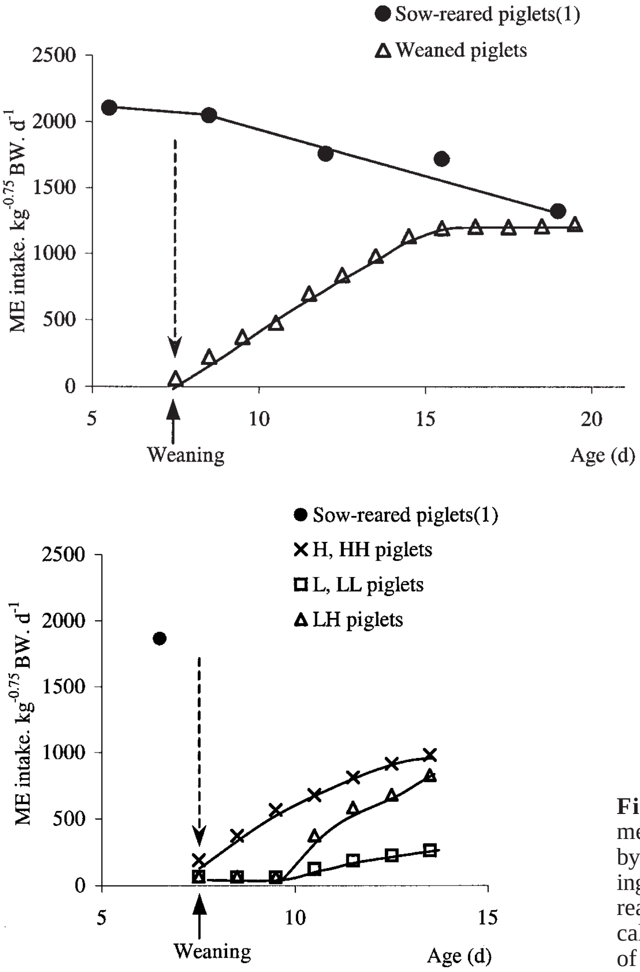

**Figure 1**. Daily amount of metabolisable energy (ME) intake by suckling and weaned piglets during trial 1 (**A**) and 2 (**B**). (1) In sow-reared piglets, milk ME intake was calculated from the conversion rate of ME into body weight gain [23].

### 2.3. Histology

In both trials, measurements of villous height and crypt depth were made under blind conditions. SI morphometry was determined using two techniques. In trial 1, small sections of SI were cut longitudinally and stored in 0.1 M (7%) formalin. Thereafter, the samples were dehydrated and stained with Schiff reagent. Samples were microdissected [13] under binocular optical. Villi and crypts were observed by light microscope at a magnification of 10 and 16, respectively, and analysed by an image analyser (Optimas v.6.5 software, Media Cybernetics, Silver Spring, USA, 1999) coupled with a light microscope via a camera. At least, 20 crypts (range 20–25) and 30 villous (range 30–42) were measured per segment, thus allowing to examine villous height distribution. The villous width was measured at mid-height of the villous.

In trial 2, SI samples were cut longitudinally, fixed in Bouin solution during 5 d, dehydrated in ethanol (70.0, 96.0 and 99.8% successively), put in xylen and embedded in paraffin. Serial, histological sections of 5 μm thickness were stained with hematoxylin and eosin for morphometry analysis under light microscope. For each intestinal segment 10 villi and 10 crypts were measured and mean villous height and width, and crypt depth per segment were calculated. Measurements were performed at a small magnification with a Nikon optical binocular microscope coupled via a Nikon camera to a PC computer with Lucia G v.4.6 software (Laboratory Imaging Ltd., Prague, Czech Republic). Measurements made on 6 samples using the microdissection technique provided average values of 879 ± 83 μm for villous height and 116 ± 29 μm for crypt depth. Corresponding values provided by the technique of paraffin embedding were similar averaging 830 ± 74 μm and 117 ± 9 μm, respectively.

### 2.4. Statistical analysis

For clarity and because there were marked differences in the BW of the piglets, digestive organ characteristics were expressed per kg BW. In experiments 1 and 2, analysis of variance was performed using the General Linear Model procedure of the Statistical Analysis System (SAS) [40] for the effect of treatments. In trial 1, differences between treatments were assessed using the Least Significant Difference (LSD) test. In trial 2, differences between treatments at 3 and 7 d post-weaning and paired comparison (L vs. LL, L vs. LH and H vs. HH groups) were assessed using the LSD test. The analysis of villous height and width, and crypt depth included treatment, site and treatment × site interaction effects. Linear and quadratic effects of post-weaning age (trial 1), level of feed intake at 7 d post-weaning (trial 2) and SI site within treatment (trial 1 and 2) were determined using the contrast method. In trial 1, villi were classified into long (> 600 μm), intermediate (400–600 μm) and short (< 400 μm). Distribution of villous height was analysed using a Chi square test. Regression equations relating villous height to energy intake were determined using the REG procedure of SAS [40].

## 3. RESULTS

### 3.1. General

Average weaning weight of the piglets of trial 1 and 2 was 2720 ± 330 and 2620 ± 360 g, respectively. No digestive disturbance was observed in both trials. As expected, due to the imposed dramatic decrease in feed intake (Figs. 1A and 1B), W piglets displayed a growth check immediately post-weaning. In trial 1, the average reduction in BW was 246 ± 115 g accounting for 9% of the weaning weight. All piglets had recovered the check in growth rate by the 3rd and 4th post-weaning day. During the overall post-weaning period (d 7 to d 21), W piglets grew at a mean rate of 152 ± 7 $g \cdot d^{-1}$ which was lower ($P < 0.001$) than the 270 ± 26 $g \cdot d^{-1}$ found in the SR piglets. At 21 d of age, W piglets were 24% ($P < 0.01$) lighter than the SR ones. In trial 2, the reduction in BW was dependent on the level of feed intake, averaging 245 ± 20 g in piglets on the low feeding level which was higher ($P < 0.001$) than the 130 ± 22 g found in those on the high feeding level. At killing, LL piglets had not recovered their weaning weight, whereas LH and HH piglets had a similar BW which was 30% ($P < 0.05$) higher than that of the LL piglets.

### 3.2. Digestive organ development and small intestine morphometry

### *3.2.1. Trial 1*

Immediately post-weaning, there was a dramatic decrease in SI and mucosa weights ($P < 0.001$, Tab. II), with the decrease being more pronounced for the mucosa (36 vs. 20%). Similarly, there was a decrease in the segmental weight ($g \cdot cm^{-1}$) of SI and mucosa, with only the decrease in the mucosa segmental weight being significant ($P < 0.001$). Thereafter, there was a linear increase ($P < 0.001$) in the SI characteristics. In the SR piglets, both SI and mucosa weights

**Table II.** Live weight, organ weight and small intestine (SI) length of sow-reared (SR) and weaned (W) pigs (trial 1).

| Treatment | SR | W | | | SR | Statistical significance[2] | |
|---|---|---|---|---|---|---|---|
| Age (d) | 7 | 10 | 14 | 21 | 21 | | Within W pigs (d 3 to d 14 post-weaning) |
| Post-weaning day | | 3 | 7 | 14 | | SEM | |
| Live weight, kg | $2.65^{d}$[1] | $2.68^{d}$ | $3.29^{c}$ | $4.93^{b}$ | $6.52^{a}$ | 0.18 | Q* |
| Stomach, g·kg$^{-1}$ BW | 6.3 | 6.2 | 6.3 | 5.9 | 5.5 | 0.4 | ns |
| SI Length, cm·kg$^{-1}$ BW | $220^{a}$ | $211^{ab}$ | $193^{b}$ | $152^{c}$ | $136^{c}$ | 10 | L** |
| SI, g·kg$^{-1}$ BW | $40.5^{ab}$ | $32.3^{d}$ | $37.7^{bc}$ | $42.8^{a}$ | $36.0^{cd}$ | 1.5 | L*** |
| g·cm$^{-1}$ | $0.185^{b}$ | $0.156^{ab}$ | $0.208^{b}$ | $0.281^{a}$ | $0.264^{a}$ | 0.009 | L*** |
| Total SI mucosa, g·kg$^{-1}$ BW | $29.0^{a}$ | $18.7^{d}$ | $23.7^{c}$ | $28.0^{ab}$ | $24.5^{bc}$ | 1.1 | L*** |
| g·cm$^{-1}$ SI | $0.117^{b}$ | $0.089^{c}$ | $0.129^{b}$ | $0.184^{a}$ | $0.178^{a}$ | 0.006 | L*** |
| LI, g·kg$^{-1}$ BW | $8.5^{cd}$ | $6.6^{d}$ | $11.5^{ab}$ | $12.4^{a}$ | $10.1^{bc}$ | 1.7 | Q* |

[1] Within a row, means with different superscript letters are significantly different ($P < 0.05$).
[2] L: linear, Q: quadratic.* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. ns: non significant.

were lower ($P < 0.05$) at 21 than at 7 d of age. At 21 d of age, SI characteristics were largely similar in the W and SR piglets. However, in both groups, SI length was 35% shorter ($P < 0.001$) than at 7 d of age, where as segmental weight of SI and mucosa were 47 and 55% heavier ($P < 0.001$), respectively. In the W piglets, large intestine (LI) weight tended ($P = 0.08$) to decrease at 3 d post-weaning and increased afterwards. At 21 d of age, the LI of W piglets was 46% heavier ($P < 0.001$) than at 7 d of age, whereas it remained unchanged in the SR piglets. It follows that at 21 d of age, LI was 18% heavier ($P < 0.05$) in W than in SR piglets. Stomach weight remained essentially unchanged in both W and SR piglets.

Data on small intestinal villous characteristics and crypt depth are presented in Table III. Because no effect of intestinal site was observed on crypt depth, only the overall mean along SI is reported. In both suckling and weaned pigs, villous characteristics were dependent on age and SI site. Irrespective of the SI site, in the SR piglets, villi were 35% ($P < 0.001$) shorter at 21 than at 7 d of age. At both ages, SI site had no significant effect on villous width. At 7 d of age, villous height was 17% higher ($P < 0.05$) in the proximal than in the medial and distal intestine, whereas at 21 d of age the effect of the site was not significant. Villous width was not significantly affected by age and intestinal site. In W piglets, regardless of the SI site, villous height and width were 41 and 15%, respectively, reduced on d 3 post-weaning, but only the reduction in villous height was significant ($P < 0.001$). Thereafter, height and width of villous remained essentially unchanged. There was a striking interaction between age and SI site on villous characteristics. On d 3 post-weaning, both villous height and width increased linearly ($P < 0.05$) from the proximal to the distal part of SI. In contrast, on 14 d post-weaning, villous height decreased linearly ($P < 0.05$) from the proximal to the distal SI. Furthermore, villous height and width of the proximal SI increased linearly ($P < 0.05$) from d 3 to d 14 post-weaning. In the distal SI there was a quadratic variation ($P < 0.08$) in villous height. At 21 d of age, both W and SR piglets had similar villous height and width. Overall mean crypt depth was 118 ± 24 μm, and only a non significant transient decrease was found on d 3 post-weaning.

**Table III.** Villous height (μm) and width (μm) at the proximal, medial and distal part of the small intestine and mean crypt depth (μm) along the small intestine in sow-reared (SR) and weaned (W) pigs (trial 1).

| Treatment | SR | W | | | SR | Statistical significance$^2$ | |
|---|---|---|---|---|---|---|---|
| Age (d) | 7 | 10 | 14 | 21 | 21 | | Within W pigs |
| Post-weaning day | | 3 | 7 | 14 | | SEM | (d 3 to d 14 post-weaning) |
| Villous height | | | | | | | |
| Proximal | $975^{a\ 1}$ | $403^{d}$ | $490^{cd}$ | $661^{b}$ | $581^{bc}$ | 41 | L*** |
| Medial | $834^{a}$ | $509^{b}$ | $488^{b}$ | $499^{b}$ | $546^{b}$ | 33 | ns |
| Distal | $827^{a}$ | $635^{b}$ | $461^{c}$ | $528^{bc}$ | $589^{bc}$ | 51 | Q ($P = 0.08$) |
| *Mean* | *$879^{a}$* | *$515^{b}$* | *$480^{b}$* | *$562^{b}$* | *$572^{b}$* | *30* | *ns* |
| *Site effect* | *L*$^{*\ 2}$ | *L*** | *ns* | *L** | *ns* | | |
| Villous width | | | | | | | |
| Proximal | $127^{ab}$ | $100^{c}$ | $115^{bc}$ | $132^{ab}$ | $146^{a}$ | 9 | L* |
| Medial | $128^{ab}$ | $109^{b}$ | $125^{ab}$ | $115^{b}$ | $138^{a}$ | 6 | ns |
| Distal | 139 | 127 | 124 | 122 | 121 | 7 | ns |
| *Mean* | *$131^{ab}$* | *$112^{b}$* | *$121^{ab}$* | *$123^{ab}$* | *$135^{a}$* | *6* | *ns* |
| *Site effect* | *ns* | *L** | *ns* | *ns* | *L (P = 0.09)* | | |
| Crypt depth | | | | | | | |
| *Mean* | *116* | *101* | *124* | *122* | *125* | *10* | *ns* |

[1] Within a row, means with different superscript letters are significantly different ($P < 0.05$).
[2] L: linear, Q: quadratic. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. ns: non significant.

There were marked effects of age, weaning and SI site on villous height distribution (Tab. IV). Regardless of the SI site, in SR piglets, the proportion of long villi (> 600 μm) was lower (42 vs. 77%, $P < 0.01$), at 21 than at 7 d of age. After weaning, the villous distribution was similar at 3 and 7 d post-weaning with, however, the proportion of long villi being lower ($P < 0.01$) than at weaning. At 14 d post-weaning there was an increase ($P < 0.01$) in the proportion of long villi and a decrease in that of short villi ($P < 0.05$). At 21 d of age the villi distribution was similar in SR and W piglets. SI site had no significant effect on the distribution of villous height in SR piglets aged 7 and 21 d. In W piglets the effect of SI site on villi height distribution was dependent on age. At 3 d post-weaning, compared with the distal SI, the proportion of long villi was lower ($P < 0.01$) and that of short villi higher ($P < 0.01$) in the proximal SI. At 7 d post-weaning, there was no effect of SI site on the distribution of villi. At 14 d post-weaning, the proportion of long villi was higher ($P < 0.05$) in the proximal than in the medial and distal SI. Within W piglets the proportion of long villi increased with age ($P < 0.01$) in the proximal SI and remained unchanged in the medial SI. In the distal SI, the proportion of long villi decreased ($P < 0.01$) between 3 and 7 d post-weaning and increased ($P < 0.01$) afterwards. At 21 d of age, the differences between SR and W piglets were a higher ($P < 0.01$) proportion of intermediate villi in the proximal and long villi in the distal intestine of SR piglets.

**Table IV.** Villous height distribution (%) at the proximal, medial and distal small intestine (SI) and villous height distribution along the SI in sow-reared (SR) and weaned (W) pigs (trial 1).

| Treatment | SR | W | | | SR |
|---|---|---|---|---|---|
| Age (d) | 7 | 10 | 14 | 21 | 21 |
| Post-weaning day | | 3 | 7 | 14 | |
| Proximal SI | | | | | |
| < 400 μm | $7.0^{c}$ | $52.9^{a, x}$ | $36.1^{ab}$ | $18.1^{c}$ | $19.0^{bc}$ |
| 400–600 μm | $14.4^{c}$ | $44.0^{ab}$ | $40.1^{a}$ | $17.1^{c, y}$ | $39.9^{b}$ |
| > 600 μm | $78.6^{a}$ | $3.1^{d, y}$ | $23.8^{c}$ | $64.8^{ab, x}$ | $41.1^{b}$ |
| Medial SI | | | | | |
| < 400 μm | $6.8^{b}$ | $29.8^{a, y}$ | $36.0^{a}$ | $30.1^{a}$ | $26.5^{a}$ |
| 400–600 μm | $16.3^{b}$ | $44.0^{a}$ | $38.7^{a}$ | $43.3^{a, x}$ | $37.4^{a}$ |
| > 600 μm | $76.9^{a}$ | $26.2^{b, x}$ | $25.3^{b}$ | $26.6^{b, y}$ | $36.1^{b}$ |
| Distal SI | | | | | |
| < 400 μm | $5.4^{b}$ | $26.0^{a, y}$ | $34.7^{a}$ | $23.5^{a}$ | $20.6^{a}$ |
| 400–600 μm | $20.0^{b}$ | $30.4^{ab}$ | $48.6^{a}$ | $39.5^{ab, x}$ | $31.4^{ab}$ |
| > 600 μm | $74.6^{a}$ | $43.6^{b, x}$ | $16.7^{c}$ | $37.0^{b, y}$ | $48.0^{ab}$ |

[a, b, c] Within a row, means with different superscript letters are significantly different ($P < 0.05$).

[x, y] Within a column and a class of villous, different superscript letters indicate a significant difference between SI site mean values ($P < 0.05$).

### *3.2.2. Trial 2*

The effects of feeding level and the length of underfeeding period during the post-weaning days on intestinal tissue characteristics are shown in Table V. At 3 d post-weaning, feeding level had an effect ($P < 0.05$) on only segmental mucosa weight. However on d 7 post-weaning, with the exception of segmental mucosa weight, characteristics of SI and mucosa were similar in the LH and HH groups and were enhanced ($P < 0.05$) as compared with those of the LL group. Between 3 and 7 d post-weaning, SI and mucosa characteristics remained unchanged in piglets on the low feeding level (L vs. LL groups), whereas in those switched to high feeding levels (L vs. LH groups) and in those on the high feeding level (H vs. HH groups), all characteristics, except SI length, were increased ($P < 0.05$). On d 7 post-weaning, both weight and segmental weight of SI and SI mucosa, weight of LI and length of SI were related to the level of metabolisable energy intake (ME), with $r$ ranging from 0.51 to 0.87 ($P < 0.05$).

The effects of the level of feed intake, age and SI site on villous height are shown in Table VI. As in trial 1, SI site had no significant effect on crypt depth and only the group mean is shown. Irrespective of the SI site, feeding level had no significant effect on the villous height on d 3 post-weaning whereas on d 7, it was similar in the LH and HH groups and 23% higher ($P < 0.001$) than in the LL group, with most of the difference being caused by the 39% increase ($P < 0.001$) in the proximal SI. Furthermore, on d 3 post-weaning, villous height increased linearly in both groups of piglets ($P < 0.01$) from the proximal to the distal SI. Between d 3 and d 7 post-weaning, villous height remained unchanged in the medial SI of piglets on the low feed intake (L vs. LL groups) but was 13 and 31% ($P < 0.05$) decreased in the proximal and distal parts of SI, respectively,

**Table V.** Effect of level of feeding on live weight, organ weight and small intestine (SI) length at 3 and 7 d post-weaning (trial 2).

| Treatment | L | H | LL | LH | HH | Statistical significance[2] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Age (d) | 10 | | 14 | | | | Effect of feeding level at 7 d post-weaning[3] | Age effect | | |
| Post-weaning day | 3 | | 7 | | | RSD | | L vs. LL | L vs. LH | H vs. HH |
| Live weight, kg | 2.40 | 2.82 | $2.36^{\text{B1}}$ | $2.91^{\text{A}}$ | $3.22^{\text{A}}$ | 0.44 | L*** | ns | $P = 0.09$ | ns |
| Stomach, $\text{g} \cdot \text{kg}^{-1}$ BW | 5.0 | 5.7 | 5.8 | 5.5 | 6.0 | 0.7 | ns | ns | ns | ns |
| SI length, $\text{cm} \cdot \text{kg}^{-1}$ BW | 205 | 200 | 243 | 208 | 196 | 29 | ns | ns | ns | ns |
| SI, $\text{g} \cdot \text{kg}^{-1}$ BW | 29.9 | 33.0 | $30.8^{\text{B}}$ | $38.5^{\text{A}}$ | $38.7^{\text{A}}$ | 4.1 | L** | ns | * | * |
| $\text{g} \cdot \text{cm}^{-1}$ SI | 0.146 | 0.166 | $0.130^{\text{B}}$ | $0.185^{\text{A}}$ | $0.197^{\text{A}}$ | 0.012 | Q* | $P = 0.07$ | ** | ** |
| Total SI mucosa, $\text{g} \cdot \text{kg}^{-1}$ BW | 13.9 | 18.2 | $15.2^{\text{B}}$ | $21.2^{\text{A}}$ | $23.6^{\text{A}}$ | 3.6 | L* | ns | * | $P = 0.07$ |
| $\text{g} \cdot \text{cm}^{-1}$ SI | $0.068^{\text{b}}$ | $0.091^{\text{a}}$ | $0.063^{\text{C}}$ | $0.102^{\text{B}}$ | $0.119^{\text{A}}$ | 0.014 | L*** | ns | ** | * |
| LI, $\text{g} \cdot \text{kg}^{-1}$ BW | 6.8 | 8.7 | $9.3^{\text{B}}$ | $11.8^{\text{A}}$ | $12.5^{\text{A}}$ | 1.2 | L*** | * | *** | *** |

[1] Within a row, means with different superscript letters are significantly different ($P < 0.05$). $^{\text{a, b}}$ differences between L and H groups; $^{\text{A, B, C}}$ differences between LL, LH and HH groups.
[2] L: linear, Q: quadratic. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. ns: non significant.
[3] At 3 d post-weaning, feeding level had an only effect ($P < 0.05$) on mucosa segmental weight.

**Table VI.** Villous height (μm) and width (μm) at the proximal, medial and distal part of the small intestine and mean crypt depth (μm) along the small intestine according to age and level of feeding (trial 2).

| Treatment | L | H | LL | LH | HH | Statistical significance$^2$ | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Age (d) | 10 | | 14 | | | | Effect of feeding level at 7 d post-weaning$^3$ | Age effect | | |
| Post-weaning day | 3 | | 7 | | | RSD | | L vs. LL | L vs. LH | H vs. HH |
| Villous height | | | | | | | | | | |
| Proximal | 416 | 450 | $360^{B\,1}$ | $485^{A}$ | $518^{A}$ | 64 | L** | * | ns | ns |
| Medial | 456 | 499 | 469 | 531 | 552 | 105 | ns | ns | ns | ns |
| Distal | 599 | 651 | $413^{B}$ | $520^{A}$ | $450^{B}$ | 90 | Q** | * | ns | * |
| *Mean* | *490* | *533* | *$414^{B}$* | *$512^{A}$* | *$507^{A}$* | *41* | *Q** | *$P = 0.06$* | | *ns* |
| *Site effect*$^{(2)}$ | *L** | *L** | *ns* | *ns* | *L** | | | | | |
| Villous width | | | | | | | | | | |
| Proximal | 84 | 94 | $88^{B}$ | $91^{AB}$ | $96^{A}$ | 6 | L* | ns | ns | ns |
| Medial | 86 | 91 | 82 | 89 | 88 | 8 | ns | ns | ns | ns |
| Distal | 84 | 90 | $84^{B}$ | $85^{B}$ | $95^{A}$ | 5 | L** | ns | ns | ns |
| *Mean* | *$85^{b}$* | *$92^{a}$* | *$84^{B}$* | *$88^{AB}$* | *$93^{A}$* | *4* | L** | *ns* | *ns* | *ns* |
| Crypt depth | | | | | | | | | | |
| *Mean* | *$90^{b}$* | *$105^{a}$* | *100* | *109* | *109* | *11* | *L ($P = 0.07$)* | *ns* | * | *ns* |

[1] Within a row, means with different superscript letters are significantly different ($P < 0.05$). $^{a, b}$: differences between L and H groups; $^{A, B, C}$: differences between LL, LH and HH groups.

[2] L: linear, Q: quadratic. * $P < 0.05$, ** $P < 0.01$. ns: non significant.

resulting in an overall decrease of 16% ($P < 0.05$). In piglets switched to high feeding level (L vs. LH groups) and in those on the high feeding level (H vs. HH groups) average villous height remained unchanged despite a 17 and 15% increase in the proximal SI, and 13 and 31% decrease ($P < 0.01$) in the distal intestine, respectively. At 3 and 7 d post-weaning, crypt depth was lower ($P < 0.05$) in pigs on the low feeding level, however the difference was only significant at d 3 post-weaning.

## 4. DISCUSSION

The results of these studies provide new information on the temporal and spatial changes in intestinal morphometry during the post-weaning period and indicate that energy (feed) intake is the major factor accounting for these changes.

Weaning is usually associated with a dramatic reduction in energy intake resulting in marked changes in the growth pattern on body and digestive organ weight and in the structure of the SI. In the present studies, with the exception of the piglets of trial 2 on the low feed intake, the maintenance energy requirement (MEm) of piglets, assumed to be 470 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ [23], was not met until d 3 to 5 after weaning, a timing similar to that reported in piglets weaned between 21 and 28 d of age [23]. As expected, due to this low energy intake immediately post-weaning, the piglets of both trials experienced a short period of growth check. Overall changes in digestive organ weights during the post-weaning period (trial 1) and with changing energy intake (trial 2) were similar to those reported earlier [10, 34]. The about 20% decrease in the relative weights of the large and small intestines observed in trial 1 was consistent with values ranging from 18 to 34% found in piglets weaned at later ages [5, 7, 19, 20, 26, 36]. Furthermore, the mucosa was the most affected SI component, being reduced by 55%. However, at 21 d of age mucosa weight was similar in weaned and suckling piglets. Following the post-weaning growth check, increase in absolute SI and mucosa weight largely exceeded that in BW. Similarly, Sève et al. [41] reported that the development of the gastrointestinal tract is of first priority at weaning. These and the marked effect of level of feed intake on the mucosa development found in trial 2 suggest that the intestinal mucosa is very plastic and may adapt rapidly to changes in luminal nutrition.

In suckling piglets, the SI morphology changed markedly between 7 and 21 d of age. The reduction in length relative to BW and the increase in segmental mucosa weight resulted in an increase in the small intestinal wall thickness. Similarly, villous height was markedly decreased. In agreement with the previous reports of Cera et al. [5], Dunsford et al. [9] and Tarvid et al. [45], these results suggest that SI morphology is at least partly dependent on age and/or on the level of milk intake which decreased during this period (Fig. 1A).Weaning resulted in more dramatic changes in mucosa morphometry, because on d 3 post-weaning, villous height was on average, reduced to 59% of the initial value found at weaning. The fact that villous characteristics and height distribution were largely similar in weaned and suckling piglets at 21 d of age indicates that recovery is complete 14 d post-weaning. Both the extent of villous atrophy associated with weaning and the duration of recovery were similar to those in earlier reports [5, 15, 19, 34, 35]. In addition, the results of our studies provide evidence that villous atrophy immediately post-weaning and recovery at 21 d of age are more pronounced in the proximal than in the other parts of the SI (Tab. III). Together, these suggest a spatial and temporal effect of weaning on villous atrophy and recovery. Using the fasting/refeeding model to investigate the changes in the morphology of the SI of adult rats, Hodin et al. [17] also reported that villous atrophy with fasting was more pronounced in the proximal intestine with the changes being reversed by refeeding in a gradual manner over time. The decreasing gradient in nutrient concentration along the SI may explain the present SI site dependent recovery gradation. Stoll et al. [43] reported that the rate of protein synthesis is more dependent on luminal content in the proximal than in the distal intestine. From these results, it is conceivable that underfeeding immediately post-weaning and refeeding thereafter had more pronounced effects on the proximal than on the distal intestine. Of paramount importance is the fact that the marked villous atrophy found in the proximal intestine on d 3 post-weaning results in a severe reduction in the mean absorptive surface area, being evaluated to 33% of the initial value assuming the villous being a cylinder [1]. The proximal intestine is the major site for digestion and absorption [21, 37]. On this basis, the severe reduction in absorptive surface area and the decrease in enzyme activity reported immediately post-weaning ([6, 16], our unpublished observations) may reduce the digestive capacity of piglets and likely play a role in the high sensitivity of piglets to post-weaning digestive disorders. Changes in villous size in both weaned and suckling piglets were associated with a reduction in the long villous population and the ensuing increase in the intermediate and short villous population. Therefore, villous atrophy may be due to an increased rate of cell loss at the most apical part of the long villi, this phenomena occurring at a higher rate than the cell renewal in crypts. Together, our data indicate that morphometrical changes of the SI are dependent on the SI site and days post-weaning. It is suggested that these factors be considered when mechanisms in intestinal alteration and recovery are being investigated.

Several factors are reported to account for the changes in villous size after weaning [29, 36]. Among the most important are the withdrawal of sow milk and hence of milk-derived growth factors [18] and glutamine, a major fuel for the developing intestine [48], and a transient hypersensitivity to antigenic components present in the diet [8, 25]. A low feed intake as a cause of villous atrophy immediately post-weaning was first reported by Kelly et al. [20] and substantiated by Pluske et al. [35] and Zijlstra et al. [49]. Our studies provide clear evidence that changes in villous height after weaning are largely dependent on the amount of energy intake. However, the level of energy intake (trial 2) marginally affected villous height during the first 3 d post-weaning. Indeed, although amount of energy intake was 6-fold higher in H than in L piglets, levels of feeding in both groups were lower than MEm and accounted only for 3 and 18% of the estimated pre-weaning milk ME intake, respectively. However, on d 7 post-weaning, compared with a low feed intake, a high feed intake improved the overall structure of the SI as reflected by the higher mucosa weight and longer villi. Assuming that villous height was similar at weaning in both trials, the relationship between energy intake and proximal SI villous height values of both trials indicates that 56% of the total variation of villous height are related to energy intake (Fig. 2A). The value increases to 73% when the SR pigs are included in the analysis (Fig. 2B). This highlights that the level of energy intake is the major factor accounting for post-weaning structural alterations of SI. In addition, the fact that the shift from a low to a high level of feeding from d 3 post-weaning (trial 2) resulted at 7 d of age in villous characteristics largely similar to those of piglets continuously fed a high feeding level suggests that the recovery of the SI epithelium is rapid, which is in good agreement with the fasting/refeeding studies of Hodin et al. [17]. Therefore, the length of the underfeeding period did not seem to alter the restoration capacities of SI.

Weaning is or not associated with crypt cell hyperplasia. Increases of crypt depth ranging from 10 to 50% in the first 4–5 d post-weaning have been reported by Hampson [15], Kelly et al. [19], Tang et al. [44] and Zijlstra et al. [49]. In contrast, only

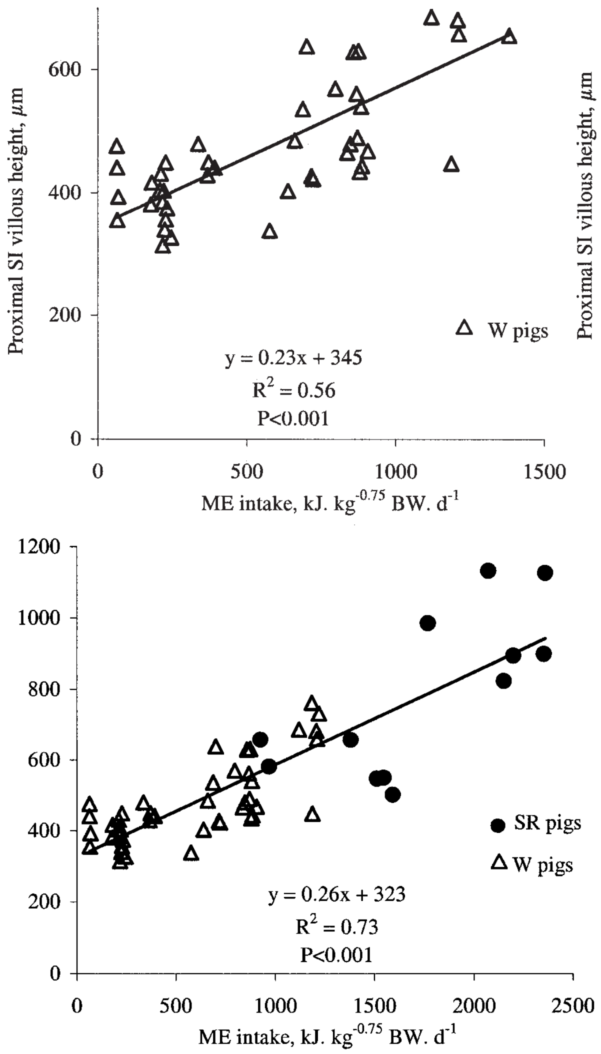

**Figure 2**. Relationships between proximal small intestine (SI) villous height and metabolisable energy (ME) intake (**A**) in only weaned (W) pigs and (**B**) in both weaned (W) and sow-reared (SR) pigs. Data of both trials are included in the analysis. In sow-reared piglets, milk ME intake was calculated from the conversion rate of ME into body weight gain [12]. In W and SR piglets, ME intake was determined on the 3 d period preceding slaughter.

a marginal effect of weaning on crypt depth was found in our studies in agreement with the findings of Spreeuwenberg et al. [42], whereas a transient decrease on d 2 post-weaning was found by McCracken et al. [28] and van Beers-Schreurs et al. [47]. Crypt depth is dependent on several factors including the level of energy intake. The absence of enteral nutrients [4, 12] or energy restriction prevents or reduces crypt cell proliferation [14] and diminishes the rate of cell migration [39]. Findings of shorter crypts on d 3 post-weaning in piglets on the low feed intake (trial 2) concur with the results of Pluske et al. [34] showing, at 5 d post-weaning, shorter crypts in piglets fed at MEm than in those fed 2.5 times MEm. Furthermore, findings that shorter crypts are found in pigs weaned into a “clean” environment compared to pigs weaned into a “conventional” environment [30, 44], suggest that the rate of epithelial renewal is to some extent dependent on pathogen exposure [11]. Our weaned pigs were raised in a very clean environment. Examination of B and T lymphocyte subsets in Peyer patches and in mucosal lamina propria in our 21 d old piglets (Quentin M., personal communication) indicated similar development of Peyer patches in both weaned and suckling piglets whereas the density of plasmocytes and lymphoblasts containing immunoglobulins was lower in the lamina propria of the weaned group, suggesting a reduced antigenic stimulation. This likely represents a plausible explanation for the largely unaltered crypt depth after weaning.

As a whole, the results of these studies indicate a spatial and a temporal effect of weaning on the SI villous atrophy and recovery. Energy intake is a major factor accounting for both the shortening of villi and the speed of recovery. It is suggested that making the nursing-weaning transition smoother by maintaining the continuity of nutrient supply, for example, by providing feed in a liquid form [2, 49] will minimise the post-weaning intestinal alterations.

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