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Original article

**Non-starch polysaccharides extracted from seaweed
can modulate intestinal absorption of glucose
and insulin response in the pig**

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Abstract — We have investigated the possible effects of algal polysaccharides on postprandial blood glucose and insulin responses in an animal model, the pig. Three seaweed fibres of different viscosities, extracted from *Palmaria palmata* (PP), *Euclima cottonii* (EC), or *Laminaria digitata* (LD), were compared to purified cellulose (CEL). Blood glucose and plasma insulin levels were monitored and intestinal absorption quantified for 8 h following a high carbohydrate test-meal supplemented with 5% fibre. Digestive contents were also sampled, 5 h postprandial. As compared to CEL, PP had no effect on glucose and insulin responses. The latter decreased with EC, but glucose absorption balance was not modified. LD addition resulted in a dramatically reduced glucose absorption balance, accompanied by a higher amount of starch left in the small intestine. Among polysaccharides tested, only the highly viscous alginates could affect intestinal absorption of glucose and insulin response.

seaweed / non-starch polysaccharides / intestinal absorption / glucose

Résumé — Les fibres alimentaires extraites d'algues peuvent moduler l'absorption intestinale du glucose et la réponse insulínique chez le porc. L'effet des fibres algales sur la réponse glycémique et insulínique a été étudié chez un modèle animal, le porc. Des fibres de viscosité différente, extraites de *Palmaria palmata* (PP), *Euclima cottonii* (EC), ou *Laminaria digitata* (LD), ont été comparées à de la cellulose purifiée (CEL). La glycémie et l'insulínémie plasmatique, ainsi que l'absorption intestinale du glucose ont été suivies 8 h après un repas-test hyperglucidique additionné de 5 % de fibres. Des contenus digestifs ont aussi été prélevés 5 h après le repas. L'addition de PP n'a pas modifié les réponses glycémique et insulínique par rapport à CEL. Elles étaient diminuées par l'addition

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de EC, mais sans répercussion sur le bilan d'absorption de glucose. En présence de LD, l'absorption de glucose était fortement diminuée, ceci s'accompagnant d'une quantité plus élevée d'amidon résiduel dans l'intestin grêle. Parmi les polysaccharides étudiés, seuls les alginates très visqueux ont pu modifier l'absorption intestinale de glucose et la réponse insulémique.

algues / polysaccharides non amylacés / absorption intestinale / glucose

1. INTRODUCTION

Although marine seaweed is the source of several phycocolloids used as additives by the food industry (alginates, carrageenans, agars), edible seaweed consumption is low in Western countries. In France, twelve species are now authorised for human consumption, as vegetables or condiments [9]. Most edible seaweeds contain large amounts of polysaccharides (30–75% on a dry weight basis) which differ from land plant polysaccharides by their chemical nature and physico-chemical properties [16]. Most of these polysaccharides cannot be hydrolysed by human endogenous digestive enzymes, and thus are considered as dietary fibres [30]. Their generally high contents in soluble dietary fibres (50–80% of total dietary fibre content, according to [16]) could be of nutritional interest.

It is now well established that soluble dietary fibres, such as pectin or guar gum, can slow down both intestinal absorption of nutrients and hormonal response when added to a meal, and that this effect is related to their capacity to increase viscosity in the digestive tract [12, 14]. Among possible mechanisms involved are a reduced rate of gastric emptying, and a decrease in starch hydrolysis or glucose transport rates, resulting from changes in the rheological properties of digestive contents [10, 12].

In the present work, we have tested the hypothesis that polysaccharides extracted from seaweed, although differing widely from land plants by their chemical nature, could affect intestinal glucose absorption and insulin response by similar mechanisms

related to their effect on the rheological properties of the digestive contents. This study was performed in the pig, which is increasingly used in biomedical research [31], especially for gastrointestinal studies. Moreover, in the present case as well as in a previous study on guar gum [11] using the pig model, quantitative data on glucose absorption and insulin response was obtained, and related to the physico-chemical properties of digesta.

This study was part of a coordinated work designed to assess the potential utility of algal polysaccharide-rich products in the human diet [3, 19, 26].

2. MATERIALS AND METHODS

2.1. Seaweed fibre extracts

Three seaweed fibre ingredients were tested in comparison to purified wood cellulose (CEL; Filtrafa, Rungis, France): soluble sodium alginates (LD) from *Laminaria digitata*, partly soluble carrageenans (EC) from *Eucheuma cottonii*, and soluble xylans (PP) from *Palmaria palmata*. LD was provided by Systems-Bio-Industries (Baupte, France). EC, provided by Colloides Naturels International (Neuilly s/Seine, France), was mostly composed of κ -carrageenans. PP was extracted as described by Bobin-Dubigeon et al. [3]. The three fibre isolates contained 567 to 712 g dietary fibre per kg dry weight, and differed greatly by their intrinsic viscosity [3]: 36 mL·g⁻¹ for PP, 591 mL·g⁻¹ for EC, and 1096 mL·g⁻¹ for LD.

2.2. Animals and surgery

Experiments were performed on a total of sixteen Large White male pigs. While under general anaesthesia induced by halothane (Fluothan, Pitman-Moore, France), twelve of them were surgically implanted with polyvinyl chloride catheters (i.d.: 1.27 mm, o.d.: 2.29 mm, Tygon Norton, Cleveland, OH, USA) in the portal vein (PV) and in the right carotid artery (CA), as described previously [25, 32], and with an ultrasonic portal blood-flow probe (12 or 14 mm probe, Transonic Systems Ltd, Ithaca, NY, USA). Carotid artery cannulation, allowing to sample blood from the thoracic aorta, has been reported to be the best technique to obtain systemic arterial blood in the pig [33]. The remaining four pigs were sham-operated by laparotomy, under general anaesthesia.

2.3. Glucose absorption experiments

After surgery, the pigs were kept in restraining cages, and progressively refed with a semi-synthetic basal diet (content in $\text{g}\cdot\text{kg}^{-1}$: casein, 178; purified maize starch, 516; sucrose, 65; soya-bean oil, 150; purified wood cellulose, 50; mineral and vitamin supplement, 41) mixed with twice its weight of water. Experiments began 8 to 10 days after surgery, when the pigs (56–62 kg body weight) had reached a normal feed intake level (800 g of flour, twice daily). Each seaweed fibre was tested on a group of four pigs. Each pig received an alternate sequence of four test-meals (basal diet supplemented with 5% fibre), two of them supplemented with seaweed fibre, and two of them supplemented with CEL. Forty grams of PP or EC vs. 40 g of CEL were added to 800 g of the basal diet. The fibres were mixed to the diet without allowing them to hydrate before hand. When LD, the highly viscous seaweed fibre, was added to the diet, it was difficult to make all the pigs eat the test-meal rapidly, that is less than 15 min. Thus, LD was tested at a level of 20 g vs. 20 g of CEL, added to

400 g of the basal diet. Test-meals were given without previous adaptation, and after a 24 h fast. Between test-meals, which were separated by 3 to 5 days, the pigs received the basal diet (800 g twice daily), without supplementation. In order to avoid interactions between treatment and time, the fibres were tested in the following order: seaweed, cellulose, seaweed, cellulose (2 pigs), or cellulose, seaweed, cellulose, seaweed (2 pigs). On the day of the experiment, from 15 min before until 8 h after the meal, portal blood-flow-rate was recorded continuously using an ultrasonic blood-flowmeter (Transonic Systems Ltd), and blood was sampled to determine blood glucose and plasma insulin concentrations. The sampling schedule was as follows: -15, 0, 10, 20, 30, 45, 60 min, each 30 min up to 5 h after the meal, and each 60 min up to 8 h postprandial.

2.4. Digesta collection experiments

After having completed the absorption experiments, or after having recovered from sham-operation, four pigs per group (57–72 kg body weight) were adapted to one of the diets for 5–6 days (twice daily 800 g with 40 g fibre added). On the day of the experiment, and after a 24 h fast, they received a test-meal (800 g with 40 g fibre added), and were sacrificed under general anaesthesia at 5 h postprandial. This time was chosen to permit digesta collection from both the stomach, and the small intestine, which was divided into 3 equal parts (I_1 , I_2 , I_3).

2.5. Analytical methods

Blood samples were collected in ice-cooled tubes; 100 μL were deproteinised in $\text{Ba}(\text{OH})_2/\text{ZnSO}_4$, as described by Somogyi [28], and immediately centrifuged (16 000 g, 5 min). The supernatant was used for assaying glucose by a specific enzymatic method [2]. Blood samples (1 mL) were collected

in ice-cooled tubes containing heparin (10 μL) and 2 mM EDTA (50 μL). Plasma was obtained by centrifugation (16 000 g , 5 min, 4 $^{\circ}\text{C}$) and stored at -80°C . Insulin concentration was measured on duplicate 50 μL samples, using a radioimmunoassay kit (INSI-PR, CIS bio international, Gif-sur-Yvette, France). The antiserum used in the test had a 100% cross-reactivity with pig insulin.

Dry matter content of the digesta was determined after drying overnight at 100 $^{\circ}\text{C}$. Total starch was assayed according to Faisant et al. [13].

2.6. Viscosity measurements

Intrinsic viscosity of seaweed fibre extracts was determined as reported by Bobin-Dubigeon et al. [3]: measurement at 37 $^{\circ}\text{C}$ in 150 mM NaCl, using an automatic capillary viscosimeter (TII, Sematech, France). In small intestinal contents, viscosity was measured with a "Rheovisco model ELV-8" apparatus (cylinder n $^{\circ}$ 3, speed: 3 turns per min), and expressed as centipoise (cPO).

2.7. Calculations and statistical analysis

The net glucose absorption rate was calculated as the difference between portal and arterial concentrations multiplied by the flow rate in the portal vein [24]. All values shown are the means \pm SEM for the number of animals indicated. The mean data from duplicate test-meals obtained from the same pigs were used to assess differences between seaweed and cellulose supplementation. Overall blood glucose and insulin responses were compared by ANOVA, taking time as a repeated factor (GLM procedure [27]). The peak values of glycemia and insulinemia, and the amounts of absorbed glucose, were compared by the Student paired t test ($df = 3$). In digesta collection experiments, data obtained from the four groups of pigs

(PP, EC, LD, CEL) were compared by ANOVA, using a one-way factorial model, followed by the Tukey studentised range test when ANOVA revealed differences among groups. Differences were considered as statistically significant for $P < 0.05$.

3. RESULTS

3.1. Blood-flow-rate in the portal vein

In each group, the portal blood-flow-rate increased by 30 to 40 % following the meal, and then decreased during the 8 h post-prandial period. There was no significant difference between mean blood-flow-rates recorded over the 8 h period following the seaweed vs. cellulose supplemented test-meals: 1683 ± 33 vs. 1739 ± 74 $\text{mL}\cdot\text{min}^{-1}$ with EC vs. CEL supplementation in the EC group ($n = 4$ pigs), 1927 ± 67 vs. 1905 ± 106 $\text{mL}\cdot\text{min}^{-1}$ with PP vs. CEL supplementation in the PP group ($n = 4$ pigs), and 1694 ± 42 vs. 1747 ± 76 $\text{mL}\cdot\text{min}^{-1}$ with LD vs. CEL supplementation in the LD group ($n = 4$ pigs.). Overall, the portal blood-flow-rate ranged from 29.9 ± 0.9 to 32.8 ± 1.4 $\text{mL}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$ live-weight.

3.2. Postprandial changes in blood glucose and insulin concentrations

Basal glycemia, averaging 3.6 ± 0.2 mM, did not differ between PV and CA, and was identical in the three groups of pigs. Following the meal intake, both glycemia and insulinemia increased in PV and CA (Figs. 1 to 6), but the time-course and peak levels reached were differently affected by seaweed addition.

There was no diet effect on the glycaemic and insulenic responses monitored after the PP vs. CEL supplemented test-meals (Figs. 1 and 2). The peak level was 7.3 ± 0.4 mM in PV and 5.2 ± 0.3 mM in CA for glucose; and 170 ± 26 $\mu\text{U}\cdot\text{mL}^{-1}$ in PV and 115 ± 25 $\mu\text{U}\cdot\text{mL}^{-1}$ in CA for insulin.

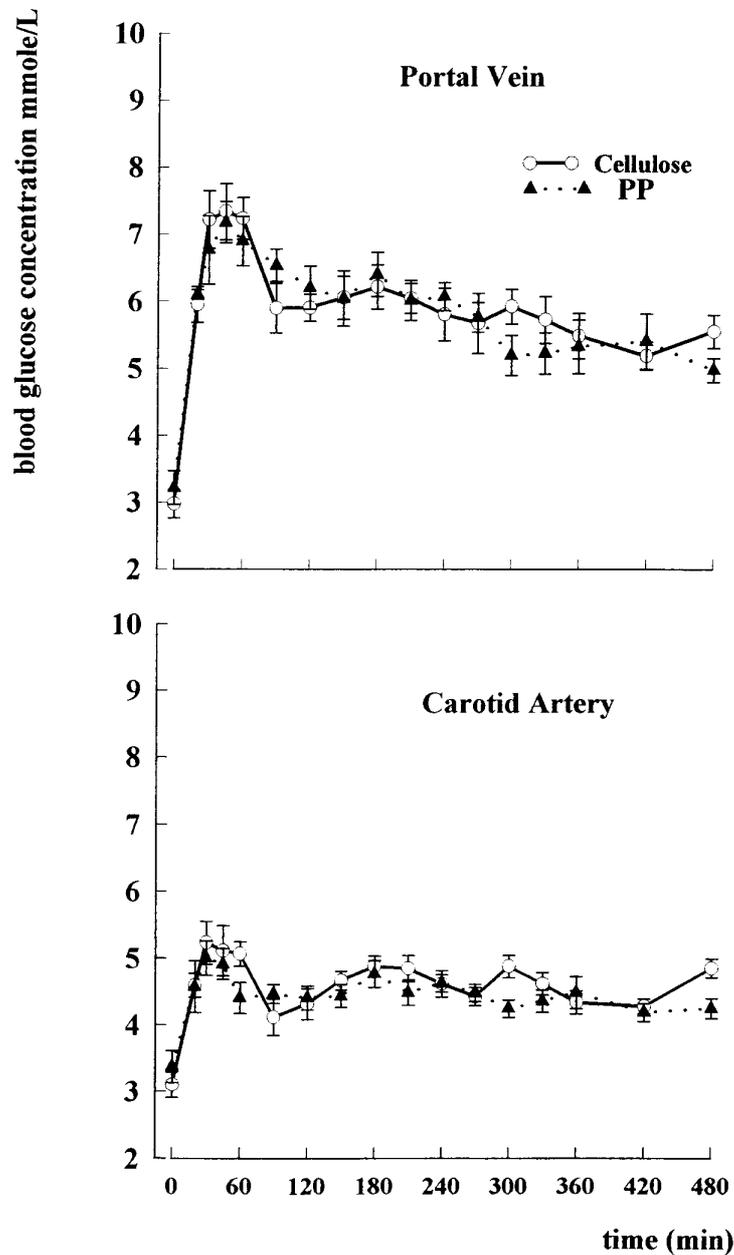


Figure 1. Effect of supplementation with the fibre extract from *Palmaria palmata* (PP) on blood glucose concentration ($\text{mmol}\cdot\text{L}^{-1}$) in the portal vein and in the carotid artery.

○ ○: control, 800 g basal diet supplemented with 40 g of purified cellulose (CEL).

▲ ▲: 800 g basal diet supplemented with 40 g of PP fibre.

Values shown are means for eight test-days performed in four pigs. Each pig received an alternate sequence of four test-meals, two of them supplemented with CEL, and two of them supplemented with PP. For details of composition of the basal diet, see the experimental section.

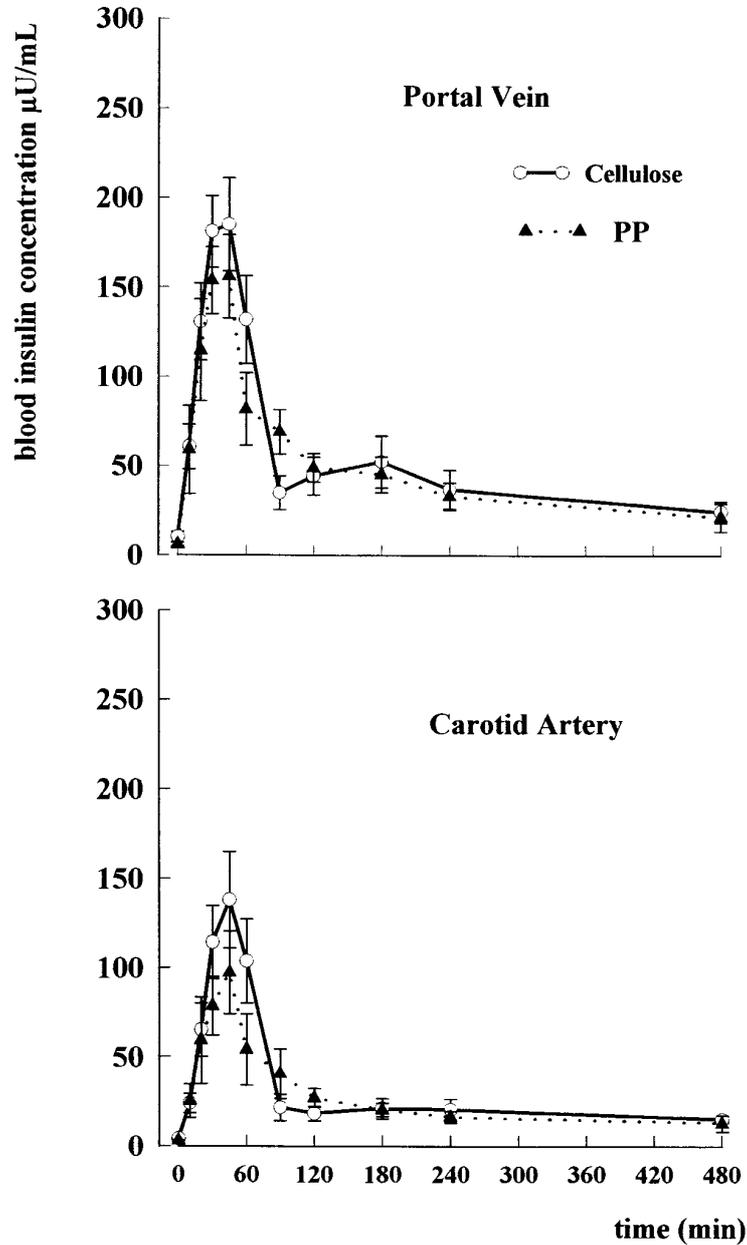


Figure 2. Effect of supplementation with fibre extract from *Palmaria palmata* (PP) on plasma insulin concentration ($\mu\text{U}\cdot\text{mL}^{-1}$) in the portal vein and in the carotid artery.

○ ○: control, 800 g basal diet supplemented with 40 g of purified cellulose (CEL).

▲ ▲: 800 g basal diet supplemented with 40 g of PP fibre.

Values shown are means for eight test-days performed in four pigs. Each pig received an alternate sequence of four test-meals, two of them supplemented with CEL, and two of them supplemented with PP. For details of composition of the basal diet, see the experimental section.

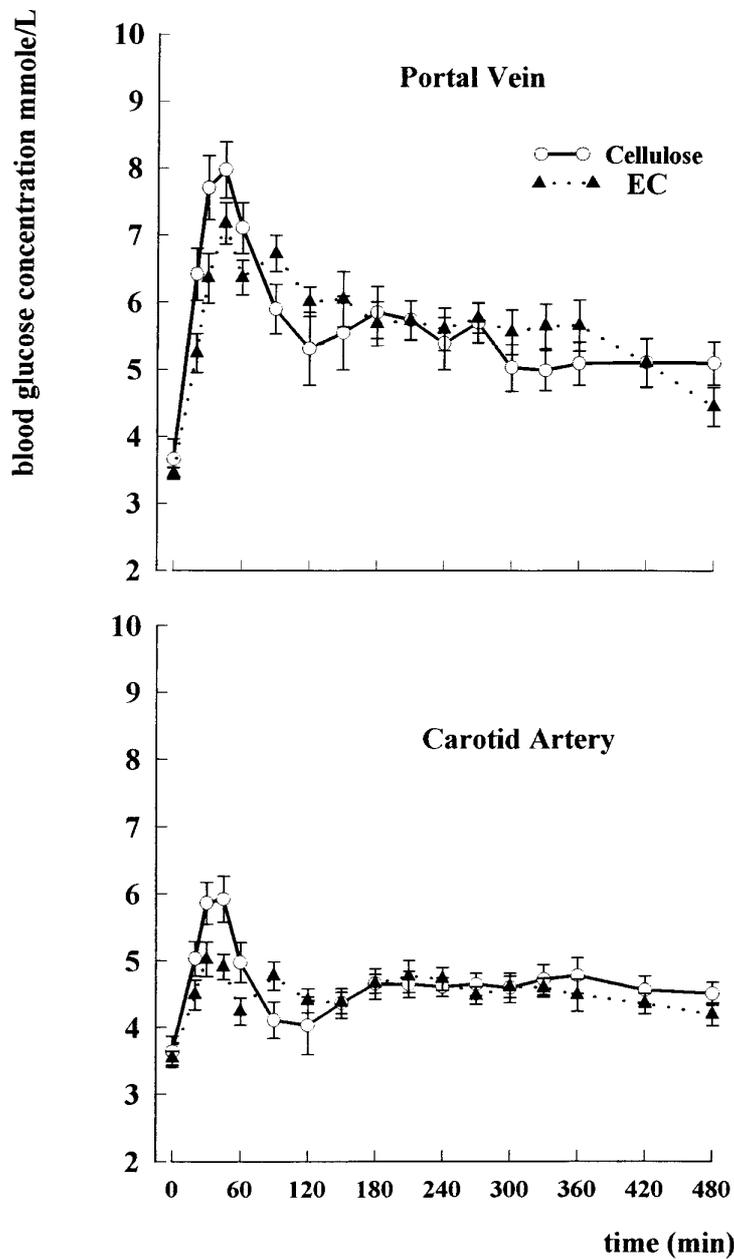


Figure 3. Effect of supplementation with fibre extract from *Eucheuma cottonii* (EC) on blood glucose concentration ($\text{mmol}\cdot\text{L}^{-1}$) in the portal vein and in the carotid artery.

○ ○: control, 800 g basal diet supplemented with 40 g of purified cellulose (CEL).

▲ ▲: 800 g basal diet supplemented with 40 g of EC fibre.

Values shown are means for eight test-days performed in four pigs. Each pig received an alternate sequence of four test-meals, two of them supplemented with CEL, and two of them supplemented with EC. For details of composition of the basal diet, see the experimental section.

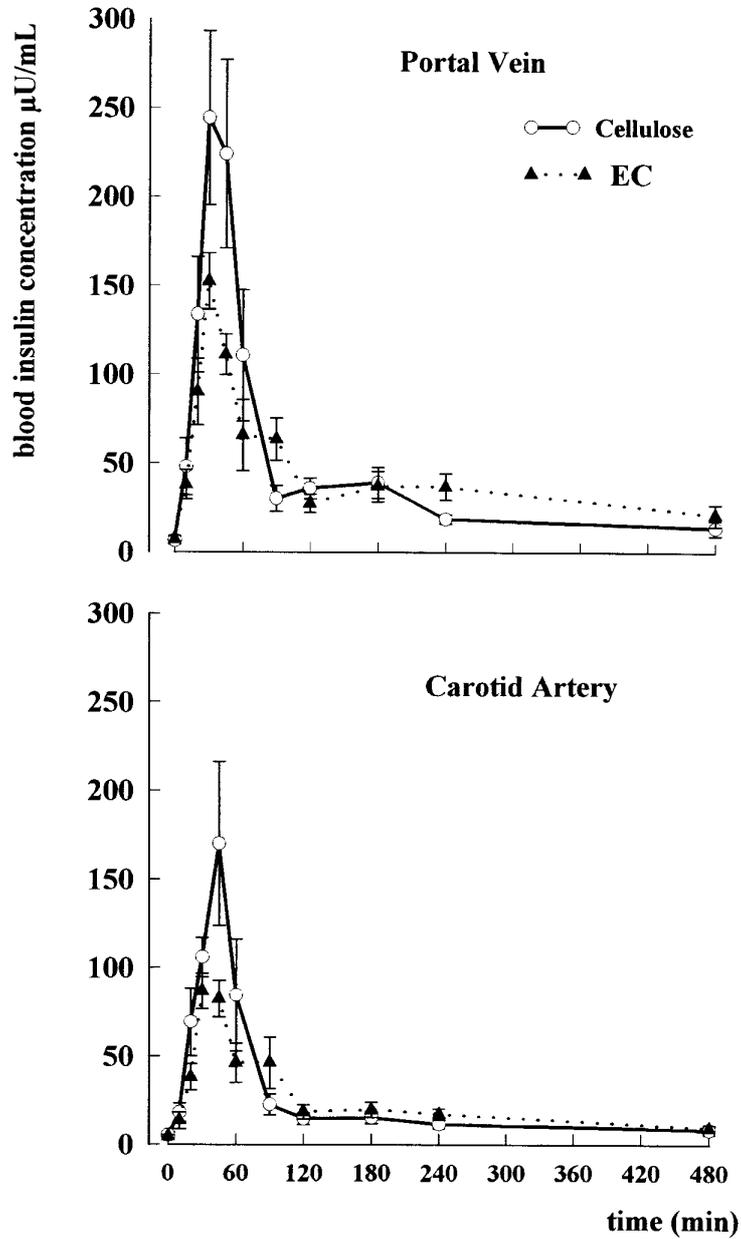


Figure 4. Effect of supplementation with fibre extract from *Eucheuma cottonii* (EC) on plasma insulin concentration ($\mu\text{U}\cdot\text{mL}^{-1}$) in the portal vein and in the carotid artery.

○ ○: control, 800 g basal diet supplemented with 40 g of purified cellulose (CEL).

▲ ▲: 800 g basal diet supplemented with 40 g of EC fibre.

Values shown are means for eight test-days performed in four pigs. Each pig received an alternate sequence of four test-meals, two of them supplemented with CEL, and two of them supplemented with EC. For details of composition of the basal diet, see the experimental section.

In contrast, the postprandial rise in blood glucose was not identical between EC and CEL supplemented test-meals, as there was a significant interaction between diet and time for portal glycaemia (Fig. 3). This was explained by glycaemia peaking from 40 to 85 min with EC, and at 40 min with CEL. In addition, the maxima reached were significantly lower with EC: 7.2 ± 0.3 vs. 8.0 ± 0.4 mM in PV, and 5.0 ± 0.3 vs. 6.0 ± 0.3 mM in CA. Moreover, as for glycaemia, the peak level of insulin (Fig. 4) was significantly lower with EC (152 ± 16 vs. 244 ± 49 $\mu\text{U}\cdot\text{mL}^{-1}$ in PV, and 87 ± 10 vs. 170 ± 46 $\mu\text{U}\cdot\text{mL}^{-1}$ in CA). Insulin concentration rose within 30–40 min after the meal, but returned more slowly to the basal level with the EC diet.

As compared to CEL addition, LD greatly modified blood glucose and insulin responses to the meal (Figs. 5 and 6), as shown by a significant diet effect, and a significant diet-time interaction for all parameters. Indeed, peak levels were reached later (60 vs. 45 min), and were significantly lower: 6.0 ± 0.3 vs. 7.6 ± 0.5 mM in PV, and 4.8 ± 0.3 vs. 5.8 ± 0.3 mM in CA for glucose; 62 ± 13 vs. 159 ± 29 $\mu\text{U}\cdot\text{mL}^{-1}$ in PV, and 35 ± 6 vs. 120 ± 25 $\mu\text{U}\cdot\text{mL}^{-1}$ in CA for insulin.

3.3. Glucose absorption balance across the small intestine

The net glucose absorption balance was calculated over the 8 postprandial hours, taking into account the porto-arterial differences in blood glucose concentrations, and the blood-flow-rate measured continuously in the portal vein.

Whatever the time after the meal, the amount of glucose absorbed was not affected by PP as compared to CEL addition (Tab. I). Although glucose absorption tended to be lower with EC in the first postprandial hour ($P < 0.05$ at 30 min), the cumulated amounts of glucose absorbed did not differ significantly following a test-meal enriched with

EC vs. CEL (Tab. I). In contrast, the cumulated amount of glucose absorbed was significantly lower for the LD supplemented diet, whatever the time after the meal (Tab. I). Over an 8 h period, glucose absorption balance expressed as a percentage of ingested starch was reduced by half after LD supplementation, whereas it was not modified by the addition of PP or EC (Tab. I).

3.4. Starch content and viscosity of digesta

The amount of starch remaining in the stomach 5 h after the meal accounted for 30 to 60% of ingested starch (360 g), and did not differ significantly according to the type of fibre added to the diet. In contrast, the amount of starch found in the small intestine was small, but higher with the LD supplemented diet (Tab. II).

In the present study, precipitation of LD in the stomach, resulted in separated liquid and solid phases in this compartment. Thus, it was impossible to measure the viscosity of gastric contents. In contrast, intestinal contents were homogeneous and viscous: the viscosity of intestinal contents collected from segment I1 or I2 (10 000–16 000 cPO) corresponded to a 2% water solution of LD (pH 7.0), whereas that of segment I3 increased 4-fold, as compared to I1 or I2. With CEL, PP, and EC diets, it was not possible to measure viscosity, because of separation of the liquid and solid phases occurring during measurement.

4. DISCUSSION

Glucose tolerance and insulin sensitivity are key-issues involved in the development of non-insulin dependent diabetes mellitus (NIDDM) in humans. Soluble dietary fibres have been shown to improve glucose tolerance and insulin sensitivity [5, 12]. Although several studies suggest that these

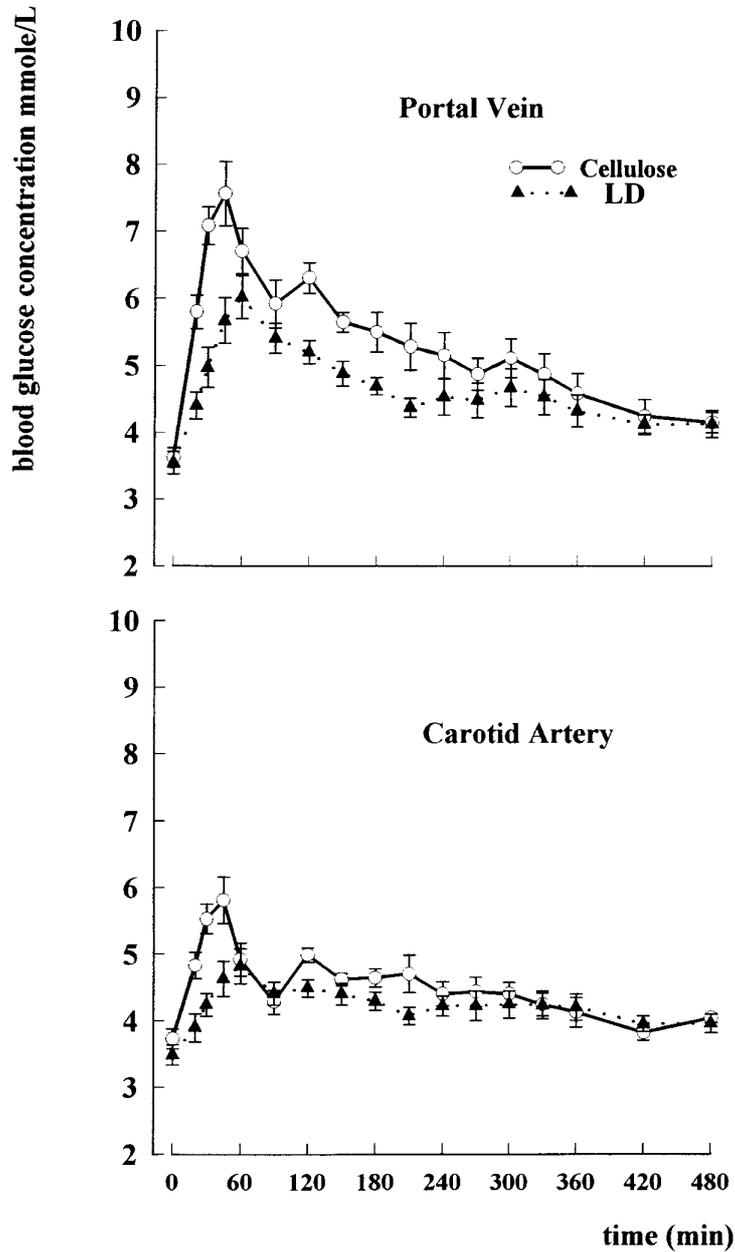


Figure 5. Effect of supplementation with fibre extract from *Laminaria digitata* (LD) on blood glucose concentration ($\text{mmol}\cdot\text{L}^{-1}$) in the portal vein and in the carotid artery.

○ ○: control, 400 g basal diet supplemented with 20 g of purified cellulose (CEL).

▲ ▲: 400 g basal diet supplemented with 20 g of LD fibre.

Values shown are means for eight test-days performed in four pigs. Each pig received an alternate sequence of four test-meals, two of them supplemented with CEL, and two of them supplemented with LD. For details of composition of the basal diet, see the experimental section.

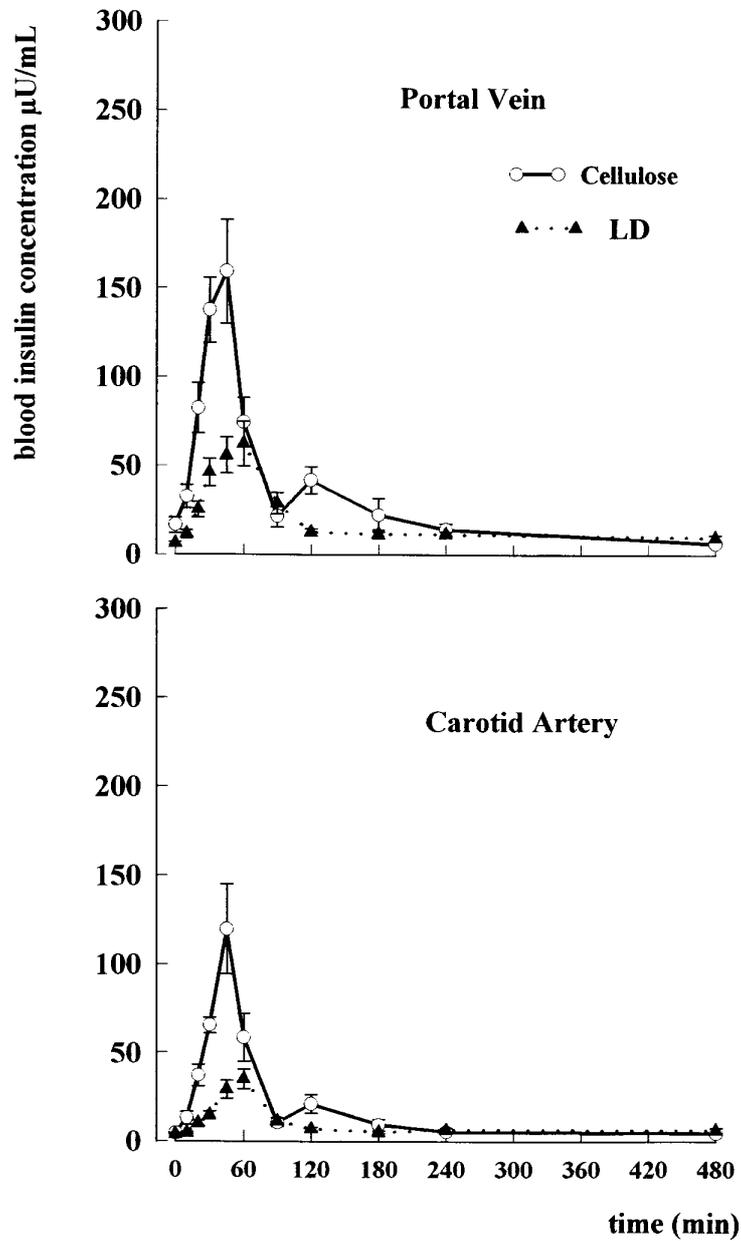


Figure 6. Effect of supplementation with fibre extract from *Laminaria digitata* (LD) on plasma insulin concentration ($\mu\text{U}\cdot\text{mL}^{-1}$) in the portal vein and in the carotid artery.

○ ○: control, 400 g basal diet supplemented with 20 g of purified cellulose (CEL).

▲ ▲: 400 g basal diet supplemented with 20 g of LD fibre.

Values shown are means for eight test-days performed in four pigs. Each pig received an alternate sequence of four test-meals, two of them supplemented with CEL, and two of them supplemented with LD. For details of composition of the basal diet, see the experimental section.

Table I. Glucose absorption balance across the small intestine following addition of 5% fibre extract from *Eucheuma cottonii* (EC), *Palmaria palmata* (PP), *Laminaria digitata* (LD), or purified cellulose (CEL) to the diet.

		(Mean values with their standard errors)				
Glucose absorbed		1 h ⁽¹⁾	2 h	5 h	8 h	
		moles	moles	moles	moles	% starch ⁽²⁾
Group 1 ⁽³⁾	EC	0.13 ± 0.01	0.34 ± 0.03	0.68 ± 0.10	0.93 ± 0.12	46 ± 6
	CEL	0.17 ± 0.03	0.35 ± 0.05	0.69 ± 0.08	0.83 ± 0.09	41 ± 5
Group 2	PP	0.21 ± 0.03	0.49 ± 0.06	1.03 ± 0.12	1.34 ± 0.12	67 ± 5
	CEL	0.18 ± 0.01	0.42 ± 0.02	0.86 ± 0.09	1.19 ± 0.13	60 ± 7
Group 3	LD	0.08 ± 0.01 ^(*)	0.19 ± 0.02 ^(*)	0.30 ± 0.03 ^(*)	0.36 ± 0.06 ^(*)	36 ± 4 ^(*)
	CEL	0.15 ± 0.01	0.33 ± 0.04	0.58 ± 0.06	0.71 ± 0.07	71 ± 8

⁽¹⁾ Data are amounts of glucose absorbed (moles) cumulated over 1, 2, 5 or 8 h after the last meal.

⁽²⁾ Data are amounts of glucose absorbed within 8 h expressed as % of starch ingested.

⁽³⁾ Pigs from group 1 ($n = 4$) received 40 g EC vs. 40 g CEL added to 800 g of basal diet (maize starch + casein). Pigs from group 2 ($n = 4$) received 40 g PP vs. 40 g CEL added to 800 g of basal diet (maize starch + casein). Pigs from group 3 ($n = 4$) received 20 g LD vs. 20 g CEL added to 400 g of basal diet (maize starch + casein). Each pig was submitted to an alternate sequence of 4 test-meals, 2 of them supplemented with seaweed fibre and 2 of them supplemented with cellulose.

^(*) Mean value was significantly different from that of CEL control (paired student t test $P < 0.05$).

Table II. Residual starch in the digestive tract following addition of 5% fibre extract from *Eucheuma cottonii* (EC), *Palmaria palmata* (PP), *Laminaria digitata* (LD), or purified cellulose (CEL) to the diet.

		(Mean values with their standard errors)			
Amount of starch (g) ⁽¹⁾		EC	PP	LD	CEL
stomach		213.6 ± 49.6	113.9 ± 34.8	117.7 ± 26.6	212.8 ± 47.4
small intestine		2.3 ± 0.2	8.6 ± 4.2	22.8 ^(*) ± 9.8	1.6 ± 0.2

⁽¹⁾ In each group (4 pigs per group), all digestive contents were collected 5 h after feeding 800 g of a basal diet (maize starch + casein) added with 40 g of EC, PP, LD or CEL.

^(*) Significantly different from other groups according to ANOVA, followed by the Tukey studentized range test ($P < 0.05$).

fibres exert such an effect by reducing the glucose absorption rate, the precise mechanisms involved are not clearly understood. In the present study, we have used the pig as an animal model. Similar physiological responses have been demonstrated in humans and pigs consuming seaweed fibres [1, 19]. Moreover, in the pig, it is possible to monitor glucose and insulin concentration

changes directly in the portal vein draining the viscera, and to quantify intestinal absorption when portal blood-flow-rate is also measured [11, 24]. In addition, the experimental design used allowed a paired comparison of the effect of seaweed fibre vs. cellulose supplementation in the same animals. Using such a design was relevant, because of relatively large inter-individual differences in

glucose absorption rates in the control situation, that is with cellulose addition.

The physiological properties of dietary fibres contained in edible seaweed have not been extensively documented [9], except for extracted carrageenans and alginates used as food additives [7, 8]. In the present work, we report contrasted effects depending on the nature of the algal polysaccharides tested. Xylanes from *P. palmata* did not affect blood glucose nor insulin response, as compared to purified cellulose used as a control. Carrageenans from *E. cottonii* modestly lowered blood glucose and insulin response both in the portal vein and in the carotid artery, but this did not result in a significant decrease of glucose absorption balance over the 8 h following the test-meal. In contrast, alginates from *L. digitata* strongly reduced blood glucose and insulin responses, which resulted in a 50% decrease of glucose absorption balance over 8 h. The latter results are consistent with previously reported observations on alginates. Alginates, at a low dose, induce a lower postprandial rise in peripheral blood glucose and serum insulin in NIDDM human subjects [29]. Alginates inhibit blood glucose and insulin levels from rising 30 min after glucose administration in an oral glucose tolerance test performed in rats [15]. The postprandial glycaemic response is also lowered in streptozotocin-induced diabetic rats receiving a diet containing 2.5% alginate [22].

The ability of land plant polysaccharides, such as pectin or guar gum, to lower blood glucose and insulin response has been shown to depend on their viscosity [12, 14]. The present data suggest that viscosity is also a major factor in the case of algal polysaccharides, as the three fibre extracts tested differed greatly in that respect, and the effects observed were correlated with their intrinsic viscosity. As already emphasised by [4] and [11], changes in the viscosity of digesta are difficult to predict from the viscosity of the fibre ingredients, and no dose-

response relationship can be found [11]. This can be explained first by dilution of secretions in the digestive tract, and second by the effect of pH and ionic conditions prevailing in the gut. These conditions, which are difficult to monitor in the complex environment provided by the digestive contents, do modify polysaccharide viscosity.

The physico-chemical properties of alginates and κ -carrageenans, as measured in vitro, depend on the ions present, ionic strength, and pH conditions [20, 23]. The rheological behaviour of LD is much more sensitive to environmental conditions (Ca^{2+} , pH, ionic strength) than that of EC [17]. LD precipitates in the stomach under the form of alginic acid [34], and solubilises in the small intestine making the intestinal contents homogeneous and viscous. As compared to LD, EC has a smaller impact on the rheological properties of the digestive contents.

Another important issue is the possible mechanisms involved in the blood glucose lowering effect. Viscosity induces changes in the rheological properties of digestive contents. This, in turn, can result in a reduced gastric emptying rate, although this is controversial for the solid phase [18], modified transit and motility in the small intestine [6], and reduced movement of nutrients from the lumen to the mucosal epithelium [12]. All these effects can result in slower or reduced intestinal absorption.

Gastric emptying rates measured in diabetic subjects are reduced in the presence of alginates [29]. Delayed gastric emptying was also reported in the rat [22], due to gel formation in the stomach, in the presence of calcium. In our study, despite alginate precipitation occurring in the stomach, the amount of starch remaining in this compartment 5 h after the meal was not increased by alginate supplementation.

Although this has been measured in vitro, alginates from *L. digitata*, as well as xylans from *P. palmata*, and carrageenans from *E. cottonii* have no effect on porcine

pancreatic amylase activity [3]. It is thus suggested that LD supplementation does not act by inhibiting starch hydrolysis. The higher amount of starch, or starch degradation products, found in the small intestinal contents 5 h after the LD supplemented meal could be explained by a slower transit in this part of the digestive tract. Another possible mechanism, which could not be specifically tested in our study, is that viscosity increases the unstirred water layer thickness, thus reducing glucose absorption rates, because of a slower diffusion through this layer. In addition, we do not know whether the reduced hyperglycemia observed in the present study was in part mediated by changes in digestive hormones, like GIP or GLP1. Previous studies have shown that a reduced secretion of these hormones could explain a reduced insulin response with soluble non-starch polysaccharides [11, 12, 21].

In the present study, we have shown that some of the non-starch polysaccharides extracted from edible seaweed can affect intestinal absorption of glucose and postprandial insulin response, when added to a high carbohydrate meal. Among the physico-chemical characteristics of the polysaccharides tested, viscosity seems to be a major determinant of this physiological effect. As for other soluble non-starch polysaccharides, viscosity probably acts by changing the rheological properties of digesta in the small intestine, thus interfering with nutrient-enzyme interaction, or with the absorption process itself.

These properties, combined with potential effects on transit time and faecal bulking [19], or colonic fermentation [17, 26] demonstrate that fibre-rich edible seaweed can be of interest in human nutrition.

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