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ORIGINAL CONTRIBUTION

Laëtitia Robert
Agnès Narcy
Edmond Rock
Christian Demigne
Andrzej Mazur
Christian Rémésy

Entire potato consumption improves lipid metabolism and antioxidant status in cholesterol-fed rat

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L. Robert · A. Narcy · E. Rock
C. Demigne · A. Mazur · C. Rémésy (✉)
Unité des Maladies Métaboliques
et Micronutriments
Institut National de Recherche
Agronomique
Centre de Clermont-Ferrand/Theix
63122 Saint-Genès Champanelle, France
Tel.: +33-047/3624-233
Fax: +33-047/3624-638
E-Mail: remesy@clermont.inra.fr

Abstract *Background*
Vegetables and fruits are rich sources of a variety of nutrients, including vitamins (E and C), trace minerals, and dietary fibers, and many other classes of biologically active compounds such as carotenoids and polyphenols, which are often assumed to protect against degenerative pathologies such as cardiovascular diseases. Although potato is considered as a starchy food, it is also included in the category of vegetables by its micronutrient content. *Aim of the study*
In the present study, we investigated in the rat the effect of a potato-enriched diet on lipid metabolism and antioxidant protection. *Results*
Feeding rats a potato-enriched diet for 3 weeks led to a significant decrease in cholesterol and triglyceride levels in plasma (respectively, −30%, $P < 0.0001$ and −36%, $P < 0.05$) and cholesterol level in liver (−42%, $P < 0.0001$). Antioxidant status was also improved by potato consumption. TBARS levels in heart were decreased and vitamin E/triglycerides ratio in plasma was improved. *Conclusions*
Our present results suggest that consumption of cooked potatoes (consumed with skin) may enhance antioxidant defense and improve the lipid metabolism. These effects could be interesting for prevention of cardiovascular disease.

Key words potato – fiber – antioxidant – cholesterol – cardiovascular diseases

Introduction

Epidemiological studies support the view that consuming diets rich in fruits and vegetables is associated with reduced incidence of degenerative pathologies such as diabetes, obesity, cancers and cardiovascular diseases [1–3]. There are several biologically plausible reasons why consumption of vegetables and fruits might delay or prevent the onset of chronic diseases. Vegetables and fruits are a rich source of a variety of nutrients, including vitamins (E and C), trace minerals, and dietary fibers, and many other classes of biologically active compounds such as carotenoids and polyphenols.

Although potatoes (*Solanum tuberosum* L.) are foods of plant origin and are sometimes included under the broad category of vegetables, most often they are considered separately [4–6]. Since potatoes are rich in starch granules, they are considered as starchy foods in the same way as rice and pasta. But potatoes also contain other nutrients of interest such as minerals and antioxidant micronutrients (vitamins, polyphenols...). Therefore, potatoes can be considered also as vegetables.

Potato is the most consumed vegetable in France, and the second plant food consumed in the world after wheat. According to the F.A.O. (Food and Agricultural Organization), potato consumption is approximately 80 and 65 kg annum^{-1} per capita in Western Europe and in France, respectively.

Potato is one of the vegetables rich in vitamin C and is also an interesting source of dietary fiber (7% of peeled potato, up to 11% of non-peeled potato). Potato fibers are mainly water-soluble fibers (55%) such as hemicelluloses and pectins (shown to have hypocholesterolemic effects on rats [7], together with water-insoluble fibers (45%) such as cellulose [7, 8]. In addition, potato contains starch (70–90% on dry basis), which is indigestible because it is encapsulated within the granules that hinder the accessibility of digestive enzymes [9]. However, when potatoes are cooked the starch granules are gelatinized and starch becomes readily digestible. The amount of resistant starch depends on the degree of gelatinization and retrogradation during cooling of the cooked food [10].

Numerous studies conducted previously have investigated the health effects of raw and/or retrograded potato starch. Mazur et al. [11] demonstrated the lipid-lowering effect of a diet rich in fermentable carbohydrates. De Deckere et al. [12] found that feeding diets containing a high amount of retrograded starch led to lower serum triacylglycerol and total cholesterol concentrations in the rat. Cherbut et al. [13] demonstrated that potato fibers increased the production of SCFA. Only a few studies investigated the impact of cooked potato consumption on rats [14] and on humans [10] and only one study found a positive association between potato intake and plasma MDA levels [15].

Potato contains high amounts of vitamin C (about 15 mg/100 g of steamed potato, contributing to 25–30% of the RDA (Recommended Dietary Allowance) for vitamin C [4, 16]), and other antioxidant micronutrients such as vitamin E, carotenoids (principally lutein) [17] and phenolic acids (mainly caffeic and chlorogenic acids) [18, 19]. These antioxidants are able to efficiently scavenge superoxides and peroxyl radicals and, together with endogenous systems of defense, they limit oxidative stress and reduce the risk of associated degenerative diseases [20, 21] such as cardiovascular diseases possibly by the protection of lipoproteins from peroxidation [22–24]. Several studies examined the health effect of consumption of fruit and vegetable in a diet (including potato) but little is known about the lipid-lowering effect of potato and its impact on antioxidant status. Taking into account its fiber content and its antioxidant content, it was hypothesized that potato consumption could improve both lipoprotein profile and antioxidant status resulting in a cardiovascular protective effect. Therefore, we investigated the effect of diet containing cooked potatoes (because potatoes are normally processed by some form of heating before consumption by man), supplemented with 0.25% of dietary cholesterol, on lipid metabolism and antioxidant status, two factors involved in the etiology of cardiovascular diseases.

Materials and methods

Animals and diets

A total of 16 male Wistar rats (colony of laboratory animals of the National Institute of Agronomic Research, Clermont-Ferrand/Theix, France) were maintained and handled according to the recommendations of the Institutional Ethic Committee (Institut National de la Recherche Agronomique), in accordance with decree N° 87–848.

Animals weighing about 180 g each were housed two per cage in a room maintained at 22 °C with a 12 h light-dark cycle (light from 8:00 to 20:00 h) and access to food from 16:00 to 8:00 h. Rats were randomized in two groups and fed *ad libitum* for 3 weeks either a control diet or a potato-enriched diet. The control diet contained (in g/kg): 180 casein, 697.5 starch, 35 AIN 93 M mineral mix, 10 AIN 96 M vitamin mix without α-tocopherol, 75 corn oil, 2.5 cholesterol. Wheat starch was obtained from wheat flour, which was mixed with water to form dough. After ripening, the resulting dough was stirred and then filtered. Wheat starch was recovered by centrifugation, refined by water washing and lyophilized. The potato diet contained (in g/kg): 110 casein, 784 potato, 2.5 AIN 96 M vitamin mix without α-tocopherol, 75 corn oil, 2.5 cholesterol. In the control diet, vitamin E is exclusively provided by corn oil, whereas in the potato-enriched diet, potatoes provide traces of vitamin E, in addition to corn oil. Potatoes were purchased from a local supplier "Jardin de Limagne". Potatoes were steamed with skin, mashed and given immediately and accounted for 78.4% (dry matter) of the total diet. During the last week of the experimental period rats were housed in metabolic cages for urine and feces collection. Daily food consumption and body weight were recorded twice a week.

Sampling procedures

Rats were anesthetized during the post-absorptive period (between 08.00 a.m. and 10.00 a.m.), when the cecal fermentation is still active, by sodium pentobarbital intraperitoneal injection (40 mg/kg of body weight). Blood was drawn from the abdominal aorta

into heparinized tubes and centrifuged at 12,000 *g* for 2 min. Plasma samples were either stored at 4 °C for lipid and lipoprotein analysis or immediately stored at −80 °C for antioxidant assay.

After blood sampling, the cecum (wall with contents) was removed and weighed. The cecal wall was flush cleaned with water, dried and weighed (cecal wall weight). Samples of cecal contents were collected, and immediately frozen at −20 °C. Supernatants were obtained by centrifuging the microtubes at 20,000 *g* for 10 min at 4 °C for short-chain fatty acid (SCFA) analysis.

The liver was freeze-clamped and stored at −80 °C for the measurement of lipid and for peroxidation assay. The heart was rapidly washed in physiological saline and immediately stored at −80 °C for lipid peroxidation assay.

Analytical procedures

SCFA were measured on aliquots of cecal supernatants by gas-chromatography as previously described [25].

Bile acids and neutral steroids were extracted twice from feces at 70 °C for 2 h with 40 volumes of alkaline ethanol (KOH 4 mmol/l). Bile acids were quantified using the reaction catalyzed by 3 α-hydroxysteroid dehydrogenase (EC 1.1.1.50; Sigma Chemical Co., L'Isle d'Abeau Chesnes, France) [26]. Neutral steroids (100 µl) were extracted three times with hexane (500 µl) after addition of 5 α-cholestane (internal standard, Sigma St Louis). The hexane extract was concentrated to 200 µl and 2 µl were injected into the gas chromatograph (Danieducational, Paris, France) fitted with a 12 m × 0.25 mm fused silica capillary column (BP 10) and a flame-ionization detector. Helium was used as a carrier gas, and an isocratic temperature (260 °C) was used for the steroid separation. Sterol concentrations were calculated from the peak area relative to the peak area of the internal standard.

Plasma total cholesterol concentration was enzymatically determined using a kit purchased from BioMerieux (Charbonnières-les-bains, France) and plasma triglyceride concentrations were determined using a kit from Biotrol (Paris, France). Liver lipids were extracted with chloroform/methanol (2:1, v/v) according to the method previously described [11].

Plasma lipoproteins were separated by ultracentrifugation (1,00,000 *g* for 24 h at 15 °C) of 2 ml plasma samples on a density gradient of potassium bromide. The gradient was divided into 24 fractions of 500 µl and cholesterol and triglyceride content of each fraction were determined as described above for plasma samples. Results were expressed for pools with $d < 1.040$ kg/l (chiefly triglyceride-rich lipoprotein: TGRLP, with a minor contribution of LDL) and $d > 1.040$ kg/l fraction (essentially HDL).

Vitamin E was analyzed by HPLC-UV [27]. Briefly, vitamin E was extracted twice from plasma after addition of α-tocoacetate (internal standard) by 2 × 2 volumes of hexane. The separation was carried out on a Vydac TP54 (250×4.6 mm; Hesperia, CA) and a Nucleosil column (150×4.6 mm; Interchim, Montluçon, France) in series. Elution was performed with methanol, at a constant flow of 2 ml/min.

Ferric reducing ability of plasma (FRAP) was determined in 100 µl plasma samples diluted 1:2 and the tripyridyltriazine complex formed with the reduced ferrous ions was measured by UV spectrometry at 596 nm [28].

The levels of TBARS in urine samples were measured using the modified procedure of Lee et al. [29] by reading absorbance at 532 nm. The quantity of TBARS is proportionate to the amount of MDA, a lipid peroxidation product generated by the oxidation of membrane lipids by reactive oxygen species. MDA reacts with TBA to form a 1:2 MDA–TBA adduct that absorbs at 532 nm. Data were normalized to urine creatinine concentrations. Results were determined as nmol/mg creatinine excreted with creatinine being measured with the kit purchased from BioMerieux (Charbonnières-les-bains, France).

MDA was also determined in heart homogenates by measuring the formation of TBARS upon induction of oxidation by a mixture with 2 mmol/l $FeSO_4$ and 50 mmol/l of ascorbic acid for 30 min at 37°C in an oxygen-free medium [30].

Statistical analysis

Values are given as the means ± SEM, and the differences between values were determined by the Student's *t*-test. Values of $P < 0.05$ were considered significant.

Results

Food intake, body and organ weight, and digestive fermentation

There was no difference between the two groups in the daily food intake (in the range of 17–18 g of dry matter/d), whilst the body weight gain was significantly lower in rats fed with the potato-enriched diet as compared to those fed with the control diet (4.33 ± 0.28 vs. 5.58 ± 0.31 g/d, $P < 0.001$). The incorporation of potato did not affect the relative weight of the heart (0.3%), whereas that of liver was lesser in rats that fed on potato-enriched diet than controls (4% vs 4.5%, respectively, $P=0.0009$) (data not shown). The fecal dry matter excretion was signifi-

cantly higher in rats fed with potato-enriched diet as compared to those that fed on control diet (2.51 ± 0.21 g vs. 0.75 ± 0.20 g/d, $P < 0.0001$). The potato diet led to a 55% increase of the cecal wall weight and to a significant acidification of the cecal content (down to 5.86 ± 0.10 in rats fed with potato-enriched diet, compared to 6.92 ± 0.07 in control rats, $P < 0.0001$). An increase of SCFA pools in the cecum of rats that consumed potato-enriched diet (Fig. 1) was observed, resulting in a rise of all SCFAs (+218% for acetate, +442% for propionate and +209% for butyrate).

Plasma and tissue lipids

Plasma cholesterol and triglycerides were significantly lower in rats that fed on potato-enriched diet than in control (−31%, $P < 0.0001$ and −36%, $P < 0.05$, respectively) (Table 1). The plasma lipoprotein profile shows a reduction of cholesterol in the TGRLP fractions (−37%) in rats fed with potato-enriched diet compared to controls (Fig. 2a), but there was no change in the d>1.04 fractions (mainly HDL). Triglyceride concentrations were 29% lower in TGRLP of rats that consumed potato-enriched diet as compared to the control (Fig. 2b). In the HDL fraction, triglycerides were slightly lower in rats fed with the potato-enriched diet than in control rats.

Liver cholesterol was significantly lesser (−42%) in rats fed with potato-enriched diet compared to the controls, whereas hepatic triglycerides were not significantly affected (Table 1).

Cholesterol intake and digestive balance of bile acids

As shown in Table 2, the daily cholesterol intake was similar in both groups. The potato-enriched diet induced a greater fecal excretion of neutral sterols (+58%, $P < 0.05$) and especially coprostanol (+146%, $P < 0.0001$). Digestive neutral sterols balance was thus significantly altered by potato-enriched diet and resulted in a decrease of apparent cholesterol absorption. An increase in bile acid excretion in rats that consumed potato-enriched diet led to a significant increase in the percentage of apparently absorbed cholesterol excreted as bile acids. This led to a significant decrease of total steroid balance in rats fed with potato-enriched diet compared to the controls. The total digestive steroids balance relative to cholesterol intake, which represents the apparent absorption of dietary cholesterol, was significantly depressed by the potato-enriched diet, representing only 3.1% of the cholesterol intake vs. 44.3% in the control diet ($P < 0.0001$).

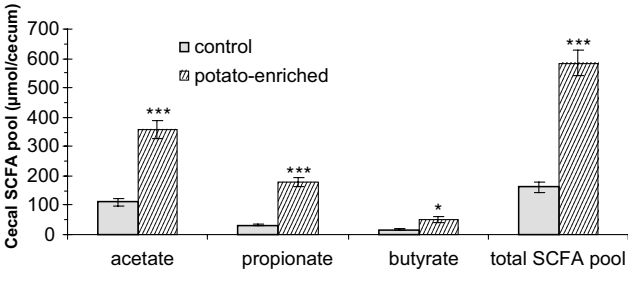

Fig. 1 Cecal short-chain fatty acids in rats fed with control or potato-enriched diet for 21 days. [1]Values are means ± SEN; n=8. *P<0.05, ***P<0.0001

Effect of potato-enriched diet on antioxidant status

Potato-enriched diet led to a significant decrease of the susceptibility to oxidation of heart lipids as assayed by an ex vivo induction of lipid oxidation by ferrous ions (−34%, $P < 0.001$). However, urine TBARS excretion was not significantly modified by potato-enriched diet. The FRAP value was increased in rats that fed upon potato-enriched diet (+66%, $P < 0.05$) (Table 3).

We also observed that potato-enriched diet led to a 30% increase of vitamin E plasma concentration (6.4 ± 0.4 vs. 4.9 ± 0.3 µmol/l, $P < 0.05$, for potato and control, respectively) and the vitamin E/TG ratio was almost two-fold higher in rats fed with the potato-enriched diet than in controls (respectively, 8.6 ± 0.9 vs. 3.9 ± 0.5 µmol/l, $P < 0.001$).

Discussion

The non-energetic moiety of vegetables (fibers, minerals, micronutrients) is complex and plays an important role by mediating various health effects, especially with regard to cardiovascular diseases [2]. Little is known about the mechanism of action of complex plant foods such as potato, one of the most consumed vegetables in many countries.

The aim of this work was to assess whether 3-weeks' of a potato-enriched diet could affect lipid metabolism and antioxidant status in rats with dietary conditions in which the macronutrient supply was relatively well equilibrated (the supplementation of the diet with 0.25% of cholesterol allowed to develop a significant hypercholesterolemia without inducing fatty liver). Since the rat is a low-responsive animal (the amount of lipoprotein fractions, especially LDL, is greater in human plasma than in rat plasma), we chose to investigate a high level (78%) of potato in the

Table 1 Plasma and hepatic concentration of cholesterol and triglycerides in rats fed with control or potato-enriched diet for 21 days[1]

Diet	Plasma		Liver	
	Cholesterol (mmol/l)	Triglycerides (mmol/l)	Cholesterol (mmol/g tissue)	Triglycerides (mmol/g tissue)
Control	2.05±0.11	1.26±0.18	13.56±0.81	31.18±3.44
Potato-enriched	1.42±0.11***	0.81±0.11*	7.82±0.6***	25.02±2.37

[1]Values are means±SEM; n=8. *P<0.05, ***P<0.0001

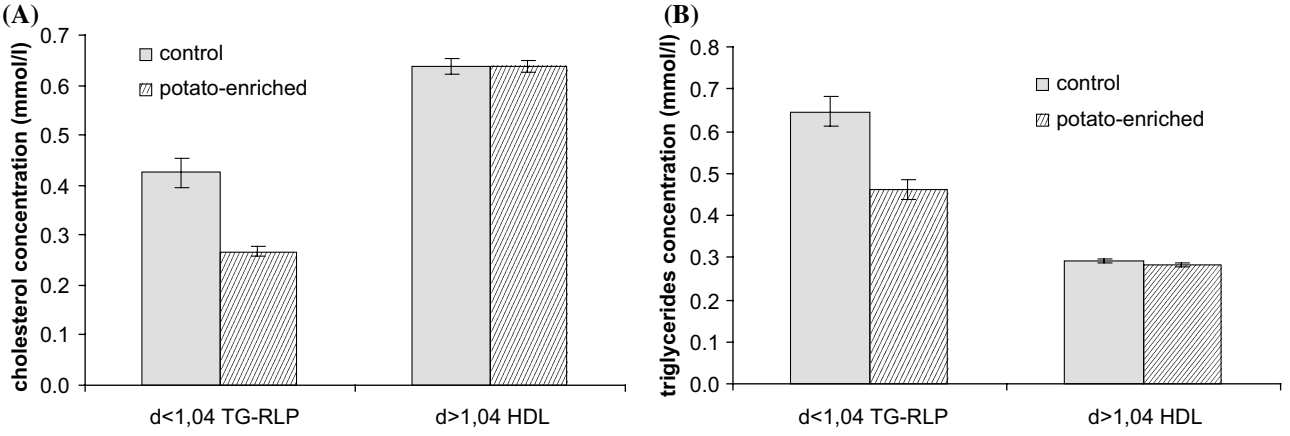

Fig. 2 (**A**) Changes in the repartition of cholesterol in the various plasma lipoprotein fractions in rats fed with control or potato-enriched diets for 21 days.[1] The fraction with d < 1.040 kg/l correspond chiefly to triglycerides-rich lipoproteins (TG-RLP) with a lower contribution of LDL. The fractions with d > 1.040 kg/l correspond essentially to HDL; (**B**) differences in the repartition of triglycerides in plasma lipoprotein fractions of rats fed with control or potato-enriched diets. Each value is a mean ± SEN of a triplicate analysis of a pool of 8 eats

diet to obtain a significant response. Potatoes were eaten with skin to keep most of fibers and antioxidant micronutrients, in order to exacerbate the impact on lipid metabolism and antioxidant status.

Table 2 Effects of potatoes on cholesterol balance in rats fed control or potato-enriched diet for 21 days[1]

	Control	Potato-enriched
Neutral sterol balance		
Cholesterol intake (µmol/d)	114.4±3.1	111.3±2.7
Cholesterol fecal excretion (µmol/d)	24.5±0.3	24.0±1.5
Coprostanol fecal excretion (µmol/d)	16.4±1.5	40.5±4.2***
Total neutral sterols (µmol/d)	40.9±1.5	64.5±6.0*
Digestive neutral sterols balance (Intake–Excreted)	73.5±2.1	46.8±1.7***
(Digestive neutral sterol balance/ cholesterol intake) × 100 (%)	64.2±2.2	42.0±2.5***
Total steroid balance		
Bile acids fecal excretion (µmol/d)	22.9±5.7	43.3±3.3**
% of absorbed cholesterol excreted as bile acids	31.1±5.1	92.6±5.3***
Total digestive steroid balance	50.6±4.6	3.5±2.4***
Cholesterol apparent absorption (Total digestive steroid balance/ cholesterol intake) × 100 (%)	44.3±4.4	3.1±0.9***

[1]Values are means ± SEM; n=8. *P < 0.05, ***P < 0.001

In these experimental conditions, potato consumption exerts a significant cholesterol-lowering effect both in plasma and in the liver. A decrease of cholesterol (−37%) in the potentially atherogenic lipoproteins (VLDL and LDL) was observed. Such an effect can be considered as beneficial for cardiovascular disease prevention. The cholesterol-lowering effect can be attributed to the fibers provided by potatoes. Indeed, previous studies have reported similar effects with high fiber diets [31]; moreover, fibers are known to affect the lipoprotein profile in cholesterol-fed rats [11].

The effect of pectin on lipid metabolism has been well studied both in humans and animal models [7, 32–34] and previous experiments demonstrated that dietary fibers can also exert cholesterol-lowering effects by increasing fecal excretion of total steroids (neutral sterols and bile acids) [35].

In the present study, we observed that potato consumption led to a significant increase of neutral sterol fecal excretion, especially of coprostanol, and to an increase in the amount of cholesterol excreted in feces as bile acids. Our data obtained from cholesterol-fed rats support the view that fibers are effective in depressing the absorption of exogenous

Table 3 Antioxidant status and oxidative stress in rats fed control or potato-enriched diet for 21 days[1]

	FRAP (μmol Fe^{2+}/L)	Urine-TBARS (nmol/mg creatinin)	Heart tissue TBARS (induced) (nmol/g)
Control	160.0±4.7	1.1±0.2	323.5±19.6
Potato-enriched	266.5±20.6*	0.8±0.1	214.8±16.3***

[a]Values are means ± SEM; $n = 8$. *$P < 0.05$, ***$P < 0.0001$

cholesterol, as previously shown in guinea pigs and rats [35, 36]. The mechanisms of inhibition of cholesterol absorption, in which viscosity is an important contributor, have been well documented; they include disturbance of micelle formation, slowing of cholesterol transfer to the brush border across the unstirred layer and inhibition of ileal bile acid reabsorption [37]. It has been shown that the physicochemical properties of soluble fibers results in important modifications in volume, bulk and viscosity in the intestinal lumen, which alter metabolic pathways of hepatic cholesterol and lipoprotein metabolism, resulting in lowering of plasma LDL–cholesterol [33]. In rats fed with diets containing fibers, the intestinal bile acid pool may be increased [36]. This could reflect an entrapment of bile acids within the viscous medium, as well as an accelerated biliary influx. It is noteworthy that in the present study, potato induced a greater elimination of bile acids.

It is well known that when cholesterol is added to the diet, the enhanced fecal losses of bile acids correspond to a less effective reabsorption [36] and to an inhibition of the HMG-CoA reductase activity [38].

Moundras et al. [36] found that in rats that fed upon guar gum diets supplemented with cholesterol, the losses of steroids were, to a certain extent, compensated by the induction of liver HMG-CoA reductase. The induction of this enzyme took place in spite of an accelerated return of bile acids to the liver; this process could limit the adaptation of cholesterol synthesis and thus contribute to the cholesterol-lowering effect of guar gum.

Fibers could also exert indirect effects on cholesterol metabolism. Their fermentation in the large intestine leads to a production of short-chain fatty acids such as propionate, which may be involved in the control of hepatic cholesterol synthesis [39]. In our experiment, we observed a rise of all SCFAs, especially of propionate (+442%). Studies on isolated hepatocytes demonstrated that propionate could inhibit cholesterol biosynthesis from acetate [40]. Nevertheless, the impact of propionate on cholesterol metabolism in the liver is likely less effective than the direct effect of fiber on digestive cholesterol absorption or their indirect effect on the cholesterol conversion into bile acids.

All together, such mechanisms are able to decrease plasma cholesterol concentration.

Potato may also provide beneficial health effects by supply of antioxidant molecules. We investigated the defense against lipid peroxidation in the heart tissue as an important target tissue for reactive oxygen species (ROS). The reaction with thiobarbituric acid to form a colored adduct is a rapid, inexpensive and sensitive technique [41]. This method, however, is subject to interferences, mainly in urine samples. Indeed, the more complex mixture of aldehyde products present in urine samples (as opposed to plasma and tissue homogenates) has probably contributed to the lack of significant lowering of lipid oxidation reported for this particular sample in our study. On the other hand, rats fed with potato-enriched diet showed a very significant lower peroxidation in heart measured by TBARS assay.

After 3 weeks of potato feedings, the plasma antioxidant capacity measured by FRAP assay was increased with potato diet. The level of α-tocopherol in plasma was also slightly but significantly improved, whereas α-tocopherol/TG ratio was increased by potato-enriched diet, suggesting a higher protection of lipid against radical attack. It is well recognized that, in addition to being able to interact with the superoxide and hydroxyl radicals, L-ascorbic acid has the ability to regenerate the activity of lipid-soluble antioxidants, such as α-tocopherol (leading to its sparing) and β-carotene, essentially in vitro [16].

In conclusion, potato consumption is often associated with bad food habits (high intake of fats, animal products, together with low intake of fruits and vegetables). In itself, potato, consumed with few fats and within the scope of a balanced diet, exerts a diversity of interesting effects on risk factors of cardiovascular diseases, all the more as potato is rich in potassium, which contributes to prevent high blood pressure [42, 43]. We have found that potato consumption can reduce plasma and hepatic lipids and improve antioxidant status. Both effects could be largely explained by the fiber content (especially when potato is consumed with skin) and by the phenolics and vitamin C supply of potato.

It is difficult to extrapolate the results obtained from rat studies to humans not only because the different metabolic response but also because of a higher food ingestion in the rat model. In our model, the diet contained 78% of potato, which could correspond to a consumption of 390 g of potato/500 g of dry matter per day. Further clinical investigations have to be conducted in humans to investigate dif-

ferent protective effects, according to the cultivar and to the cooking process, since antioxidant micronutrient content varies according to these conditions [18, 44]. Otherwise, investigations have to be also conducted to examine potential beneficial effects of a lesser percentage of potato intake to explore the translatability of our results obtained from a rat model to a human population.

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