



The case for a legal definition of sourdough bread

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This Real Bread Campaign document outlines the case for a clear and simple single legal definition of sourdough bread. The key reasons are to help protect the livelihoods of bakers who make *genuine* sourdough bread (see below), and to help prevent shoppers from being misled, for whatever reasons they want or need to choose it.

Introduction

There are various reasons that people want (or, in some cases, find that they *need*) to choose sourdough bread. At present, people are not adequately protected from being misled by the use of the word sourdough in the naming and marketing of fundamentally different products. Current, but outdated, legislation is also failing to protect makers and retailers of genuine sourdough bread from unfair competition.

An increasing number of products are being named and marketed using the word sourdough, which have not been made by a sourdough long fermentation process. Some are manufactured using additives that an average consumer would reasonably expect not to be found in sourdough bread, which is generally considered to be less processed and more 'natural'. Legislation is needed now to stop the genie getting any further out of the bottle.

Key points this document outlines include that:

- This is more than a subjective matter of taste and flavour. The making of genuine sourdough bread is a substantively different process that results in products that are, objectively, fundamentally different from baked goods made by other methods/processes.
- There is an increasing general awareness that genuine sourdough bread is fundamentally different to other baked products and a growing perception that it might even be 'healthier', 'more natural', of higher quality or otherwise 'better'. This is underpinned by a growing body of evidence, and driven by producers, retailers, the media and even the NHS.
- Some manufacturers seek to profit from this growing demand (sometimes using premium branding and charging premium prices) but without investing the time, knowledge and skill needed to make genuine sourdough bread. Their use of production methods, perhaps because they are quicker and cheaper, result in fundamentally different products.
- People are selecting such products with an understanding and expectation that they are purchasing something 'premium', 'better', 'more natural' or at least substantively different to, other baked products.
- When presented with complaints about the (mis)use of the word sourdough, consumer protection bodies do not enforce existing food information or trading standards legislation, typically citing the lack of a legal definition of the word as the reason they are unable to do so.
- The effectiveness of voluntary, industry-led, opt-in schemes is far more limited than regulation.

What is genuine sourdough bread?

Rather than a flavour, look, style or trend, the sourdough process is simply the oldest way of leavening dough. Bread of every type can be (and is) made using a genuine sourdough process by bakeries of all sizes around the world.

Yeasts and bacteria are present all around us, including on the surface of wheat and other grains. When grain is milled into flour, some of the yeasts and bacteria are incorporated. Given suitable conditions (basically warm and wet, with additions of more flour to metabolise) yeasts and lactic acid bacteria (LAB) will thrive, multiply and can be nurtured into a sourdough starter culture. More flour, water and (if the baker chooses) other natural ingredients can then be added to a portion of sourdough starter culture to make a dough. Allowed sufficient time, carbon dioxide generated by the yeast cells as a by-product of their respiration will make the dough rise.

In the hands of a skilled, knowledgeable baker, the production of enzymes, organic acids and other substances by the yeasts and LAB during this long fermentation process can be controlled to have <u>beneficial effects on the</u> <u>organoleptic properties</u> (flavour, texture and aroma) of the resulting bread. This transformation cannot happen to the same extent if the fermentation time is shortened by the use of additional raising agents. In the absence of a live sourdough starter culture, it cannot happen at all.

Good (and even great) bread *can* be leavened using baker's yeast alone or in combination with a sourdough starter culture, but neither process results in genuine sourdough and so should not be marketed as such. A comparison might be that neutral grain spirit can produce good vodka in a short time, but could not be called whisky unless it goes through a particular process to make it such. Nor is adding a splash of whisky to neutral spirit sufficient for the word to be used to name or market a bottle of it.

Genuine sourdough bread falls into the processed (rather than the ultra-processed) food category of the UN FAO recognised <u>NOVA classification</u>. People generally and reasonably expect sourdough bread not to be an ultra-processed product. As such, the production of genuine sourdough bread does not involve any so-called 'processing aid' or other additive, all of which are, by definition, totally unnecessary to produce bread of any kind.

Potential health benefits

The need for a legal definition of sourdough bread does not rely on proof that making bread using a genuine sourdough process has one or more nutritional or other health benefits greater than making bread without a live LAB starter culture, or if the fermentation time has been shortened, such as by the use of baker's yeast. A growing body of evidence (see appendix) suggests, however, that it might.

The strains and concentration of yeast cells in a sourdough starter culture produce carbon dioxide at a slower rate than baker's yeast, meaning that dough made by a genuine sourdough process takes longer to rise. During this extended fermentation time, the LAB in particular cause biochemical changes in the dough that go beyond subjective improvements to the organoleptic properties of the resulting bread.

Published in the February 2021 issue of Trends in Food Science & Technology, <u>Thirty years of knowledge on</u> <u>sourdough fermentation: A systematic review</u> is based on an examination of 1230 peer reviewed research articles published between 1990 and 2020 on the subject of sourdough. Its authors note: "The most recent literature showed how the sourdough fermentation mainly increased mineral bioavailability, enabled fortification with dietary fibers, lowered glycemic index, improved protein digestibility and decreased the content of anti-nutritional factors." Researchers have also found how sourdough fermentation can modify and reduce the proteins that trigger the coeliac response - see the appendix for links to selected studies.

The lactic acid bacteria in bread making are related to those that act as natural preservatives in the production of foods including some cheeses, sauerkraut, kimchi, yoghurt and charcuterie. While not a health benefit, LAB fermentation has been shown to <u>slow staling</u> and <u>inhibit fungal activity</u>, both useful in helping to reduce food waste.

Again, none of this can happen to the same (or even sufficient) extent if the fermentation time is shortened by the use of additional raising agents. In the absence of a live sourdough starter culture, it cannot happen at all. The Real Bread Campaign calls for more research to be funded and carried out on the potentially beneficial effects of sourdough fermentation. In the meantime, people who experience benefits for themselves need protection from being misled.

Perception

Consumer research in the UK and elsewhere suggests that people who seek out products marketed as 'sourdough' typically do so wanting more natural food, understanding or believing that it is some way 'better'. For example, a <u>market analysis report</u> published by Grand View Research in August 2019 noted: "Sourdough-based baking products are considered to be healthier alternatives to those made using regular dough."

There are many drivers to this general perception. In addition to any knowledge of existing scientific research/evidence a person has, they include: exposure to articles, broadcasts and other social and traditional media content; word of mouth; advice from dieticians; nutritionists or others in healthcare. Some of these sources are official or at least generally understood to be factually accurate. For example, sourdough appears on a list of <u>'tummy-friendly breads'</u> in Eat Well guidance published by the NHS, and the BBC has published a list of <u>Top 5 health</u> benefits of sourdough, written by a registered nutritionist. This all aligns with many instances of people reporting that they experience negative effects of eating cereal products but that they can enjoy eating genuine sourdough bread.

The perception is also being driven by marketing messages from producers and retailers, including some of the UK's largest baked product manufacturers. Examples include Allinson's promoting <u>a baker's yeast-leavened factory loaf</u> as a premium product that's 'that extra bit special because it is baked with sourdough for a distinctive, full-flavoured white bread' and Warburtons similarly marketing <u>a yeast-leavened industrial loaf</u> as 'ideal for making that weekend brunch a little bit extra special with its unique texture and taste. Baked based on a traditional artisan process, this is really in the 'upper crust' in loaves!'

Meanwhile, additive/ingredient suppliers are promoting products to bakers and encouraging them to pass on to customers messages about the potential benefits of sourdough, whilst supplying products that are intended to reduce or eliminate sourdough fermentation time. An example is Puratos, which promotes its products with messages such as this line from an advertorial in the October 2021 issue of Out of Home Magazine: 'educating consumers on the nutritional benefits, flavour, formats and versatility of sourdough may help justify the price of the product.' A similar message appears in a media release by Puratos, the basis of this article on the Bakery Business website, which also mentions 'O-tentic active bakery blends for baking delicious Italian style breads with just four ingredients: flour, water, salt and O-tentic.' Puratos advertise this as a 'clean(er) label' product to be 'the start of all your breads with just 4 ingredients: flour, water, salt and O-tentic'. Rather than being just dehydrated, powdered sourdough starter, however, the product also contains a further two baker's yeast and the additive E300. One recipe on the Puratos website for using O-tentic is called High Street Baker French Sourdough, despite having a

fermentation time of a mere 90 minutes at most. It is doubtful that this long enough to develop all, or any, of the benefits the company is using to sell its products to bakers and encouraging them to use as marketing messages to shoppers.

Supporting fair competition

Since at least the 1990s, Real Bread bakers around the UK have created and been nurturing a British tradition of genuine sourdough breadmaking. The majority of those doing so commercially are at locally-owned SME bakeries, which support more jobs per loaf than larger, more automated baked products manufacturers, and (in common with other small, locally-owned businesses) help to keep more money circulating in their local economies.

In parallel with helping to develop awareness that sourdough breadmaking it is a fundamentally different process that results in a substantively different product, these bakers have been building up goodwill around its subjective qualities including taste, flavour, texture, aroma and appearance. The existing (and future) makers of genuine sourdough bread need a legal definition to help protect them from unfair competition by any manufacturers that act to benefit from this goodwill to sell fundamentally different products.

SME bakeries in particular need legislative support to help create equity in the marketplace. Genuine sourdough bread is fundamentally different to products that are sourdough in name alone. Against the multi-million pound marketing budgets of businesses in the multi-billion pound industrial loaf manufacturing and retailing sectors, however, SME bakeries simply do not have an individual, or even collective, 'voice' loud enough for this truth to be heard.

Many (perhaps most) of the current commercial custodians of the evolving UK tradition of genuine sourdough breadmaking are amongst more than 1000 small-scale bakeries in the Real Bread Campaign's network. The Campaign is, however, keen to see and encourage bakeries of all types and sizes making genuine sourdough bread available to more people across the UK. Genuine sourdough bread *can* be made at every scale by every bakery business willing to use a genuine sourdough process. This is demonstrated by the likes of The Village Bakery Melmerby and The Bertinet Bakery, both of which have national distribution. Outside the UK, there are national market leaders, such as Fazer in Finland, whose ranges include lines of genuine sourdough bread. Rather than preventing plant and other larger scale bakery manufacturers entering this marketplace, our proposed legal definition would reinforce the USP of those that choose to invest in making genuine sourdough bread.

Industry self-regulation

Industry self-regulation in any sector tends to be led by a small, but hugely powerful, group representing larger businesses to accommodate and serve their own needs, limitations and abilities. Typically, such voluntary schemes do not help to create a level playing field, failing to accommodate adequately the needs, limitations and abilities of SMEs, individuals, communities, animal welfare and the environment, or a combination of these. As noted in Sustain's case for a Children's Food Bill, industry self-regulation/voluntary schemes have been shown to fail time and again. Leaving industry to self-regulate the use of trans fats has meant that, despite evidence of negative impacts on health dating back to at least the 1990s (and perhaps as far as the 1950s), they are still in use. More generally, a 2015 RSPB review of the effectiveness of over 150 voluntary schemes across a range of sectors and found that: "the impact of most voluntary schemes is limited. Over 80 per cent of schemes were found to perform poorly on at least one key measure." Regulation (such as the Soft Industry Drinks Levy, introduced following the Sustain report and campaigning alongside Jamie Oliver and others) has been shown to be more effective.

When it comes to sourdough, leaving it to 'the market' to self-regulate clearly is not working. In September 2018, one of the UK's largest industrial loaf manufacturers launched <u>a sliced white loaf marketed using the word</u> <u>sourdough</u> that was in fact made using baker's yeast and a mere 3% dried sourdough starter. Despite this it had a recommended selling price of around 66% more than the company's otherwise apparently identical regular white loaf in the same range.

In another example, a <u>trade advert for a packet mix</u> noted that genuine sourdough normally requires a "bulk fermentation period of up to 24 hours" and promised commercial bakers the ability to make "sour dough" [sic] with just 60 minutes' fermentation. Despite stating that the longer that dough ferments, "the better quality the product and customers are prepared to pay a premium for this," the advertiser encouraged bakers to take "the opportunity to enter this lucrative market without the need to invest in specialist staff." The ad reinforced this with the egregious assurance of an "easy way" to "an excellent profit margin", all without any "learning needed on pH and acidity."

Custodians kept out of code creation

In 2019, a so-called 'UK Baking Industry Code of Practice for the Labelling of Sourdough Bread and Rolls' was sent to Defra. We believe that that this proposed code would make things more, not less, confusing for shoppers and would legitimise what, in intellectual property law, might be considered as extended passing off. It sought to redefine what sourdough bread is in order for businesses (perhaps such as those represented by the authors) to profit from fundamentally different products manufactured using quicker, easier (and therefore cheaper) processes. It went as far as stating: "Where space and skills are lacking, bakers have recourse to an increasing number of ingredients and raw materials that help to simplify the process."

Underlining the point about industry self regulation in the section above, rather than being written by and for bakers and buyers of genuine sourdough bread, this proposed code was produced by a group of industrial entities* that, until relatively recently, had little to no experience or involvement in making genuine sourdough bread. They include bodies that represent the companies behind examples cited in this document. Another is the Craft Bakers' Association, which in June 2019, ran an event encouraging bakers to use 'sourdough' products, made by the ingredients/additives company that sponsored the event, as shortcuts around processes necessary for genuine sourdough breadmaking.

When writing the code, the authors chose not to work with the Real Bread Campaign. This was despite them knowing that our organisation has been active and vocal on this subject since 2009 and that many (perhaps the majority) of the UK's genuine sourdough bakers and experts are in the Campaign's network. When in June 2019 we discovered from a third party that a code had been drafted, we began contacting the authors, asking to be involved in the process. It was not until October that they sent us a copy. We responded with our comments and an offer of helping to rewrite it, but after another month of us following this up, the authors advised us that they had rejected any input from us and sent the document to Defra unchanged.

* The Association of Baking Ingredients Manufacturers, The British Sandwich and Food To Go Association, Craft Bakers ' Association, Federation of Bakers, Pizza, Pasta and Italian Food Association.

Protected names

It has been suggested that the Real Bread Campaign could establish a Traditional Speciality Guaranteed, or other protected name, status for sourdough bread. Such a measure is not suitable in this case. It would not be possible to gain protected name status for 'sourdough bread' and prefixing it with a qualifier (eg genuine, traditional, British, real) would not protect buyers (or bakers) of any other product named or marketed using the word sourdough www.realbreadcampaign.org www.sustainweb.org Charity registered number: 1018643

without the specific qualifier. Furthermore, this proposal is broadly rejected by Real Bread Campaign supporters on the grounds of the unnecessary and disproportionate cost and administrative burden that participation would place on SME bakeries.

Around 100 bakeries participate in the Real Bread Campaign's <u>Real Bread Loaf Mark scheme</u>, which since 2020 has included The Sourdough Loaf Mark option. This self-certification scheme has only ever been intended as an affordable interim measure as it is limited by weaknesses inherent in voluntary schemes, including lack of participation, visibility / consumer awareness, and enforceability.

Existing legislation

Protection of consumers' interests should be covered by legislation including <u>Article 8(1)(c) of Regulation (EC)</u> <u>178/2002</u>, laying down the general principles and requirements of food law, which is given substance by <u>Article 7 of</u> <u>Regulation 1169/2011 (EC)</u>, aka Food Information to Consumers.

This is, however, proving inadequate to prevent the misuse of the word sourdough. Time and again, consumer protection bodies (notably the Advertising Standards Authority) have declined to take action in <u>cases like these</u>, stating that the absence of a legal definition of sourdough makes it hard for them to decide upon what to base a judgement of what is and isn't misleading.

International comparisons

Regulations that contain a definition of sourdough include Spain's <u>Real Decreto 308/2019</u>, <u>de 26 de abril, por el que</u> <u>se aprueba la norma de calidad para el pan</u>; and the '<u>Décret de pain'</u> in France. While British shoppers and genuine sourdough bakers need and deserve similar legal protection, the historical context and market conditions in the UK are not the same as those in other countries and so adopting their legislation or definitions is not appropriate.

The current British tradition is a relatively modern one, started and nurtured over several decades by bakers for whom the use of baker's yeast or additives is antithetical to crafting sourdough bread. Unlike countries with longer traditions, into which such additions might have become customary before current legislation was introduced, the UK still has the opportunity to preserve and protect its sourdough tradition.

A legal definition of sourdough bread that excludes the use of additives and baker's yeast will not hinder export from the UK. It could in fact help to build trust in, and reinforce the reputation of, British food at home and abroad, and so might actually improve export sales. It could also help to prevent British baking businesses from being undercut by more quickly and cheaply made imported products.

Changes to The Bread and Flour Regulations

The Real Bread Campaign recommends amending the interpretation of bread to:

"bread" means a food of any size, shape or form that -

(a) is usually known as bread, and

(b)consists of a dough made from flour of any type and water, with or without other ingredients (but no additives), which is unleavened or has been fermented by yeast or a live sourdough starter culture and subsequently baked, steamed, fried, or otherwise cooked

We also call for the following to be added:

www.realbreadcampaign.org

Restrictions on the use of the word 'sourdough'

(1) The word 'sourdough' shall not be used in the labelling or advertising of bread, or as part of the name of the bread, whether or not qualified by other words, unless it is leavened only by a live sourdough starter culture.(2) No person shall sell or advertise for sale any bread in contravention of this regulation.

Supporting clarity

To avoid confusion, <u>The Bread and Flour Regulations 1998</u> require that the word wholemeal can only be used to name or market flour and baked products if 100% of the flour used is unrefined. Similarly, we call for the word sourdough to be reserved for use in naming and marketing products leavened using only a sourdough starter culture.

Though the word 'with' might sometimes be useful when naming a characteristic ingredient in a food, it is not appropriate when referring to sourdough, which is a process. Returning to the earlier analogy, a bottle of neutral grain spirit with a small amount of <u>single malt Scotch whisky</u> added could not be marketed using the phrase 'with single malt Scotch whisky' and nor should 'with sourdough' be allowed to market a product leavened using baker's yeast. Similarly adding qualifiers such as 'style' should not be permitted as a loophole through which the word sourdough can be used to market fundamentally different products made by different processes.

Invitation

To help Defra, the FSA, the Secretary of State, ministers or other MPs and civil servants with their research into these issues, and get first-hand accounts from business owners (and, potentially, their customers) we are happy to help arrange visits to bakeries in the Real Bread Campaign network.

We are also happy to work with Defra and other members of the BFTWG to draft the wording for surveys of business owners, and of a public consultation to assess consumer understanding of, and attitudes towards, these issues and proposals.

Contact: Real Bread Campaign coordinator Chris Young: chris@sustainweb.org

The Real Bread Campaign was launched in November 2008 by the baker Andrew Whitley and Sustain, the charity that runs it. Starting with a universally accessible definition of bread as made without additives, the Real Bread Campaign finds and shares ways to make bread better for us, better for our communities and better for the planet.

The Campaign has welcomed thousands of supporters in more than 20 nations, within a wider network of tens of thousands of friends in many more countries. They include the owners of more than 1000 Real Bread bakeries, baking schools, mills and related enterprises. <u>www.realbreadcampaign.org</u>

Sustain: The alliance for better food and farming advocates food and agriculture policies and practices that enhance the health and welfare of people and animals, improve the working and living environment, enrich society and culture and promote equity. As a membership organisation, Sustain represents around 100 national public interest organisations working at international, national, regional, and local level. <u>www.sustainweb.org</u>

Appendix

Between 1990 and 2020 more than 1230 peer reviewed research articles were published on the subject of sourdough. The following small selection of studies highlights just some of the potential benefits of sourdough fermentation. Note that each study had specific parameters/criteria, such as the type of grain/flour, the strains of lactic acid bacteria and yeasts in the starter, fermentation time and temperature etc.

Reducing the Glycaemic Index (GI) of bread

De Angelis, Maria et al. "<u>Use of sourdough lactobacilli and oat fibre to decrease the glycaemic index of white wheat</u> <u>bread</u>." The British journal of nutrition vol. 98,6 (2007): 1196-205. doi:10.1017/S0007114507772689

De Angelis, M., Damiano, N., Rizzello, C.G. et al. <u>Sourdough fermentation as a tool for the manufacture of low-glycemic index white wheat bread enriched in dietary fibre</u>. Eur Food Res Technol 229, 593–601 (2009). doi.org/10.1007/s00217-009-1085-1

Maioli, Mario et al. "<u>Sourdough-leavened bread improves postprandial glucose and insulin plasma levels in subjects</u> with impaired glucose tolerance." Acta diabetologica vol. 45,2 (2008): 91-6. doi:10.1007/s00592-008-0029-8

Najjar, Anita Mofidi et al. "<u>The acute impact of ingestion of breads of varying composition on blood glucose, insulin</u> and incretins following first and second meals." The British journal of nutrition vol. 101,3 (2009): 391-8. doi:10.1017/S0007114508003085

Reducing phytic acid

Cereal bran contains phytic acid, the main form in which plants store phosphorus. Phytic acid combines with minerals including calcium, zinc, magnesium and iron in a way that makes the human body unable to absorb and make use of them. Phytase breaks down the phytic acid, increasing the bioavailability of those nutrients, ie allowing the body to absorb higher amounts of those present.

Lopez, Hubert W; Duclos, Virgile; Coudray, Charles; Krespine, Virginie; Feillet-Coudray, Christine; Messager, Arnaud; Demigné, Christian; Rémésy, Christian (2003) <u>Making bread with sourdough improves mineral bioavailability from</u> <u>reconstituted whole wheat flour in rats.</u> Nutrition, Volume 19, Issue 6, June 2003, Pages 524-530.

Leenhardt, Fanny et al. "<u>Moderate decrease of pH by sourdough fermentation is sufficient to reduce phytate</u> <u>content of whole wheat flour through endogenous phytase activity</u>." Journal of agricultural and food chemistry vol. 53,1 (2005): 98-102. doi:10.1021/jf049193q

Reducing acrylamide

Acrylamide is formed from the amino acid asparagine and sugars naturally present in carbohydrate-rich foods when they are cooked at temperatures higher than 120°C in low moisture conditions, such as baking and frying. Acrylamide has been declared a carcinogenic substance by the European Food Standards Agency.

Emadi, A., Yousefi, B., Eslami, M. et al. <u>Reduction of acrylamide formation in bread and fried potato products using</u> probiotic microorganisms: a systematic review and dose–response meta-analysis. Food Measure 15, 4277–4287 (2021). doi.org/10.1007/s11694-021-00997-5

Nasiri Esfahani, Behnaz et al. "<u>Reduction of acrylamide in whole-wheat bread by combining lactobacilli and yeast</u> <u>fermentation</u>." Food additives & contaminants. Part A, Chemistry, analysis, control, exposure & risk assessment vol. 34,11 (2017): 1904-1914. doi:10.1080/19440049.2017.1378444 www.realbreadcampaign.org www.sustainweb.org Charity registered number: 1018643

Reducing FODMAP levels

Cereals are high in Fermentable Oligo-, Di-, Monosaccharides And Polyols (FODMAPs), which are widely considered to be triggers of irritable bowel syndrome (IBS) for many sufferers. Sourdough fermentation has been shown to reduce FODMAPs, for example in rye bread.

Laatikainen, R et al. <u>"Randomised clinical trial: low-FODMAP rye bread vs. regular rye bread to relieve the</u> <u>symptoms of irritable bowel syndrome.</u>" Alimentary pharmacology & therapeutics vol. 44,5 (2016): 460-70. doi:10.1111/apt.13726

Producing lunasin

Lunasin is a peptide chain of amino acids, which has been found to block the action of some carcinogens.

Carlo G. Rizzello, Luana Nionelli, Rossana Coda & Marco Gobbetti (2012) <u>Synthesis of the Cancer Preventive Peptide</u> <u>Lunasin by Lactic Acid Bacteria During Sourdough Fermentation</u>, Nutrition and Cancer, 64:1, 111-120, DOI: 10.1080/01635581.2012.630159

Producing antioxidants

Coda, Rossana et al. "<u>Selected lactic acid bacteria synthesize antioxidant peptides during sourdough fermentation</u> of cereal flours." Applied and environmental microbiology vol. 78,4 (2012): 1087-96. doi:10.1128/AEM.06837-11

Modifying / reducing proteins some people find problematic

Prolamins are proteins, mainly found in cereal grains. They include gliadin in wheat (which combines with glutenin to form gluten), hordein in barley, secalin in rye and avenin in oats. These can trigger the coeliac response, allergies and intolerances in some people.

Di Cagno, Raffaella et al. "<u>Sourdough bread made from wheat and nontoxic flours and started with selected</u> <u>lactobacilli is tolerated in celiac sprue patients</u>." Applied and environmental microbiology vol. 70,2 (2004): 1088-96. doi:10.1128/AEM.70.2.1088-1096.2004

Rizzello, Carlo G et al. "<u>Highly efficient gluten degradation by lactobacilli and fungal proteases during food</u> processing: new perspectives for celiac disease." Applied and environmental microbiology vol. 73,14 (2007): 4499-507. doi:10.1128/AEM.00260-07