Fermented Vegetables as Vectors for Relocation of Microbial Diversity from the Environment to the Human Gut

Ilenys M. Pérez-Díaz

Abstract The discovery of yeasts as living cells able to produce ethanol in fermented foods and beverages in the 1920s continues to captivate our imagination with respect to the functionality and role of microbes in food preservation and human health. Mounting evidence confirms the ability of microbes to deliver nutrition, flavor and many bio-functionalities to fermented foods and the gastrointestinal (GI) tract of mammals. The microbial diversity found in fermented foods, particularly vegetables, can benefit the human GI tract microbiome. Critical functions for microbes associated with fresh vegetables include the contribution to growth, development and defense of host plants. In parallel, plants have evolved to select and maintain beneficial microbes, including those within their tissue. Fermentation then serves as an instrument to pre-adapt beneficial microbes indigenous to fresh vegetables to the acidic pH and high lactic acid concentration characteristic of the colon and to the metabolism of dietary fiber, particularly pectic substances naturally present in the plant material and the gut. Fermented vegetable products enjoy a long-lasting record of safety upon consumption and are an appropriate vector for the translocation of microbial diversity from plants to the gut. Fermented vegetables can enhance prebiotic fiber and beneficial microbes content and consequently augment the catalog of metabolic functions needed in and available to the gut for building resilience in a healthy individual. It is the indigenous microbiota of fermented vegetables and intrinsic chemical composition of substrates, particularly dietary fibers, which can enable beneficial health claims from the consumption of pickles.

Keywords Vegetables microbiome · Natural fermentation of vegetables · Spoilage · Cucumber fermentation · Sauerkraut · Lactic Acid Bacteria (LAB)

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Introduction

Studies of the indigenous microbiota in fermented vegetables began in the 1920s, a few centuries after the discoveries of microbes as living cells capable of producing ethanol and fermenting milk by Antonie van Leeuwenhoek, Cagnard-Latour, Louis Pasteur and Joseph Lister occurred (Brock 1961; Nanniga 2010). There was no concept or understanding of microbial diversity in the early 1900s and the tools available for microbiological studies were limited compared to the knowledge base and tools available in the twenty-first century.

Lacking an understanding of the microbiology behind a desirable fermentation, past generations performed what is known as "back slopping" or the use of cover brines or doughs from fermentations with desirable attributes to initiate fresh fermentations in an attempt to perpetuate specific organoleptic attributes in the desired fermented foods (Cogan 1996). The fermentation of vegetables in the twentieth century consisted of dry-salting of shredded cabbage, turnips and lettuce and whole grains of corn, lima beans and green peas to support a vigorous conversion of the sugars to lactic and acetic acids and possibly ethanol (Etchells et al. 1947). Bulky vegetables, some with a low water content, were chopped prior to brining or brined whole with varied sodium chloride concentrations (Etchells et al. 1947). When and exactly how the preservation of vegetables by fermentation began is unknown but it is chronologically situated between the first and third centuries before Christ (B.C.). Records of mixed vegetable fermentations date back to the third century B. C. during the construction of the Great Wall in China (Anderson et al. 1988; Lee 2001). Sauerkraut production was described as early as the first century by Plinius the elder (Buckenhüskes et al. 1990). The diverse preparation forms of table olives were also described by Columela in the book *The Re Rustica* in the I century (Columela 1979, 45). Early written records of cucumber pickles come from surviving fragments of a play (*The Taxiarchs*) by the Greek writer Eupolis (429–412 BC), and pickles are mentioned several times in the Christian bible. Today the consumption of vegetables is widespread in the world and represents an important component of the human diet.

This chapter addresses the advances made in understanding the indigenous microbiota in fermenting and fermented vegetables and the influence of modern industrial production practices on microbial diversity. The consequent role of fermented vegetables as a delivery vehicle for microbes to the human gut is also described. The many metabolic and physiological functionalities of the cultures present in fermented vegetables is beyond the scope of this chapter.

For the purpose of this chapter fermented vegetables are defined as low acid vegetables subjected to the action of acid producing microorganisms that will naturally achieve and maintain a pH of 4.6 or lower, regardless of whether acid is added (Pérez-Díaz et al. 2014). If the fermentation proceeds to completion and good manufacturing practices are applied, spoilage organisms capable of rising the pH above 4.6 are prevented from growing in the product and pathogens of public health significance are destroyed during the process, thus making the final product safe for consumption (Ito et al. 1976; Breidt and Caldwell 2011).

The Microbiota of Fresh Vegetables

Microbial diversity on fresh vegetables primarily derives from the soil. A low incidence of lactic acid bacteria occurs in fresh vegetables.

The cucurbits rhizoplane is known to predominantly host *Rhizobium* and *Cellvibrio* and to a lesser extent *Saccharophagus*, *Devosia*, and *Pseudomonas* (Ofek et al. 2014). *Cellvibrio*, a Pseudomonadaceae, may reach up to 20% of the cucumber plant rhizoplane microbial population and can degrade plant cell wall components and other complex polysaccharides which enables microbes to penetrate and colonize the plant tissue (DeBoy et al. 2008). Dried seeds used for planting a new crop are known vectors of microbial diversity for plants, flowers and fruits (Lemanceau et al. 2017). Although microbial diversity could also come from the soil and/or bioaerosols, it is documented that seeds richer in oil (50%), protein (35%) and DNA, contribute the most to the selection and evolution of endophytes, which are microbes that reside in the internal plant tissues without adverse effects on their host (Lemanceau et al. 2017).

Microbes that colonize plant tissue contribute to the host growth and development in multiple ways. *Bacillus* species contribute to cucumber plants through nitrogen-fixation and scavenging (converting such gas into a solid and usable form), deaminase activity and protease, pectinase or cellulose activity. *Bacillus* spp., Enterobacteriaceae and LAB assist with phosphate solubilization through the production of organic acids or phosphatases (Khalaf and Raizada 2016). The Enterobacteriaceae family and *Pseudomonas*, are also able to produce auxin, a plant growth hormone, and siderophores used to chelate iron. Interestingly, *Bacillus* species isolated from cucumber seeds cluster apart from Bacilli isolated from other cucurbit seeds (Khalaf and Raizada 2016). Given the specialized functionality of the plant derived endophytes, it is speculated that they may be transmitted by seeds and conserved for future generations to help secure this important symbiotic relationship between plants and their microbiomes.

The relationship between microbes and plants is enabled by the nutritional and anti-nutritional factors (i.e. oxalate, lectins, tannins, phytic acid) intrinsically present in the later (Filannino et al. 2018). The response of lactic acid bacteria (LAB) to various stresses on the vegetation results in nutrient enhancement, stress reduction and consequently plant growth promotion (Filannino et al. 2018). Concomitantly, the plant-produced food is enriched in bioavailable and bioactive compounds (Filannino et al. 2018). Plants select their microbiome in the vicinity of the plant roots or rhizosphere, and seeds are involved in the transmission of microorganisms to future generations (Lemanceau et al. 2017). Microbes associated with vegetation have evolved to benefit from specific plants because of the easy access to nutrients (Khalaf and Raizada 2016). Microbes with a positive impact on plant growth and health are selected and maintained to evolve within the system.

Plant growth and development involves both biotic and abiotic factors. The range of abiotic factors produced by plants including oxygen, organic acids, vitamins and sugars can be used as nutrients and signals by microbes. Conversely, abiotic factors

produced by microbes including hormones, volatile compounds and small molecules impact plants immunity and growth. The close association of vegetables with the soil promotes higher microbial density and diversity in fresh produce (Samish and Etinger-Tulczynsky 1962). The availability of oxygen promotes microbial colonization of the blossom end, seed cavity and the outer 6 mm layer of cucumbers, including the exocarp and a portion of the mesocarp, consisting of 5–6 log of CFU/g of total aerobic microbes (Mattos et al. 2005). In tomatoes, microbial colonization is more frequently found near the stem-scar and central core and decreases closer to the exocarp (Lemanceau et al. 2017; Rastogi et al. 2012). Cabbage contains the greatest numbers of bacteria on the outer leaves and lower numbers toward the center of the head (Pederson and Albury 1969). The adhesion of bacteria to cucumber exocarp depends on contact time, cell species and density, and temperature. These factors impact the adhesion of *Salmonella*, *Staphylococcus*, *Lactobacillus* and *Listeria* to fresh cucumber surfaces in an aqueous solution (Reina et al. 2002). Bacterial adhesion to the cucumber exocarp is less extensive at lower temperatures and shorter contact times (Reina et al. 2002). While Gram-negative bacteria, which are mostly motile, migrate to the cucumber mesocarp and persist commensally, inoculated gram positive LAB establish on the exocarp (Samish and Etinger-Tulczynsky 1962). Enterobacteriaceae, in particular the motile rods *Erwinia* spp., are known to colonize the internal cucumber tissue and produce carbon dioxide (CO_2) from fermentative metabolism in the presence of oxygen (Samish and Etinger-Tulczynsky 1962).

The core bacteriome of fresh vegetables including fresh cucumbers, corn, cabbage, carrots, spinach and peas is composed of the two taxonomical families, Enterobacteriaceae and Pseudomonadaceae (Lopez-Velasco et al. 2013; Manani et al. 2006; Samish et al. 1963; Samish and Etinger-Tulczynsky 1962; Shi et al. 2009; Weiss et al. 2007) (Figs. 1 and 2). However, fresh produce contains a diverse range of epiphytic microbiota. Average aerobic colony counts for fresh cucumbers, cabbage, and olives are estimated at 5.16 ± 0.76, 4.84 ± 0.26 and 1.90 ± 0.50 CFU/g, respectively (Pérez-Díaz et al. 2014). Colony counts from Violet Red Bile agar plates for lactose fermenting coliforms from cucumber, cabbage and olive have been estimated at 4.58 ± 0.98, 4.36 ± 0.06 and below detectable levels, respectively (Pérez-Díaz et al. 2014). *Pseudomonas*, *Pantoea*, *Chryseomonas* and *Enterobacter* colonize tomatoes, lettuce and Chinese cabbage (Lee et al. 2017; Ottesen et al. 2016; Shi et al. 2009). *Bacillus* species are present in lettuce, tomatoes and cucumbers (Ottesen et al. 2016; Shi et al. 2009; Rastogi et al. 2012; Ofek et al. 2014). The microbiome of tomatoes include *Microvirga*, *Sphingomonas*, *Brachybacterium*, *Rhizobiales*, *Paracocccus*, *Microbacterium*, *Cyanobacterium*, *Hafnia*, and *Erwinia* (Ottesen et al. 2016; Shi et al. 2009). The lettuce core microbiota includes the microorganisms listed above for tomatoes plus *Massilia* and *Arthrobacter* (Rastogi et al. 2012). Furthermore, *Acinetobacter, Burkholderia, Dickeya, Klebsiella, Pectobacterium, Rahnella, Serratia* and *Stenotrophomonas* colonize fresh lettuce and Chinese cabbage (Lee et al. 2017). A study of the fresh cucumber microbiota showed the dominance of the Gram-negative bacteria *Rhizobium*, *Pseudomonas*, *Acinetobacter*, *Sphingomonas*, *Sphingobacterium*, *Methylobacterium*,

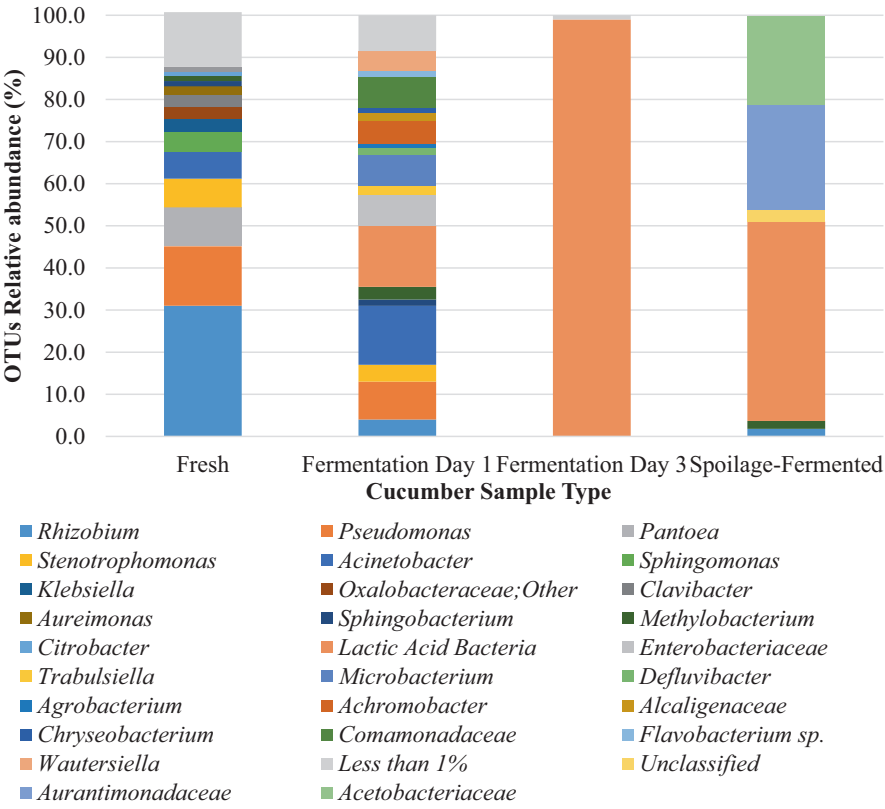

Fig. 1 Description of the relative abundance of OTUs found in samples of fresh and fermented cucumbers as determined by high throughput sequencing. Cucumber fermentation cover brine samples were obtained from batches brined with 6% sodium chloride. Only the bacterial communities are represented. Data was adapted from Medina-Pradas et al. (2016) and Pérez-Díaz et al. (2016, 2018)

Stenotrophomonas, *Citrobacter* and *Klebsiella* spp. (Pérez-Díaz et al. 2018). Despite the variations in the microbiota of specific vegetables in terms of density and diversity induced by type, variety, lot and harvesting location (Samish et al. 1963), more recent investigations revealed the occurrence of a vegetable-specific core microbiota (Rastogi et al. 2012). However, a noticeable difference exist between the microbial load of vegetables cultivated in greenhouses and those grown in the field (Meneley and Stanghellini 1974; Leben 1972; Geldreich and Bordner 1971). The numbers of internally-borne bacteria in healthy cucumbers grown in trellises and covered by a glasshouse was below detection levels (Meneley and Stanghellini 1974). Coliforms are absent in indoor-cultivated-foliage as well (Geldreich and Bordner 1971).

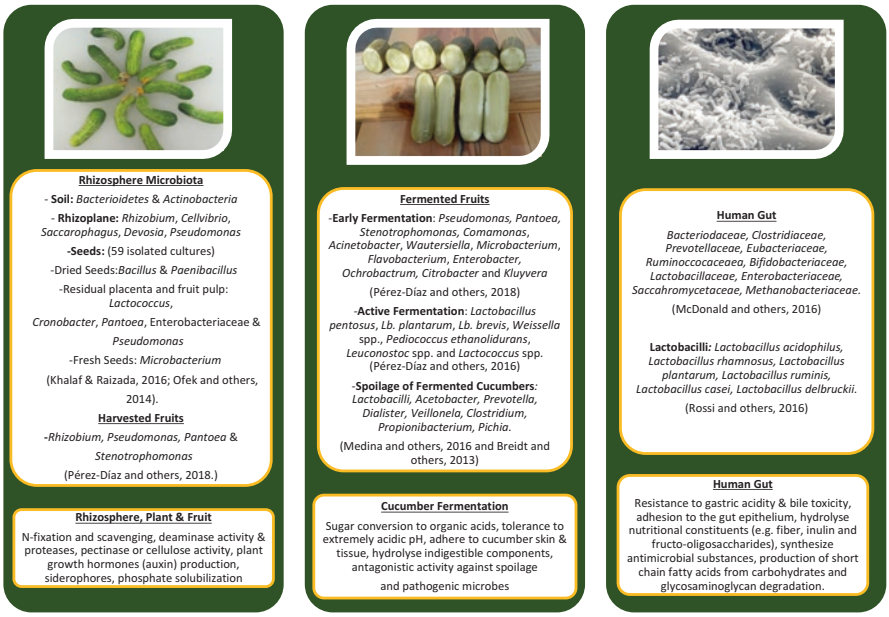

Fig. 2 Summary of microbes found in a cucumber plant and the fresh fruit (left panel), in cucumber fermentations (central panel) and the human gut (right panel), followed by an abbreviated list of functions needed to compete in the various habitats

Of interest is the fact that the LAB that dominate in vegetable fermentations are present in the corresponding fresh substrate in minimal numbers. Colony counts from MRS agar plates, typically used for the enumeration of LAB, particularly lactobacilli, from fresh cucumbers and cabbage are estimated at 3.84 ± 1.21 and 3.18 ± 0.33 Log CFU/g, respectively (Pérez-Díaz et al. 2014). In fresh olives the colony counts from MRS agar plates tend to be below detection levels, presumably due to its natural antimicrobial phenolic content (Pérez-Díaz et al. 2014). A characterization of the population forming colonies on MRS agar plates inoculated with fresh cucumber homogenate revealed lack of selectivity by such medium (Pérez-Díaz et al. 2018). *Enterococcus* (25%), *Exiguobacterium* (15%), *Lactococcus* (15%), *Staphylococcus* (13%), *Lactobacillus* (11%) and *Leuconostoc* (10%) are frequently isolated from MRS plates and three genera are infrequently encountered including *Bacillus* (6%), *Aerococcus* (4%) and *Clostridium* (1%) (Pérez-Díaz et al. 2018). Only 8.6% of the colonies formed in MRS agar plates belonged to the *Lactobacillus plantarum* cluster, a species that prevails in vegetable fermentations and are widely used as starter cultures. However, presumptive LAB have been found in plant material in substantial numbers with seasonal-related variability (Mundt 1970; Mundt and Hammer 1968).

The Microbiota of Natural Fermentations

LAB Consistently Prevail in Vegetable Fermentations

The diversity of the microbial population found associated with fresh vegetables is drastically reduced during the fermentation process, which supports the safety record of such preserved foods. It is generally accepted that the vegetable fermentation microbiota is dominated by three stages: initiation, primary fermentation and secondary fermentation (Garrido Fernández et al. 1997). During the initiation stage, the various Gram-positive and Gram-negative bacteria that colonize the fresh vegetable compete for dominance. The Enterobacteriaceae, *Bacillus* spp., LAB and a few other bacteria and yeasts may be active for several days or weeks depending on the temperature, water content, oxygen availability and salt concentration (Fuccio et al. 2016; Nychas et al. 2002; Panagou et al. 2008; Pérez-Díaz et al. 2016, 2018; Botta and Cocolin 2012; De Angelis et al. 2015). Eventually, the LAB prevail during primary and secondary fermentation due to the low pH from the conversion of sugars to organic acids. Seven species of LAB prevail in vegetable fermentations: *Enterobacter* spp., *Leuconostoc mesenteroides, Pediococcus* spp., *Lactobacillus brevis, Lb. plantarum*, *Lb. pentosus* and *Weissella* spp. (Bleve et al. 2015; Botta and Cocolin 2012; De Angelis et al. 2015; Etchells et al. 1973; Hong et al. 2016; Kyung et al. 2015; Lee et al. 2016, 2017; Nychas et al. 2002; Park et al. 2012; Plengvidhya et al. 2007; Pérez-Díaz et al. 2016, 2018). *Leuconostoc*, *Lactococcus* and *Weissella* tend to lead during the primary fermentation of vegetables such as cabbage. *Lactobacillus plantarum* and *Lb. pentosus* are typically found in the finished vegetable fermentations due to their resistance to extreme acidic pH (McDonald et al. 1990). A succession of microbes is often needed to complete a vegetable fermentation. The complete fermentation of cabbage requires the activity of *Leuc. mesenteroides, Leuc. citreum* and *Weissella* spp. which decrease the pH to approximately 6.5, and are followed by *Lb. plantarum*, *Lb. curvatus* and other lactobacilli, which continue to drop the pH to about 4.5 (Plengvidhya et al. 2007). *L. brevis* ends the production of acids in a cabbage fermentation spearheading the final decrease in pH to ~4.0. The fermentation of kimchi proceeds at 18 °C for a few days followed by a longer incubation period at refrigerated temperatures to promote microbial stability and reduce the development of excess sourness (Pérez-Díaz et al. 2014). This type of temperature control provides advantageous conditions for the proliferation of heterofermentative *Leuconostoc* spp. at the outset, followed by the growth of homofermentative lactobacilli and *Weissella* spp. (Jung et al. 2012). The use of *Leuc. citreum* as a starter culture for kimchi fermentation has proven to prevent over-ripening and growth of yeasts during refrigerated storage (Chang and Chang 2010).

Even though, salting is a critical step in vegetable fermentations, the function of sodium chloride with regards to the fermentation microbes is intrinsically restricted to the modulation of the density of certain species (Pérez-Díaz et al., submitted). The fermentation of cucumbers in water and 0.1% potassium sorbate to inhibit

yeasts results in the dominance of the heterofermentative lactic acid bacterium, *Leuconostoc* and the homofermentor, *Lactococcus* (Pérez-Díaz et al., submitted). Supplementation of cover brines with NaCl compromises the proliferation of *Leuconostoc* and *Lactococcus,* opening an opportunity for *Weissella* to prevail. Additionally, in systems brined with NaCl, *Weissella*, a heterofermentative lactic acid bacterium, competes with a number of Gram negative bacteria that are likely to compromise the quality of the finished product. *Lactobacillus* and *Pediococcus* are noted in salt free fermentations by day 3. The addition of a salt in cucumber fermentation cover brines results in the dominance of *Lactobacillus* by day 7. Conversely, a lack of a salt in the fermentation cover brines yields comparatively more microbial diversity with less acid production even after 14 days. *Pediococcus*, *Leuconostoc*, *Lactococcus* and *Weissella* are present in salt free cucumber fermentations by day 14. The spoilage associated *Enterobacter* is also present in salt free cucumber fermentations by day 14. The microbes present in cucumber fermentations can produce acid and tolerate some salt and extremely acidic pH.

Bacteria present in fresh cucumbers such as *Rhizobium*, *Pseudomonas*, *Acinetobacter*, *Sphingomonas*, *Stenotrophomonas*, *Sphingobacterium*, *Methylobacterium, Klebsiella, Pantoea* and *Citrobacter* are also present on the first day of cucumber fermentations (Pérez-Díaz et al. 2018) (Figs. 1 and 2). However, the density of such populations start to decrease as a function of time and acid production. The presence of opportunistic pathogens such as *Citrobacter freundii*, *C. brakii*, *Enterobacter* spp., *Pseudomonas fluorescens, Stenotrophomonas maltophilia* and *Kluyvera cryocrescens*, and the antibiotic resistant pathogen *Serratia marcescens* during the initial stage of commercial cucumber fermentations is jeopardized by temperature, sodium chloride content of at least 3.5%, a pH below 4.5 and oxygen availability (Rothwell et al., unpublished; Olsen and Pérez-Díaz 2009). The population density corresponding to these organisms reaches undetectable levels in commercial cucumber fermentations by day 10 (Pérez-Díaz et al. 2018). It is presumed that upon initiation of the fermentation, the majority of the microbial population on fresh cucumbers, which localizes on the cucumbers exocarp (Mattos et al. 2005), is exposed to the full strength cover brine containing between 12 and 18% NaCl, a known preservative. A study of the salt tolerance of various LAB isolated from Spanish-style fermented olives and natural black olive fermentations suggests that 66% are inhibited by 6% NaCl and those that are resistant cannot grow in the presence of 9% of the salt (Balatsouras 1985). Salt content is gradually increased to7% in Spanish-style table olive fermentation as a function of equilibration to maintain stability (Garrido Fernández et al. 1997).

Some particularities apply to the fermentation of certain vegetables. The microbiota of watery kimchi is dominated by *Leuconostoc*, Enterobacteriaceae, Lactobacillaceae and *Pseudomonas* regardless of fermentation temperature (Kyung et al. 2015). A study of the microbiota in traditional Korean cabbage kimchi revealed the presence of, in order of prevalence, *Pediococcus pentosaceus*, *Leuconostoc citreum*, *Leuconostoc gelidum*, *Leuconostoc mesenteroides*, *Tetragenococcus*, *Pseudomonas* and *Weissella* (Hong et al. 2016). Household and commercial kimchi fermentations were found to harbor the organisms listed above and *Psychrobacter*,

Hafnia, *Lactococcus*, *Rahnella*, *Enterobacter*, and *Pantoea* (Lee et al. 2017). A study of ten representative kinds of kimchi that were refrigerated at 4 °C for 30–35 days found that although some microbial diversity is present in the early stage of the fermentation, *Weissella*, *Leuconostoc* and *Lactobacillus* are dominant in the later stage (Park et al. 2012). Sauerkraut fermentations are characterized by the presence of *Lc. mesenteroides*, *Lc. citreum*, *Lc. argentinum*, *Lactobacillus plantarum*, *Lb. paraplantarum*, *Lb. coryniformis*, *Pediococcus pentosaceous*, *Lb. brevis* and *Weissella* (Plengvidhya et al. 2007). Commercial cucumber fermentations are dominated by *Lactobacillus pentosus*, *Lb. brevis* and *Lb. plantarum* regardless of salt type or content, and are followed, in relative abundance, by *Pediococcus*, *Leuconostoc*, *Lactococcus* and *Weissella* (Pérez-Díaz et al. 2018). The fermentation of other vegetables products such as capers consist of lactic acid production by predominantly *Lb. plantarum* and to a lesser extent *Lb. paraplantarum*, *Lb. pentosus*, *Lb. brevis*, *Lb. fermentum*, *P. pentosaceus*, *P. acidilactici*, and *Enterococcus faecium* (Pérez Pulido et al. 2005).

Although, many researchers associated yeast with cucumber fermentations as early as the 1910s, given that gas production and bubbling was observed in the commercial process, a systematic classification study was not conducted until 1941. The average yeast population count in commercial cucumber fermentations is estimated to initiate at 3 log of CFU/g and increases to 5–6 log of CFU/g in about 10 days (Etchells 1941). Such population remains somewhat stable until about days 20–30 of the fermentation followed by a gradual decline to undetectable levels (Etchells 1941). Fluctuations in yeast counts are commonly observed in cucumber fermentations with salt concentrations between 5 and 10% (Etchells 1941), with a peak of activity on days 15 and 20, respectively (Etchells 1941). Yeast cells are primarily found on the skin of the cucumber fruits, exposed mesocarps and the fermentation cover brines. The size of yeast cells prevents their penetration into the mesocarp through the fruits exocarp (Daeschel et al. 1985). A study classified 47 surface film-forming yeasts isolated from fermentations containing between 5 and 19% NaCl from various locations in the USA in the following genera: *Debaryomyces membranaefaciens* var. *Hollandicus* (18), *Debaryomyces* sp. (4), *Endomycopsis ohmeri* (12), *Zygosaccharomyces halomembranis* (9) and *Candida krusei* (4) (Etchells and Bell 1950b, Fig. 3). *Pichia* was also isolated by the same group from fermentations containing less than 5% NaCl (Etchells and Bell 1950b). A study carried out to identify 1226 subsurface yeast isolated from 42 commercial cucumber fermentations revealed four predominating genera in increasing order of abundance: the tiny yeast *Torulopsis caroliniana* (718), acid producing *Brettanomyces versatilis* (559), hyperosmophilic *Zygosaccharomyces halomembranis* (59), *Hansenula subpelliculosa* (49), *Torulaspora rosei* (6), *Torulopsis holmii* (4), *Brettanomyces sphaericus* (2), and *Kloeckera magna* (1) (Etchells and Bell 1950a, Fig. 4). In the fermentations studied, *T. caroliniana* dominated until day 30 of the fermentations and was followed by *B. versatilis* and *Zygosaccharomyces* spp. until the end of the study at 100 days (Etchells and Bell 1950a). *T. holmii* and *Torulaspora rosei* were detected towards the end of the *T. caroliniana* fermentation. *Brettanomyces* spp. were found to

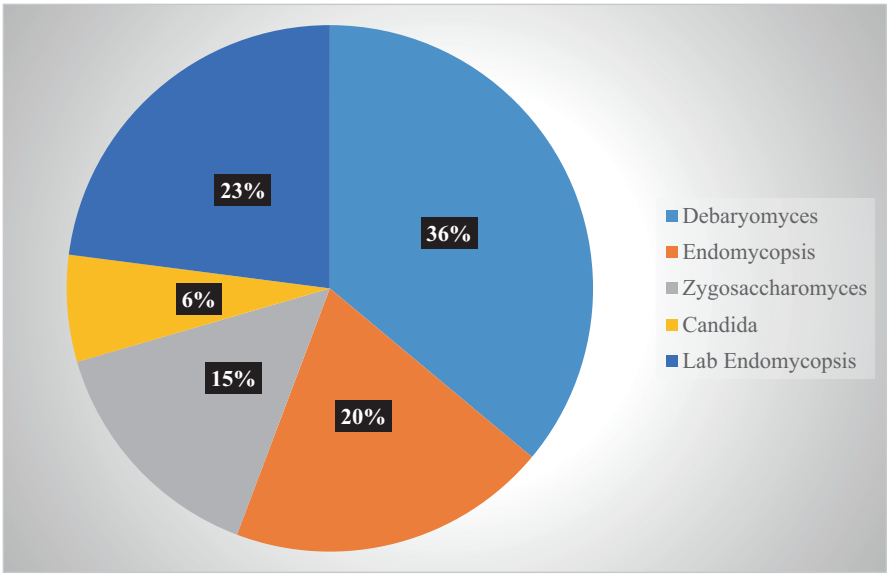

Fig. 3 Populations of surface oxidative yeasts isolated from commercial cucumber fermentations brined with 5–19% NaCl and conducted in 40 outdoor vats packed between 1947 and 1948. Data adapted from Etchells and Bell (1950b)

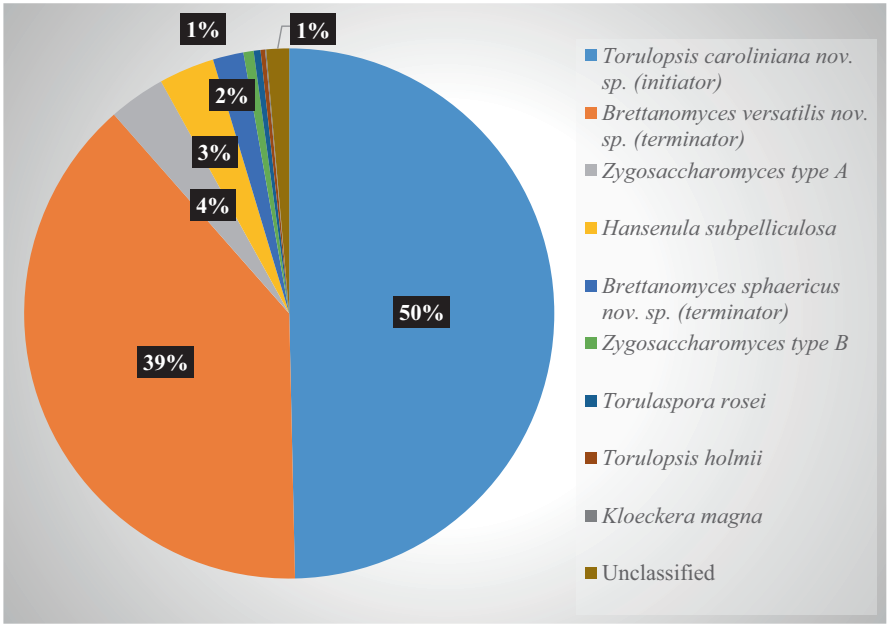

Fig. 4 Populations of subsurface fermentative yeasts and molds isolated from commercial cucumber fermentations brined with 6 ± 2% NaCl and conducted in outdoor vats packed between 1946 and 1947. A total of 1226 cultures were classified. Data adapted from Etchells and Bell (1950a). The yeasts *Torulopsis caroliana, Brettanomyces versatilis, Brettanomyces sphaericus*, and *Torulaspora rosei* are currently known as *Candida lactiscondensi, Candida versatilis* and *Torulopsis versatilis, Pichia subpelliculosa, Candida etchelsii* and *Torulaspora delbruckii*, respectively

overlap with those species present between days 23 and 77 and suspected to derive energy from compounds other than glucose or fructose, possibly acetic acid, lactic acid or ethanol (Etchells and Bell 1950a). A follow up study confirmed the following genera dominate in cucumber fermentations, in particular those performed in the USA midwest: *Brettanomyces* (*versatilis* and *sphaericus*; 29%), *Torulopsis* (*holmii* and *caroliniana*; 23%), *Torulaspora* (*rosei*; 15%), *Hansenula* (*subpelliculosa*; 13%), *Zygosaccharomyces* (*halomembranis*, *pastoris*, *globiformis*; 10%), *Saccharomyces* (*globosus*; 5%), *Candida* (*krusei*; 2%) and *Debaryomyces* (*membranaefaciens*; 2%) (Etchells et al. 1952). Attempts to study the population of yeasts present in commercial cucumber fermentations using DNA sequencing technology have been hampered by the inability to classify yeasts OTUs to the genera and species taxonomical levels. Such studies have been restricted to the identification of *Capnodiales* and *Tremellales* in fresh cucumbers with colony counts from Yeast and Molds agar plates to 2.82 ± 0.95 CFU/g, and *Saccharomycetales*, mostly *Candida* spp. and *Aureobasidium*, *Hanseniaspora*, *Torulaspora*, *Cryptococcus* and *Hannaella* in commercial cucumber fermentation cover brines containing 4.15 ± 0.68 CFU/g (Pérez-Díaz et al., unpublished).

Although colony counts for the population of yeast and molds from olives are below the detection level, their presence in fermentations is desirable for the development of specific flavors (Arroyo-López et al. 2008). Yeasts only propagate and predominate in olive fermentations (5.1 ± 0.86 CFU/g) if the fruits are neither properly lye treated nor heat shocked before brining (Mark et al. 1956). Yeasts present in olive fermentations include species of the genera, in order of prevalence, *Candida*, *Debaryomyces*, *Pichia*, *Saccharomyces*, *Rhodotorula* and *Kluyveromyces* (Mark et al. 1956; Marquina et al. 1992). Yeasts naturally present in olives may form mixed biofilms with the LAB prevailing in fermentations, which is evaluated for the delivery of probiotics to the human digestive tract upon the ingestion of fermented olives (De Bellis et al. 2010).

Significantly less information is available with regards to the yeast and molds population in cabbage and sauerkraut given that most of the research pertaining to such fermentations focuses on the LAB and quality issues. Yeast and mold colony counts from fresh cabbage is 2.87 ± 0.79 CFU/g (Pérez-Díaz et al. 2014). The biosurfactant producing yeast, *Pseudozyma*, was isolated from fruits and vegetables of the *Brassica* family and is been studied for the production of mannosylerythritol lipids (Konishi et al. 2014).

The community of bacteriophages, viruses that infect bacteria, in fermented foods is significantly less diverse than the counterparts found in many environmental habitats such as seawater, marine sediment, the human gut and soil (Park et al. 2010). Although, many bacteriophages have been isolated from fermented vegetables, particularly sauerkraut and cucumber fermentations, three viral families have been implicated including *Myoviridae*, *Siphoviridae* and *Podoviridae* (Barrangou et al. 2002; Lu et al. 2003a, b, 2005, 2010, 2012; Yoon et al. 2002, 2007). Bacteriophages are known to have a relevant function in the modulation of the microbiota during commercial fermentations, particularly in the manufacture of dairy products. The presence of bacteriophages in vegetable fermentations is concomitant with the abundance of the hosting LAB species. In cucumber fermenta-

tions, bacteriophages infect primarily *Lb. plantarum*/*Lb. pentosus* and *Lb. brevis*, the most abundant LAB (Lu et al. 2012; Pérez-Díaz et al. 2016). The genomic organization of bacteriophages from fermented vegetables and dairy products is similar (Lu et al. 2005, 2010). It is estimated that about 10% of the LAB population is sensitive to bacteriophages (Lu et al. 2012). The infection ability of specific bacteriophages found in a commercial cucumber fermentation may be limited to a species or strain, however, few of the viruses can also infect multiple species (Lu et al. 2012). Bacteriophages able to infect multiple genera are rare (Lu et al. 2012). Bacteriophages able to infect *Enterobacter* spp. naturally present in commercial cucumber fermentations have also been found (Lu et al., unpublished).

Microbially Induced Spoilage of Fermenting and Fermented Vegetables

Increased microbial diversity exists in spoiled fermented vegetables at the cost of acceptable sensorial attributes.

Industrial vegetable fermentations mostly rely on the indigenous microbiota, which occasionally results in the growth of undesired microbes or microbial spoilage during long term storage. The presence of residual sugars and viable microbes in finished products can alter appearance. Undesirable microbes in vegetable fermentations include *Enterobacter*, *Pantoea*, *Eschericia*, *Acetobacter*, *Clostridium*, *Propionibacterium*, *Desulfovibrio*, *Pichia*, *Zygosaccharomyces*, *Saccharomyces*, *Wicherhamomyces, Rhodotorula, Alternaria, Mucor, Fusarium, Aerobacter*, *Aeromonas*, *Achromobacter*, *Paracolobactrum* and *Lactobacillus buchneri* (Garrido Fernández et al. 1997; Nychas et al. 2002; Panagou et al. 2008; Gililland and Vaughn 1943; Levin and Vaughn 1966; Moon et al. 2014; Duran-Quintana et al. 1979; Vaughn et al. 1969, 1972; Ruiz-Cruz and Gonzalez-Cancho 1969; Franco and Pérez-Díaz 2012; Hernandez et al. 2007; Moon et al. 2014; Costilow et al. 1980; Arroyo-López et al. 2008; Golomb et al. 2013; King and Vaughn 1961; Franco and Pérez-Díaz 2012; Johanningsmeier and McFeeters 2013; Medina-Pradas et al. 2016; Fred and Peterson 1922).

The initiation of a vegetable fermentation is prone to produce butyric acid and/or sulphrydic compounds under anaerobiosis. A putrid olive fermentation, characterized by a manure-like and decomposing aroma, and a rancid butter odor develops as the consequence of the proliferation of *Clostridium* and *Desulfovibrio* species (Gililland and Vaughn 1943). Prevention of anaerobiosis at the bottom of fermentation tanks by air purging is used to impede the growth of the strict anaerobe and culprit, *Clostridium*. The emergence of sulphur-like aroma generated by *Desulfovibrio* spp. is commonly prevented by the implementation of good sanitation practices for fermentation vessels and potable water (Levin and Vaughn 1966).

A delayed decrease in pH during the initiation of a vegetable fermentation results in the proliferation of *Enterobacteriaceae* (Garrido Fernández et al. 1997; Nychas et al. 2002; Panagou et al. 2008; West et al. 1941) regardless of oxygen content.

Certain *Enterobacteriaceae*, such as *Enterobacter* spp., can metabolize the sugars naturally present in the vegetables and produce lactic acid, acetic acid and CO_2 (Garrido Fernández et al. 1997; Etchells et al. 1945; Samish and Tulczynsky 1962). Production of CO_2 in olive and cucumber fermentations leads to bloater defect caused by the accumulation of the gas just below the epidermis or in the meso- and endocarps forming hollow cavities that mimic an internal bubble (Garrido Fernández et al. 1997; Fleming 1979). Cucumber and olive bloating represents the most costly spoilage in the production of the fermented products. Uncontrolled growth of *Saccharomyces cerevisiae* and *Wicherhamomyces anomalus* can also cause bloater defect in olive fermentations given the ability to produce CO_2 from sugars (Duran-Quintana et al. 1979; Garrido Fernández et al. 1997; Vaughn et al. 1972).

Softening of vegetables during fermentation is a defect associated mainly with the activity of yeast and is difficult to prevent. *Rhodotorula minuta*, *W. anomalus*, *Debaryomyces hansenii*, *P. kudriavzevii*, *Alternaria*, *Fusarium* and *Mucor* are known to produce proteases, xylanases or pectinases in vegetable fermentations causing softening of the plant tissues by degrading their pectin, cellulose, hemicellulose and polysaccharide content (Hernandez et al. 2007; Moon et al. 2014; Costilow et al. 1980; Arroyo-López et al. 2008; Golomb et al. 2013). Pectinolytic bacteria, able to cause tissue softening have also been isolated from vegetable fermentations. Gram negative bacteria such as *Aerobacter*, *Aeromonas*, *Achromobacter*, *Escherichia* and *Paracolobactrum* produce tissue softening of black olives during the oxidation step, if applied at high temperature (Garrido Fernández et al. 1997; King and Vaughn 1961; Vaughn et al. 1969).

Pink sauerkraut is one of the most common defects in the production of such commodity. Although pink sauerkraut has been reported to be edible and is often sold at a lower price, it has been related to undesirable changes in texture, flavour and odour (Fred and Peterson 1922). Sodium chloride concentrations above 3%, high acidity, and extrinsic factors such as temperature and the supply of oxygen can be manipulated to control the pink sauerkraut defect (Fred and Peterson 1922).

As described above oxidative yeast are capable of proliferating on the surface of cucumber fermentation cover brines and cause a rise in pH, tissue softening and/or off odors and taste. *Pichia manshurica* and *Issatchenkia occidentalis* consume lactic acid in aerobic or air purged cucumber and olive fermentations, which induces an increase in pH (Ruiz-Cruz and Gonzalez-Cancho 1969; Franco et al. 2012). *Pichia kudriavzevii* causes kimchi spoilage characterized by undesirable changes in organoleptic properties (Moon et al. 2014).

The extreme acidic pH, high organic acid concentrations and lack of monomeric fermentable sugars ensure the long-term stability of fermented vegetables. Even though conditions are unfavourable for microbial growth at the end of a complete fermentation, some especially unique microbes can initiate spoilage. *Propionibacterium* spp. metabolize sugars, or the lactic acid formed during primary fermentation, to produce propionic acid, acetic acid and CO_2, inducing an increase in pH and volatile acidity (Gonzalez-Cancho et al. 1970). Rising pH spoilage of fermented cucumbers results in the development of cheese and manure-like aromas (Franco et al. 2012). *Acetobacter* spp. and *Lb. buchneri* are present in fermented cucumber spoilage at pH 3.3 (Franco and Pérez-Díaz 2012; Johanningsmeier and

McFeeters 2013; Medina-Pradas et al. 2016). *Acetobacter* spp. are commonly used in the production of vinegar and are known for converting lactic acid to water and carbon dioxide or acetic acid, concomitantly with the conversion of ethanol to acetic acid (Raj et al. 2001; Lefeber et al. 2010). *Lb. buchneri* is able to produce acetic acid and 1,2-propanediol from lactic acid during the first stage of the undesired secondary fermentation (Johanningsmeier and McFeeters 2015). Should the undesired secondary fermentation enable the increase in pH above 4.2, *Propionibacterium* and *Pectinatus* species, and *Clostridium bifermentans* and *Enterobacter cloacae* are able to convert lactic acid to propionic acid and butyric acid imparting the characteristic putrid aromas (Breidt et al. 2013b; Franco et al. 2012). The activity of *Propionibacterium* spp. in olive fermentation spoilage and of *L. buchneri* in fermented cucumber spoilage can be prevented by controlling the end of fermentation pH and salt concentrations (Garrido Fernández et al. 1997; Johanningsmeier and McFeeters 2015).

Spoilage associated LAB include *Lb. plantarum*, *Lb. brevis*, *Lb. casei*, *Lb. paracasei* and as mentioned above, *Lb. buchneri*. *Lb. brevis* is associated with the formation of a water-soluble red pigment in sterile cabbage juice at a pH of 5.7 ± 0.5 and it is suppressed by anaerobic conditions (Stamer et al. 1973). *Lb. casei* and *Lb. paracasei* have been implicated in sporadic cases of red colored fermented cucumber spoilage in fermented cucumber products (Díaz-Muñiz et al. 2007). *Lb. casei* and *Lb. paracasei* are able to degrade the azo dye tartrazine (FD&C yellow no. 5) used as a yellow colouring in cover brines. This type of spoilage is prevented by the addition of 0.1% sodium benzoate (Díaz-Muñiz et al. 2007). *Lb. plantarum* is the cause of the so-called yeast spots in fermented olives (Vaughn et al. 1953, 1969). A strains of *Lb. plantarum* (3.2.8) capable of producing exopolysaccharides and dominant over *Lb. pentosus* in cucumber fermentations was also found responsible for the production of yeast spots in such fruit (Pérez-Díaz et al., unpublished).

Mass Production Parameters for Vegetable Fermentations That Consistently Yield Finished Products with Acceptable Attributes for Consumers

A rapid decrease in pH and stability during long term storage are key to controlling the fermentation of vegetables.

There are three parameters that must be controlled in vegetable fermentations to obtain an acceptable product including a rapid initiation and acid production, the complete conversion of freely available sugars to organic acids and/or ethanol and a stable post-fermentation pH. The quick production of acids from sugars ensures a drop in pH below 4.6, which is critical for preventing growth of the deadly toxin producer, *Clostridium botulinum* (Ito et al. 1976). This is particularly relevant in vegetable fermentations conducted in closed vessels that support the development of anaerobiosis, a strict requirement for the proliferation of the spore former, *Cl.*

botulinum. At least 0.9% acetic acid in cover brines is needed to achieve the inhibition of the clostridial species in a cucumber fermentation (Ito et al. 1976). Artisanal preparations of table olives have been associated with botulinum outbreaks (Medina-Pradas and Arroyo-López 2015). As mentioned above a delayed decrease in pH creates an ideal scenario for the Enterobacteriaceae, naturally present in vegetables, to proliferate and produce excess CO_2 conducive to bloater defect. A drop in pH to levels that are inhibitory for growth of *Lb. plantarum*/ *Lb. pentosus* before a complete sugar conversion occurs, results in the availability of energy sources for spoilage microbes as described above. Unstable vegetable fermentations result in the establishment of conditions that allow growth of undesired microbes capable of utilizing lactic acid and thus, of rising the pH above 4.6, generating a public health concern from the potential production of the botulinum toxin. Thus, control of pH before, during and after a vegetable fermentation is a critical parameter and the most important one in the production of a safe preserved food.

The use of sodium chloride in vegetable fermentation cover brines has five main functions including the densitometric modulation of specific members of the microbiota, the speed of the fermentation, prevention of softening caused by salt sensitive microbes, imparting a salty flavour in the finished fermented product and assisting with the equilibration of the vegetable content with the cover brine by weakening the tissue membranes (Bell and Etchells 1961; Bell et al. 1950). For instance, more than 8% sodium chloride is needed in table olive fermentation for long term bulk storage to inhibit spoilage by *Propionibacterium* spp. (Garrido Fernández et al. 1997). A combination of pH 3.3 and 4% salt is needed in cucumber fermentations to prevent spoilage by *Lb. buchneri* (Johanningsmeier and McFeeters 2013). Although, sodium chloride has become synonymous with vegetable fermentations for centuries, the fermentation of certain vegetables, such as cucumber, was demonstrated in closed containers with cover brines supplemented with calcium chloride as the only salt (McFeeters and Pérez-Díaz 2010). Sodium chloride-free cucumber fermentations in commercial open top tanks requires the addition of a preservative to inhibit yeasts and the growth of undesired microbes (Pérez-Díaz et al. 2015). Cucumber fermentations in closed containers without salt and with potassium sorbate results in a complete conversion of the sugars to lactic acid and a more diverse community of LAB, sustaining the growth not only of *Lb. plantarum* and *Lb. pentosus*, but also that of *Pediococcus*, *Weissella*, *Lactococcus* and *Leuconostoc* after 14 days (Pérez-Díaz et al., *submitted*). Although the absence of sodium chloride in a fermentation can support a greater microbial diversity, other factors must be applied to control the growth of microbes that can impart less appealing organoleptic characteristics in the finished product and compromise safety. Sauerkraut fermentations with reduced sodium chloride, from 2 to 0.5%, resulted in an undesirable flavour profile (Johanningsmeier et al. 2005). Consuming vegetables that have been fermented without sodium chloride or any additive other than water is like playing the lottery where the winning price is a delicious and freshly putrefied fermented vegetable and the loosing ticket is food poisoning or diarrhea.

A starter culture is a critical factor in low salt vegetable fermentations and in achieving finished product consistency for mass production (Etchells et al. 1964;

Etchells et al. 1973; Vega Leal-Sánchez et al. 2003). It is also a main factor in the reduction of the microbial diversity in the industrial production of fermented vegetable products. Pure starter cultures were introduced commercially in New Zealand in 1934 (Cogan and Hill 1993) beginning the era of "controlled" fermentations. Utilization of *Lc. mesenteroides* as a starter culture for low salt sauerkraut fermentations prevents off-flavour and odors (Johanningsmeier et al. 2005). The use of a *Lb. plantarum* starter culture for caper berry fermentation induces a consistent process and faster sugar catabolism (Palomino et al. 2015). Fermented vegetable products manufactured with a starter culture enjoy higher acceptability by consumers and improved nutritional characteristics (Martínez-Villaluenga et al. 2012; Di Cagno et al. 2012). Starter cultures of *Lb. delbrueckii* and *Lb. paracasei* reduce the nitrite content in Chinese cabbage (Han et al. 2014). *Lb. pentosus* and *Lb. plantarum* are among the LAB species with major applications as starter cultures in fermented vegetables such as cucumber, capers and tables olives, albeit *Lc. mesenteroides* is also occasionally used in low salt fermentations such as sauerkraut (Corsetti et al. 2012; Pérez-Díaz et al. 2015). However, the dominance of a starter culture in a vegetable fermentation intrinsically eliminates or reduces biodiversity selecting for those microbes that can tolerate a number of stresses associated with the specific habitat.

The exclusion of air from cucumber fermentations with nitrogen purging results in a higher quality pickle (Costilow et al. 1980). Air purging is commonly applied in cucumber fermentations to displace the carbon dioxide produced during the fermentation and prevent bloater defect characterize by the formation of hollow cavities within the flesh (Fleming 1979). The incorporation of air in cucumber fermentations results in the proliferation of yeasts and molds and tissue softening (Costilow et al. 1980). Although, air purging could potentially increase the diversity of yeasts and molds in a cucumber fermentation, the resulting sensory attributes are undesirable. The need to reduce bloater defect and maintain product quality demands the incorporation of preservatives such as sorbic acid in cucumber fermentation cover brines to inhibit yeasts (Borg et al. 1972). Incorporation of sorbic acid additionally aids in the elimination of film-forming yeasts on the superficial cover brines that occasionally leads into a decreased acidity. Additionally, natural cucumber fermentations without preservatives can sustain yeast growth after the primary fermentation stage by LAB is initiated (Etchells 1941).

Processing Parameters for Vegetable Fermentations That Could Increase the Delivery of Microbial Diversity to the Gut

Lower salt content and more diversified starter cultures are key parameters in augmenting the diversity of desirable microbes in commercial scale fermentations.

Obviously, the processing parameters currently in place for the mass production of fermented vegetables have evolved to accommodate for consistency, acceptable sensorial characteristics and food safety. The incorporation of a more diverse

microbiota in a fermented vegetable product has not been prioritized. A commonality of vegetable fermentations, as it is done to date, is the reduction of biodiversity to accomplish a controlled fermentation that consistently delivers a healthy product of quality.

There is an emerging sector of the population with a preference for the consumption of raw spoiled vegetables, coagulated soups and putrid fermented foods hoping to gain a beneficial health effect from the consumption of a broader microbial diversity. People willing to rescue vegetables from the dumpsters, irrigate their root crops in their gardens with the sink effluent and pickle leftovers to enable the consumption of live foods expected to inoculate the gut, at the risk of sporadic diarrhea and food poisoning, to boost the immunological system (Holes 2010). Fermentation is considered by this sector of the population as one of the initial conditions of civilization that facilitated a sedentary lifestyle, before refrigeration developed (Holes 2010).

While there may be some truth in Sandor Katz saying that "we are killing ourselves with cleanliness by killing every microbe that could enter our stainless-steel kitchens"; an intermediate point that preserves the safety hurdles in a fermentation process must be found. A middle point between the industrial perspective and the interest to boost the microbial biodiversity in the gut is achievable with the application of science and a more flexible consumer base. Compromises are needed from both sectors to achieve healthy products with long term stability. But, how would the fermented vegetable product with a diverse microbiota be prepared? What would this elixir contain?

The main objective of food fermentation is to achieve long term preservation and extend the shelf-life of a fresh or about to spoil food. Thus, it is an intrinsic function of the fermentation to reduce or minimize microbial diversity and activity. A primary objective of fermentation is to transform the sugars naturally present in the vegetables and render them unavailable as an energy source for the proliferation of a number of microbes. Additionally the conversion of sugars to acids and alcohol causes a decrease in the pH of a vegetable matrix which ends up suppressing a number of microbes resulting in microbial stability. So, can fermented vegetables truly be carriers of a diverse microbiota?

Only the resistant microbes survive in a fermentation, which happen to belong to the same taxonomical genera present in the gut, as the colonic habitat is also characterized by an acidic pH, limiting oxygen and the availability of complex undigestible sugar polymers and amino acids as primary energy source for microbes. If only fermented vegetables are considered, the list of survivors tends to be short, leading with *Lb. plantarum* and *Lb. pentosus* and followed by *Leuconostoc, Weissella* and *Pediococcus*. A number of other lactobacilli are also present in fermented vegetables in lower abundance. Thus, if the microbial diversity in a fermented vegetable is to be expanded the obvious choices are those microbes that survive a fermentation, which often times end up causing spoilage. Suffice it to remind the reader that spoilage is defined as undesirable changes in organoleptic properties as define by consumers. As described above, spoilage microbes in fermented vegetables tend to convert the lactic acid, acetic acid and ethanol commonly produced in the bioconversion to

propionic and butyric acids imparting putrid and manure-like aromas to an otherwise perfectly edible food (Gonzalez-Cancho et al. 1970; Raj et al. 2001; Lefeber et al. 2010; Johanningsmeier and McFeeters 2015). The fermented vegetable spoilage bacteria tend to be those that can use lactic and acetic acids and ethanol including among others *Clostridium*, and *Propionibacterium*, which are also able to colonize the human gut. Such microbes assist in the conversion of undigestible fibers in the gut to short chain fatty acids like propionic and butyric acids that are utilized as energy sources by the epithelium. So, do we need to adapt to eating stinky fermented vegetables?

Preservation by fermentation must continue to remove the sugars naturally present in the produce and yield a finished product with an extended shelf-life. Factors that science and consumers can modify, at least in theory, is the desirable metabolic product in a vegetable fermentation and the definition of an acceptable finished product, respectively.

A vegetable fermentation processing parameter that cannot be changed is the initiation of the fermentation in a closed container at a pH below 4.6. This parameter not only represents the exclusion of the deadly botulinum toxin in fermented vegetables (Ito et al. 1976) but also assures the eventual die off of microbes of public health significance, such as *Listeria monocytogenes*, *Salmonella* spp. and acid resistant strains of *Escherichia coli* (Breidt and Caldwell 2011). *Listeria monocytogenes,* a food-borne pathogen, has become a major concern to the food industry over the past 30 years, mainly for refrigerated and ready-to-eat products. The bacterium is commonly found in the environment and has been isolated from various plant materials, including silage (Fenlon 1985), soybeans, corn (Welshimer 1968; Welshimer and Donker-Voet 1971) and cabbage (Seelinger and Jones 1986; Beuchat et al. 1986). Outbreak strains of *L. monocytogenes* are also able to grow on raw cabbage and in cabbage juice (Beuchat et al. 1986), but not if the pH is adjusted to 4.6 or below (Conner et al. 1986). *Listeria monocytogenes* can additionally survive and grow in green table olives after 2 months of storage (Caggia et al. 2004). The die off of *Escherichia coli* O157:H7 in cucumber fermentation cover brines takes 3 and 24 days at a pH of 3.2 and 4.6, respectively (Breidt and Caldwell 2011). The development of fermentation in the same cover brine reduces the die off of this pathogen to 1 and 16 days. The survival of *Salmonella* spp. at a pH below 4.6 is also assured, given that it is less sensitive to acidic conditions than *E. coli* (Breidt et al. 2013a, b). Fermentation should continue to function as a sanitizer for fresh vegetables that could be potentially contaminated with agricultural run offs or the fecal matter from handlers. It is not necessary to push its limits by inoculating vegetables with microbes that are outside of the plants habitat. Compromises with regards to food safety parameters jeopardizes consumer's health and are thus not negotiable.

There is flexibility within the existing processing parameters for vegetable fermentations to host a diverse microbial population. A fully or partially fermented vegetable could be safely consumed by healthy adults if the equilibrated pH is between 4.5 and 3.3. The closer the pH is to 4.5 the greater the likelihood of consuming the most diverse microbiota a fermented vegetable can provide, which would be likely restricted to some *Enterobacteriaceae, Pseudomonadaceae* and

LAB. *Enterobacteriaceae* such as *Enterobacter* and presumptive *Klebsiella* and *Pseudomonas* were isolated from cucumber fermentations with a pH of 4.04 ± 0.15 (Pérez-Díaz et al. 2018). These microbes are also present at the initiation of numerous vegetable fermentations as described above. The reduction of sodium chloride in the fermentation of some vegetables may enable a more diverse fermentative microbiota. However, such an approach may not consistently deliver an edible and safe product. Additionally, with the elimination of salt other more permissive factors would have to be incorporated to achieve a complete and stable fermentation that produces an acceptable product.

The use of mixed starter cultures also offers an opportunity to enhance biodiversity in a fermented product. Yeasts have robust enzymatic diversity, are considered bioprotectants in vegetable fermentations, enhance the growth of LAB and improve the organoleptic properties of certain pickles (Arroyo-López et al. 2008). The application of starter cultures composed of yeasts and LAB, such as *Lb. plantarum* and *Saccharomyces oleaginosus*, leads to more complete sugar consumption in the fermentation of carrots, cabbages, beets and onions, with a consequently higher acidity as compared to spontaneous fermentation (Gardner et al. 2001; Montaño et al. 1997). The development of green and black olives containing probiotics has been achieved by the selection of compatible yeasts and LAB that can form biofilms on the fruits (Rodríguez-Gómez et al. 2014; Bleve et al. 2015). Mixed starter cultures of yeasts and LAB in green table olives also modify the concentration of free amino acids, phenols and volatile compounds and generates finished products with increased consumer's acceptability (De Angelis et al. 2015). Additionally, the successful fermentation of certain vegetables such as green beans necessitates mixed starter cultures to remove different sugars such as glucose, fructose, mannitol and cellobiose (Chen et al. 1983a, b). The use of *Lb. plantarum* LPCO10 as a starter culture and of *Enterococcus casseliflavus* cc45 and *Lb. pentosus* 5138A in sequential inoculations has proven effective in accelerating acid production and the die off of pathogenic microbes as compared to spontaneous fermentation of green table olives (De Castro et al. 2002; Leal-Sánchez et al. 2002; Vega Leal-Sánchez et al. 2003). Further advancement in the understanding of the contributions of individual microbes to specific vegetable fermentations will offer the opportunity to develop fully functional and safe products that taste like fresh produce.

Can Fermented Vegetables Aid in Augmenting Biodiversity in the Gut or Repopulating It?

Lactobacillus plantarum will continue to be central to the ability of fermented vegetables to deliver beneficial health effects.

The human body is estimated to host 10^{14} bacteria, with the stomach and lower small intestine contributing the lowest amount (10^7 each) and the colon contributing the highest (10^{11}) (Sender et al. 2016). Intermediate values of bacterial counts are contributed by the skin, saliva, dental plaque and the upper small intestine to the

human microbiome (Sender et al. 2016). It is also estimated that the number of eukaryotic cells are equal to the number of bacteria at 10^{14}, with woman and newborns carrying twice as many bacteria as eukaryotic cells (Sender et al. 2009). The number of LAB rarely reach 10^9 CFU/g in a fermenting vegetable, which translates into 0.001% of the gut microbiota (Fig. 1). Fully fermented cucumbers host a microbial load of lactobacilli and yeasts at 5.01 ± 3.75 (MRS agar plates) and 5.28 ± 4.81 (Yeast and Mold agar plates) log of CFU/g, respectively, during long term storage (Pérez-Díaz et al. 2014). If the most active microbial population in a still fermenting vegetable survives passage through the digestive tract and reaches the colon, it will encounter a microbial jungle. A particular niche for the transiting microbes would have to exist, so that colonization can take place. The newly formed colony would have to metabolize the fibers, proteins, fat and polyphenols that are not digested by the host and are thus available in the gut to establish itself in the new habitat, sense its surrounding and efficiently compete with the indigenously diverse population. Alternatively, the transiting microbes may have the ability to simply attach to the existing microbial mass or epithelial gut, conquer a niche and establish itself in the gut. A more complex model for establishment in the gut would be through the association of certain less fitted microbes to a robust colonizer. It is likely that the result of this type of establishment in the gut would result in the production of compounds that could be beneficial or detrimental to the host's health. However, there is evidence suggesting that the human gut microbiome is resistant to colonization by foreign species (Salonen and deVos 2014; a review).

The human microbiome project directed by the US National Institute of Health reported that the metabolic activity of the microbes in the gut produce beneficial compounds such as vitamins and anti-inflammatories that the human genome cannot produce (Lloyd-Price et al. 2016). In achieving the metabolism of compounds that are undigestible by humans, it becomes more relevant for the gut microbiome to contain a complete set of metabolic enzymes rather than specific microbes. Consequently, a variety of microbes would fulfill the need to metabolize fat or polyphenols and become a part of a stable healthy gut microbiome.

The human gut microbiome changes among healthy people with age, medical interventions and diet. Taking antibiotics causes an imbalance in the microbiome resulting in lower microbial diversity (McDonald et al. 2018). The necessary functionalities are restored as a function of time even if the new microbiome composition is different. Despite the many advancements that have been made in understanding the human gut microbiome, its holistic microbial diversity is still unknown (McDonald et al. 2018). The influence of lifestyle, health state and diet on the composition of the human microbiome is still unclear. However, recent evidence has unexpectedly emerged on the influence of the consumption of 30 types of plants versus 10 on the human gut microbiome. This is specifically related to short-chain fatty acid fermenters (McDonald et al. 2018). The microbial fermentation of undigested plant derived components suggests that diversity in the microbiome is related to the availability of a variety of dietary fibers and resistant starches.

The microbial diversity in the gut has been recognized as limited when compared to the environmental counterpart, but enormous if compared to the indigenous

fermented foods microbiota (McDonald 2018). With the variability rate in the human gut metagenome the definition of a healthy human gut will continue to be elusive (Lloyd-Price et al. 2016), giving birth to the need for personalized nutrition. Contrary to the microbial diversity in the gut microbiome, with only a 30% conserved metagenome (Lloyd-Price et al. 2016), the fermentome is composed of less than 50 genera in the initial stage of the process and a handful of genera during the active fermentation period. However, expansion of the diversity in the fermentome promises to better position fermented foods to contribute to the human gut metagenome.

Consumption of various vegetables in significant amounts is a main component of the food consumption guidelines around the world. But, should this translate into a recommendation for the consumption of a higher diversity of fermented vegetables regularly? A definitive answer to this question may not exist. As discussed above the raw vegetables microbiome is more diverse than that found in a fully fermented vegetable with acceptable sensorial characteristics by consumers. However, fermented vegetables have the potential to host more of those microbes commonly found in the human gut such as *Clostridium*, *Lactobacillus*, *Enterococcus*, *Dialister*, *Veillonella*, *Prevotella*, *Bacteroides*, *Escherichia* and *Shigella* at comparatively higher abundance (Barko et al. 2018). About to spoil of spoiling fermented cucumbers undergoing secondary fermentation at a pH of 3.7 contain all the genera listed above, except for *Escherichia* and *Shigella* (Medina-Pradas et al. 2016). However, even if fermented cucumbers undergoing secondary fermentation with exotic aromas were to be consumed, the effectiveness of such an elixir in the microbial diversity of the gut would depend on the individual microbiome composition and need to fulfil a metabolic niche.

Data generated from human feces suggests that a stable community of lactobacilli is found in the human gut (Rossi et al. 2016). *Lb. rhamnosus*, *Lb. ruminis*, *Lb. delbrueckii*, *Lb. plantarum*, *Lb. casei* and *Lb. acidophilus* are among the 58 lactobacilli species that have been found in human feces at densities fluctuating between 6 and 8 log CFU/g (Rossi et al. 2016). Other lactobacilli species have been found at concentrations between 4 and 5 log of CFU/g of feces. Among the most prevalent lactobacilli found in the gut, only *Lb. plantarum* is consistently present in fermented vegetables in high concentrations (8 log of CFU/g).

The delivery of *Lb. plantarum* as probiotic to the human gut by consuming fermented or partially fermented vegetables is considered a low-calorie, lactose-free alternative for obtaining beneficial health effects (Cauley 2016). Challenges exist with regard to the delivery of an effective dose of *L. plantarum* per serving size of a fermented vegetable to the gut including the subsequent establishment of the specific culture in the gut and positioning in a way that expresses the necessary genes associated with probiotic properties. Many studies have been conducted to elucidate the mechanism by which *Lb. plantarum* could impact human health (Hemert et al. 2010; McDonald et al. 2018; Kishino et al. 2013; Marco et al. 2006). *Lb. plantarum* is one of the most competitive LAB with the ability to resist extremely acidic pH, high salt concentrations (>8% sodium chloride), colonize a variety of habitats, possesses a comparatively large genome among LAB and acquires genes by horizontal

transfer (McDonald et al. 1990; Siezen and van Hylckama Vlieg 2011). Several strains of *Lb. plantarum* contain genes coding for N-acetyl-glucosamine/galactosamine phosphotransferase system, LamBDCA quorum sensing system, and components of the plantaricin biosynthesis and transport system potentially responsible for the stimulation of anti- or pro-inflammatory immune response in the gut (Hemert et al. 2010). *Lb. plantarum* is also known to convert linoleic acid to conjugated linoleic acid, a metabolic reaction identified as a marker for microbes impacting gut health in individuals consuming more than 30 plants as part of a regular diet (McDonald et al. 2018; Kishino et al. 2013). Strains of *Lb. plantarum* isolated from various fermented vegetables are able to survive in simulated gastric and intestinal conditions, adhere to intestinal Caco-2 and HT29 MTX cell tissues, catabolize fructooligosaccharides as the only carbon source and cholesterol, and inhibit pathogens from human sources (De Angelis et al. 2017; a review). *Lb. plantarum* is known to transit the mouse gastrointestinal tract in about 4 h. This probiotic maintains a presence in the stomach and small intestine and the cecum and colon for 4 and 8 h, respectively, in addition to displaying specific and differential responses at various sites along such mammalian gastrointestinal tract (Marco et al. 2006). Although, a strong body of evidence has been generated with regard to the potential of *Lb. plantarum* to deliver a beneficial health effect in the human gut, its ability to colonize a healthy gut and modulate specific responses/needs is still somewhat elusive. This task is further complicated by the fact that the healthy microbiome composition varies among individuals, the lack of in-depth knowledge of the metabolic potential needed in the gut to effectively process a plethora of food-derived undigestible compounds and access to a developing wealth of knowledge on how the gut microbiome impacts body functions at large.

Potential Impacts of Fermented Vegetables in the Human Gut Microbiome

Fermented vegetables can deliver prebiotics and pre-adapted probiotics to the Western gut.

The concept of nutrition has changed from the consumption of foods that satisfy our biological needs to personalized probiotic and prebiotic containing diets that boost our gut microbiome and health. Support of the gastrointestinal tract microbiome diversity imparts a resilience that buffers against dysbiosis, a transient change in permeability, inflammation, pre-disposition to illness and infection and psychological imbalance (Karl et al. 2018). As described above, vegetable fermentations sustain a diverse bacterial, bacteriophage and yeast ecosystem that can serve to expand the catalog of reactions available to the gut microbiome during a perturbation of health. The health promoting lactobacilli naturally prevailing in vegetable fermentations offer basic functionalities related to simple and complex carbohydrate catabolism and short chain fatty acid production to the gut (Gänzle 2015; a review). These functions are associated with the reduction of the gut pH to inhibit

pathogens and the production of energy for the epithelium, respectively. Similarly, as a vegetable fermentation proceeds a number of undesirable acid sensitive microbes in the indigenous microbiota are suppressed reducing the probability of the fermented finished product to deliver pathogenic microbes to the gut and consequently functions associated with protein fermentation, production of sulfate and sulfites and the induction of inflammation (Pérez-Díaz et al. 2018; Gililland and Vaughn 1943; Karl et al. 2018, a review).

Microbes in the gut derive energy from dietary components that are not digested (degraded nor absorbed) by the host and are secreted in the intestine or carbohydrates produced by the gut microbiome itself (Tingirikari 2018; a review). A substantial proportion of carbohydrates available to the microbiome in the human gut derives from plant material, particularly dietary fiber which is composed of cellulose, hemicellulose, pectic substances, and lignin (Rincón-León 2003). Cellulose, hemicellulose and lignin can trigger and regulate bowel movement (Viuda-Martos et al. 2010). Pectic substances are water-soluble and abundant in the soft tissue of vegetables and fruits (15–20%) (Grigelmo-Miguel et al. 1999; García et al. 1995). Pectic substances influence the gel-forming and water holding capacity of the gut and serve as energy sources for the microbiome to induce an acidic pH in the colon and the production of short chain fatty acids and gases (Roberfroid 1993). Together the delivery of natural dietary fibers and of a diversity of microbes by a fermented vegetable represents a theoretical elixir for the gut. Dietary fibers that remain whole after transiting the digestive tract can be digested by the indigenous vegetables microbiome. Co-existence of dietary fibers and the vegetable microbiome in a fermentation process prior to consumption is an opportunity to pre-adapt the microbes to the degradation of such complex carbohydrates and thus enable them to make a difference in and acidic habitat such as the gut upon colonization or transient passage. Consumption of un-pasteurized fermented vegetables is thus a natural vehicle for the re-introduction of energy sources for the microbiome and microbial diversity not commonly present in the Western-like individuals with low intake of plant-derived-foods, such as *Prevotella* (Sonnenburg et al. 2016). While the enrichment of cucumber fermentations with *Prevotella* indicates the development of spoilage, in the gut it can serve as a biomarker for dietary interventions (Medina-Pradas et al. 2016; Salonen and deVos 2014; Gorvitovskaia et al. 2016; Kovatcheva-Datchary et al. 2015; Verbeke et al. 2015). The dominance of *Prevotella* in the human gut is associated with the exposure to complex plant-derived carbohydrates (Salonen and deVos 2014).

The delivery of lactic acid producing microbes and possibly of lactic acid itself by fermented vegetables to the gut can also be advantageous. Production of lactic and acetic acids by LAB in vegetable fermentations consequently generates a need to resist the negative effect of the acids on the cells. LAB are notorious for their ability to produce mM concentrations of such acids and tolerate pH as low as 3.3 (McDonald et al. 1990). Consequently, fermented vegetables can deliver significant concentrations of L- and D-lactic acid to the GI tract. Some lactobacilli incorporate D-lactic acid on the cell wall (Delcour et al. 1999). Nanomolar concentrations of D-lactic acid are produced by the human body from methylglyoxal metabolism

(Ewaschuk et al. 2005; Spencer et al. 2009). To date D-lactate acidosis is a rare condition in human and has not been associated with the consumption of fermented foods, but with surgical intervention (Uribarri et al. 1998). The millimolar concentration of L-lactic acid produced in mammals can be increased by excess microbial activity in the gut (Ewaschuk et al. 2005). L-lactic acid is currently recognize as an energy source for the human skeletal muscles (Lund et al. 2018). Lactic acid is microbially converted to propionic and butyric acids in the gut which are energy sources for the gut epithelium and other organs (Fitch and Fleming 1999). Thus the availability of lactic acid in the gut, should it not be absorbed in the upper digestive tract, could serve as an energy source for the microbiome and the epithelium.

Conclusion: Can Fermented Vegetables Seed the Gut-Associated Microbiota?

The ability of fermented vegetables to deliver bacterial consortia to the human gut is still undefined. Logically, one would think that the higher microbial diversity a fermented vegetable can sustain the higher the probability of such product to deliver diversity to the gut. It can also be deduced that a freshly fermented vegetable containing viable cells of *Lb. plantarum* could serve as a vehicle for inoculation of the gut. Once in the gut, *Lb. plantarum* could establish itself, should a niche exist for its many genome encoded functionalities or leave a footprint in the gut as it transits. While it seems to be premature to hypothesize whether other LAB found in vegetable fermentations such as *Leuconostoc*, *Pediococcus*, *Lactococcus*, *Weisella* would colonize the gut, there is circumstantial evidence implicating a niche for fermented vegetable spoilage associated microbes in the gut including *Prevotella*, *Veillonella*, *Dialister*, and *Clostridium* among others. Regardless of the specific microorganisms delivered to the gut by fermented vegetables, such microbes would be advantageously pre-adapted to the utilization of dietary fibers, particularly pectic substances, an acidic pH and to substantial concentrations of lactic acid, acetic acid and ethanol. Such pre-adaptation could represent a competitive advantage for their establishment in the gut.

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