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The cutting type of spontaneously fermented vegetables impacts their fermentation rate

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ABSTRACT

Fermented vegetables are essentially produced by spontaneous fermentation of raw vegetables, which are roughly or thinly cut, salted and incubated in an oxygen-free environment. Despite the variety of types of cutting and its potential role in the rate of diffusion of solutes from vegetable tissue, and thus the fermentation rate, the effect of this factor has been scarcely studied. Our aim was to investigate how the cutting and small variation of salt concentration impact the microbial and biochemical changes during the spontaneous fermentation of vegetables.

A 2 × 3 experimental design was set up with vegetable type (carrot / cabbage), cutting type (thin / rough), and salt concentration (0.8% / 1%) as factors. Vegetables were pressed down in 500 mL-jars and filled up with brine, and two independent jars used at 4 stages to characterise the microbial dynamics and biochemical changes by combining culturomics, 16S rRNA V5-V7 and gyrB metataxonomics, and targeted metabolomics.

Culturomics and metataxonomics results showed a similar succession of the main bacterial groups in both vegetables, with *Enterobacteriaceae* quickly replacing the initial microbiota,

44 further replaced within a few days by lactic acid bacteria, mainly represented by *Leuconostoc*
45 sp. Cabbage and carrot fermentation rates quantitatively differed. Maximal *Enterobacteriaceae*
46 counts were higher in cabbage (8 vs 7 logCFU/g), while lactic acid bacteria counts were higher
47 in carrot (9 vs 8 logCFU/g). The acidification rate was faster in carrot (e.g. pH decreased to 3.8 in
48 40 h vs approx. 5.0 in 86 h in cabbage). Mannitol, lactic and acetic acids were the main
49 metabolites produced in both vegetables, but concentrations were two-fold higher in carrot.
50 Viable *Enterobacteriaceae* were not detected anymore after two-week fermentation, except for
51 some roughly-cut cabbage samples. No pathogenic bacteria were detected. Taxonomic profiles
52 varied according to the marker used, e.g. *Leuconostoc* was only detected with gyrB and vice-
53 versa for *Clostridium*. The gyrB marker provided a markedly better resolution at the species-
54 level (for 97% of ASV vs only 20% for the 16S marker). Significant effects of cutting type, and not
55 of NaCl concentration, were observed. Thinly-cut vegetables globally showed a quicker
56 fermentation compared to roughly-cut ones and exhibited a higher titratable acidity, e.g. 0.8%
57 vs 0.3%, respectively, in grated and sliced carrot at 64 h incubation. In line, a quicker production
58 of acids and a quicker decrease of viable enterobacteria were observed in thinly-cut vegetables,
59 in particular for cabbage, for which the surface generated by the cutting was ~20-fold greater in
60 shredded cabbage than in leaf cabbage. Some leaf cabbage samples displayed atypical
61 fermentations, with the presence of particular taxa and atypical metabolite profiles with high
62 amounts of ethanol produced. These general trends were modulated by quantitative and
63 qualitative differences between replicate jars.

64 This study confirms the highly diverse microbiota of spontaneously fermented vegetables
65 and the tight competition between *Enterobacteriaceae* and lactic acid bacteria in their
66 colonisation, and documents for the first time the effect of the type of cutting on the
67 fermentation rate.

68

69 **Keywords** : Fermented carrot/ sauerkraut / cutting / lactic acid bacteria / leuconostoc /
70 enterobacteria / natural fermentation

71

Introduction

72 Fermented vegetables are traditionally consumed in central Europe and Asia, and have
73 recently received a renewed interest in Western countries, for many possible reasons that
74 include consumers' demand for more natural and sustainable foods and the growing proportion
75 of vegetarian or vegan diets (Medina-Pradas et al., 2017; Thierry, Baty, et al., 2023). In Asian and
76 Eastern countries, where fermented vegetables have been part of the tradition, a wide variety
77 of vegetables are fermented and commonly consumed (Gänzle, 2022; Thierry, Baty, et al., 2023).
78 Cabbage is the main vegetable used worldwide, either in mixture with other vegetables, as in
79 the Korean kimchi or the Chinese paocai, or alone in sauerkraut in the East of France and in
80 Germany, produced at industrial scale (Tamang et al., 2020). In Western countries, sauerkraut,
81 olives, and cucumber are the main fermented vegetables commonly consumed. The other
82 fermented vegetables are principally produced at domestic and artisanal scale (Thierry, Baty, et
83 al., 2023). In a recent study we showed that French domestic and artisanal productions of
84 fermented vegetables include a large variety of vegetables. Indeed, in the frame of a citizen
85 science project, the 75 collected samples from citizens included 23 types of legumes, mainly
86 cabbage (27%), followed by carrot (19%) and beets (12%), and 40% of them contained mixtures

87 of vegetables (Thierry, Madec, et al., 2023). The potential health effects of plant-based
88 fermented foods have only begun to be scientifically documented, even if they make the buzz
89 in social media without scientific support. Some vitamin concentrations can increase, or be
90 preserved during fermentation but the effect depends on the microbial community and the
91 conditions of production, among other factors, and contrasted results have been observed
92 (Thierry, Baty, et al., 2023). All fermented vegetables are manufactured according to a quite
93 simple process, which consists in cutting and tightly packing raw vegetables added with salt or
94 brine, so that vegetables are covered with brine or with the juice released from vegetables
95 (Buckenhueskes, 2015). Fermentation is most generally spontaneous and due to an endogenous
96 lactic acid bacteria (LAB) community. A wide variety of recipes are used in terms of number,
97 nature, and mixture of vegetables, and use of minor ingredients, i.e. spices and condiments (Di
98 Cagno et al., 2013; Ashaolu & Reale, 2020).

99 Several bacterial groups succeed one another over time during the spontaneous
100 fermentation of vegetables, and some of them are alive at the time of consumption. According
101 to a meta-analysis on various fermented food covering 400 articles over 50 years, the average
102 number of alive microorganisms in fermented vegetables such as sauerkraut, kimchi, pickles,
103 and olives varies from 2 to 8 log colony-forming units (CFU)/g (Rezac et al., 2018). The
104 environmental aerobic or facultatively anaerobic microorganisms first grow and are
105 progressively replaced by a succession of heterofermentative and then homofermentative LAB.
106 For example, in a study on carrot juice spontaneous fermentation, bacteria of the
107 *Enterobacteriaceae* family first grew and reaching about 8 log CFU/g from the first hours of
108 fermentation, then decreased to totally disappear after 10 days of fermentation (Wuyts et al.,
109 2018). In parallel, during the first 3 days of fermentation, LAB actively grow, reaching around 9
110 log CFU/g and are responsible for rapid decrease of pH. The first LAB that grow are typically
111 members of the *Leuconostoc* genus, followed by the *Lactilactobacillus* and *Lactiplantibacillus*
112 genera, at cell numbers of about 9 log CFU/g (Wuyts et al., 2018). Similar pictures were observed
113 in other vegetables, e.g. in pepper (Li et al., 2024), sauerkraut (Müller et al., 2018), cucumbers
114 (Stoll et al., 2020). Most kinetic studies on fermented vegetables are carried out over relatively
115 short periods and do not exceed one month, which is generally considered as the final stage of
116 fermentation since the pH is stabilised (Wuyts et al., 2018; Müller et al., 2018; Wang et al., 2020).
117 In a recent study, carried out on 75 samples produced at a domestic scale, the age of samples
118 ranged from 2 weeks to 4 years with a median value of 6 months. 84 % of analysed samples still
119 contained alive LAB. LAB represented the majority of living microorganisms but also the
120 majority of 16S reads recovered by 16S rRNA gene metataxonomics while bile-tolerant
121 *Enterobacteriaceae* were detected in only four samples (Thierry, Madec, et al., 2023). Besides
122 bacteria, yeasts and bacteriophages can also grow and survive in fermented vegetables
123 (Tamang et al., 2016). Yeasts have been reported in various fermented vegetables (Liu et al.,
124 2021; Wang, Chen, Tang, Ming, Huang, Li, Ye, Fan, Yin, et al., 2022) and were found in half of the
125 75 fermented vegetable homemade analysed (Thierry, Madec, et al., 2023). Given the microbial
126 changes over fermentation time, it is crucial to combine cultural methods with culture-
127 independent methods such as 16S metataxonomics or shotgun metagenomics, to better
128 understand the dynamics of the microbiota of fermented vegetables. Cultural methods allow
129 access to the living part of the cultivable microorganisms present and therefore potentially
130 metabolically active at the time of analysis. Culture-independent methods provide access to all

131 the microorganisms present in the sample, whether or not they are viable at the time of analysis.
132 The complementarity of these two approaches is all the more important as each method
133 contains numerous potential biases (Parente et al., 2022). Concerning the 16S metataxonomics
134 method, one of these biases lies in the specificity of the 16S primers used; the combination of
135 several primers can make it possible to overcome these biases (Poirier, 2018; Guo et al., 2022).

136 Some steps are essential for a successful fermentation, notably salting and packing. The
137 main function of salting is to withdraw water and nutrients from vegetable tissue, thus providing
138 microorganisms with the substrates they need for growth. The NaCl concentration generally
139 ranges from 1% to 3% of the final product. Sliced vegetables are filled and pressed in glass jars,
140 a tight packing being crucial to eliminate air pockets and promote an anaerobic environment to
141 limit the growth of undesirable aerobic microbiota, potentially responsible for spoilage.
142 Products are then let to ferment at ambient temperature for at least 3 to 4 weeks before being
143 consumed or further stored at lower temperatures. These conditions of incubation
144 (temperature, NaCl concentration, oxygen availability, ...) determine the start-up speed of the
145 fermentation process and thus shape the microbial community (Thierry, Baty, et al., 2023). The
146 rate of fermentation, in particular the time course of pH decrease, is crucial to limit the growth
147 of undesirable microbiota. Temperature and salt concentrations influence the dynamics of LAB
148 species. The higher the temperature of fermentation is, the faster pH decreases, the earlier the
149 dominance of (former) lactobacilli, which have a greater acid tolerance. In contrast,
150 leuconostocs were present at a higher abundance at temperatures < 15°C (Wang et al., 2020). As
151 for salt concentration, early studies showed its impact on the rate of acidification and the
152 growth dynamics within the main LAB species, e.g. the growth of *Leuconostoc mesenteroides*,
153 which is less salt-tolerant than other, homofermentative, LAB species (Pederson & Albury, 1969).

154 The type of cutting markedly varies in domestic productions, as recently observed in a recent
155 study (Thierry, Madec, et al., 2023). Vegetables can be used either thinly cut (grated, shredded),
156 or more roughly cut (into slices, dices, or simply cut in two lengthwise, for example), or even
157 whole in the case of some small size vegetables. For example, carrot can be thinly or more
158 roughly grated, or cut into small dices or slides, or only roughly cut. However, to our knowledge,
159 the role of this factor has only been rarely addressed. In an original study that explored the
160 survival of inoculated *Escherichia coli* O157:H7 and *Listeria monocytogenes* during fermentation
161 of whole heads and shredded cabbage, both pathogens declined faster in shredded cabbage
162 (Niksic et al., 2005). This was explained by the significantly higher total titratable acidity in
163 shredded cabbage, compared to whole head cabbage. In summary, a thin cutting is expected to
164 facilitate the withdrawal of water and nutrients from vegetable tissue and thus to increase the
165 buffering capacity of juice and accelerate the rate of (lactic acid) fermentation.

166 Our aim was to investigate the effect of two factors, the type of cutting and a slight reduction
167 of the amount of salt added, on the microbial and biochemical changes during spontaneous
168 fermentation of vegetables. We chose to study a root vegetable, carrot, and a leafy vegetable,
169 cabbage, either thinly or roughly cut. We thus compared fermentation between grated carrot
170 and sliced carrot, and between grated cabbage and whole cabbage leaves. We also studied two
171 slightly different salt concentrations, a concentration of 1%, which is the minimum
172 concentration of salt normally used, and, with a view to reduce salt rates to follow health
173 recommendations, a concentration of 0.8%. We performed fermentations of carrot and cabbage
174 under controlled conditions and the various conditions studied were carried out in duplicate.

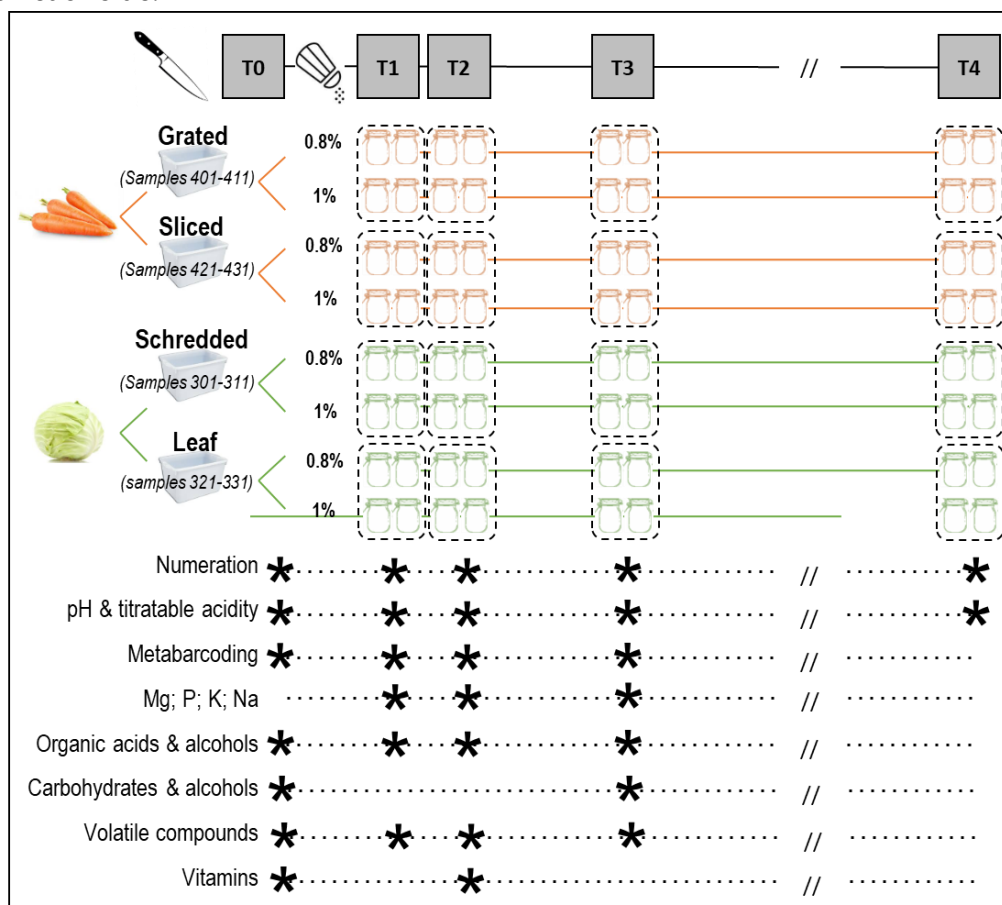
175 On these duplicates, we characterised the microbiological and biochemical changes over one
 176 month by combining culturomics, 16S rRNA gene and *gyrB* metataxonomics analysis for
 177 bacterial community, and targeted metabolomics.

178 **Material and methods**

179 **Ingredients and experimental design**

180 Two vegetables, carrot and white cabbage, were collectively chosen by the partners of the
 181 FLEGME project among the most frequently used in the manufacture of fermented vegetables,
 182 so as to include a root and an aerial vegetable. Non-washed organic carrots were provided by
 183 the Ferme Ty Coz farm, Saint-Pol-de-Léon, France. Non-washed organic white cabbages
 184 (*Brassica oleracea* L.), were provided by Coopérative des Producteurs Légumiers, Doué en
 185 Anjou, France. Dry (< 0,1 % humidity) grey coarse sea salt was used. Tap water was used to
 186 prepare the brine, water was boiled for carrot brine. 500 g-jars with glass lid and rubber seal were
 187 used (Korken, IKEA).

188 A 2³ experimental design was set up with (i) vegetable type (carrot / cabbage), (ii) cutting type
 189 (thin / rough) and (iii) salt concentration (0.8% / 1%) as factors. The two chosen vegetables,
 190 cabbage and carrot, were either thinly or roughly cut, firmly pressed down in 500 mL-jars and
 191 filled up with brine to reach final NaCl concentrations of 0.8% or 1.0%, expressed as gram of raw
 192 salt per 100 g of the mixture of vegetable and brine (**Figure 1**). More precisely, carrot was either
 193 grated or cut into slices, and cabbage were either shredded or cut into pieces of leaf of about 6-
 194 8 cm on each side.



195

196 **Figure 1:** Experimental design used to prepare fermented vegetables and sampling. The
197 three factors tested were vegetable type (carrot and cabbage), cutting type (either thin or
198 rough) and salt concentration (0.8% and 1%, expressed as g raw salt per g of preparation
199 (vegetable and brine). Sampling was done in duplicate (two independent jars) at each
200 sampling point, represented by a star, except for volatile analysis and vitamins, done in
201 triplicate (three independent jars), at five points: T0, initial time, T1, 1.7 day, T2, 2.7
202 (carrot) or 3.6 day (cabbage), T3 (4 weeks), and T4 (7 months). A few analyses were also
203 performed at 2 weeks (stage T2b).

204 After removing the external leaves, cabbages were either shredded by using a professional
205 Dito Sama TRS vegetable slicer, equipped with a 2 mm disk. Cabbage leaves were manually cut
206 into ~9 cm x ~9 cm pieces of leaves. Then, 205 g shredded cabbage and 282 g of brine, or 232 g
207 cabbage leaf and 246 g of brine, were successively weighed in each jar. As for carrots, they were
208 washed, hand-peeled, grated in 3 mm pieces or cut in 5 mm-slices at the CTCPA pilot facility
209 (agri-food technical centre and Oniris, Nantes, France). Then, 285 g grated carrot and 215 g of
210 brine, or 285 g sliced carrot and 230 g of brine, were successively weighted in each jar. To ensure
211 the final expected salt concentrations of 0.8% and 1%, preliminary tests were performed to
212 determine the maximum amount of vegetables that could be packed in a jar, which varied
213 between 205 g to 285 g according to the vegetable and the cutting types (**Supplementary Table**
214 **S1**), and, consequently, the quantity of liquid (brine) that could be added (215 to 282 g), so as to
215 calculate the salt concentration of brine in each case. The details of brine concentration are
216 given in Supplementary Table S1.

217 Twenty jars of each type (vegetable, cutting type, salt concentration) were prepared, leading
218 to a total of 160 jars. Jars were transported (1 h of transport between manufacturing site and
219 laboratory) at ambient temperature (approx. 20°C) just after manufacturing to be incubated at
220 the STLO laboratory at 19°C for 7 months. Two independent jars were characterised at each time
221 point. One sample of raw vegetable was transported in a cooler (approx. 6°C upon arrival) to be
222 analysed before fermentation (T0).

223 Samples were characterised for viable microorganisms, metataxonomics profiles and pH
224 measurement at four sampling times. The first sampling was at the very beginning of
225 fermentation, two samplings (named T1 and T2) covered the initial acidification period and the
226 last (T3) was after four weeks incubation. Due to differences in the acidification rates, the first
227 two sampling times were 40 h (T1) and 64 h (T2) for carrot and 40 h (T1) and 86 h (T2) for cabbage.
228 A late sampling (T4) was performed after seven months of incubation, for microbial
229 enumeration and pH measurement only (**Figure 1**). In addition, some intermediary sampling
230 times were performed between T2 and T3 for volatile analysis and isolate identification (T2a,
231 T2b, and T2c: 10, 15 and 21 days, for carrot samples and T2b and T2c: 14 and 22 days, for
232 cabbage).

233 Sample names were coded as follows: 301 and 311 for shredded cabbage at 0.8% and 1.0%
234 salt, respectively, 321 and 331 for cabbage leaf at 0.8% and 1.0% salt, respectively, 401 and 411
235 for grated carrot at 0.8% and 1.0% salt, respectively, and 421 and 431 for sliced carrot at 0.8%
236 and 1.0% salt, respectively (Figure 1). For example, the sample 331-a-T3 was the replicate 'a' of
237 a cabbage leaf sample prepared at 1.0% salt, sampled after 4 weeks fermentation.

238 **Culturomics conditions**

239 Samples of 10 g of fermented vegetables (5 g of juice plus 5 g of drained vegetables) were
240 suspended in 90 mL of a Tryptone Salt diluent (TS, sodium chloride 8.5 g/L, tryptone 1 g/L)
241 heated at 48°C and homogenised in a filter bag (BagPage+, Interscience), in which vegetable
242 debris was separated from the filtrate. Microbial analyses were performed on 14 different
243 nutritive and selective media and incubated under aerobic (air atmosphere) or anaerobic
244 conditions (Anaerocult® A, Merck, Darmstadt, Germany) at 37°C, 30°C, or 25°C depending of the
245 medium, as previously detailed (Thierry, Madec, et al., 2023). In brief, seven media targeted the
246 following microbial groups: LAB, total aerotolerant bacteria, halotolerant bacteria, aerotolerant
247 Gram-negative bacteria, yeasts and filamentous fungi, bile-tolerant *Enterobacteriaceae*, and
248 enterococci (**Supplementary Table S2**). In addition, three media targeted spore-forming
249 bacteria (Supplementary Table S2). *Bacillus cereus*-typical colonies on BCA were further
250 examined, by observing their aspect on the agar medium Compass Bacillus cereus (Biokar),
251 incubated at 30°C for 24 h and 48 h, microscopical observation and *panC* gene sequencing.

252 In addition, four pathogens, namely, *Escherichia coli*, coagulase-positive staphylococci
253 (*Staphylococcus aureus*), *Salmonella*, and *Listeria monocytogenes*, were searched by a
254 subcontracted laboratory (LABOCEA, Fougères, France), following the ISO 16649-2, ISO 6888-2,
255 BRD 07/11-12/05, and AES 10/03-09/00 standards, respectively.

256 **Microbial isolation and identification**

257 To collect LAB strains, 1 to 3 isolates were picked up on the several culture media used for
258 agar plate containing 20 to 100 colonies, according to visual aspect of the colonies (size, colour,
259 morphology), to favour the diversity of the isolates collected. Yeast isolates were collected
260 following the same methodology. The isolates were collected from T0 to T4 with an
261 intermediate collection stage at 15 days which corresponds to the stabilisation of the pH.
262 Bacteria and yeast clones were identified by 16S rRNA gene and D1/D2 domain of 26S rRNA gene
263 sequencing, respectively. Bacterial and yeast identification were performed following the
264 procedures previously described (Thierry, Madec, et al., 2023).

265 **16S rRNA gene and gyrB metataxonomic analysis**

266 DNA was extracted from the samples, using the Nucleospin Tissue kit (Macherey-Nagel,
267 Düren, Germany) as previously described (Thierry, 2024). DNA sequences were amplified in 16S
268 rRNA gene V5-V7 region for bacteria using primers 799F/1193R (Forward-
269 AACMGGATTAGATACCCCKG, Reverse-ACGTCATCCCCACCTTCC) and PCR conditions as previously
270 described (Beckers et al., 2016). In parallel, the degenerate primers F64 (5'-
271 MGNCCNGSNATGTAYATHGG-3') and R353 (5'-CNC CRTGNARDCCDCCNGA-3') were used to
272 amplify a ~280-bp region of *gyrB* (Poirier et al., 2018). The 16S rRNA and *gyrB* amplicons were
273 sequenced at Génome Quebec sequencing platform (Montreal, Quebec) using Illumina MiSeq
274 PE250 technology, which generated 2 x 250 bp reads and a total of 2.45 Gb of data for amplicons.

275 **Bioinformatic analyses**

276 The raw sequences of 16S rRNA gene sequencing were processed as previously described
277 (Thierry, Madec, et al., 2023). The raw sequences of *gyrB* gene sequencing were also processed
278 using DADA2 package v 1.20.0 (Callahan et al., 2016), following the authors guidelines: we

279 successively applied the functions filterAndTrim, learnErrors, dada, mergePairs,
280 makeSequenceTable, removeBimeraDenovo, and assignTaxonomy. The gyrB database from
281 (Poirier et al., 2018) was used for the taxonomic affiliation. The amplicon sequence variants
282 (ASV) count table, the ASV taxonomy table, and the sample metadata were combined into one
283 phyloseq object (McMurdie & Holmes, 2013; Canon et al., 2020) for each target gene. The
284 phyloseq (v1.44) R package was used to visualise barplots. Data were transformed into relative
285 abundances before computing beta diversity (Bray-Curtis dissimilarity). The ComplexHeatmap
286 (v2.16.0) R package was used to visualise the relative abundance of the different genera on a
287 heatmap with a complete clustering based on Bray-Curtis dissimilarity computed after depth
288 normalisation. Principal coordinate analyses (PCoAs) based on Bray-Curtis dissimilarity,
289 calculated from the relative abundances of different genera, were conducted to evaluate the
290 beta diversity of the samples using gyrB and 16S markers.

291 **Biochemical analyses**

292 The pH of juice samples was measured with a pH-metre (Hanna Instruments HI 2020-02).

293 Total titratable acidity (TTA), was determined on centrifuged (18000 g for 10 min at 20°C)
294 juice samples, by titrating approximately 10 mL juice with 0.1 M NaOH to pH 8.3. It was estimated
295 as follows: total acidity (%) = $V_{\text{NaOH}} \times 0.1 \times m / S / 10$ and expressed as percentage (w/w) of lactic
296 acid, with V_{NaOH} , volume of 0.1 M NaOH (mL); 0.1, factor corresponding to NaOH normality; m =
297 90, molar mass of lactic acid, S, mass of sample used (g), and was

298 *Sample preparation*

299 Before metabolite analysis except volatiles and vitamins, aliquots of juices were first
300 centrifuged at 8000 g for 10 min at 4°C to eliminate vegetal debris, and the supernatant
301 deproteinized by ultrafiltration on Vivaspin 2 centrifugal concentrator columns
302 (polyethersulfone, 10 kDa cutoff, Sartorius) at 8000 g for 15 to 30 min at 4°C. Two
303 chromatographic systems, High-Performance Liquid Chromatography (HPLC) coupled to UV
304 and refractometry detection, and high-performance anion-exchange chromatography coupled
305 to pulsed amperometric detection (HPAEC-PAD) were combined to analyse a range of organic
306 acids, carbohydrates, and alcohols.

307 Before mineral analysis, juice samples were centrifuged at 18000 g for 10 min at 4°C, and the
308 supernatant 40-fold (for Mg and P analysis) to 1000-fold diluted (for Na and K analysis) in a 2%
309 v/v HNO₃ (Thermo fisher scientific, Waltham, MA, USA).

310 For volatile metabolites, triplicate samples, taken from three independent jars, were directly
311 analysed from juice, using headspace (HS) gas chromatography- mass spectrometry (GC-MS).
312 Juice aliquots (2.5 mL) were placed in Perkin-Elmer 22 mL vials (B0104236, 20 mm),
313 hermetically sealed, and the vials stored at -80°C until analysis.

314 Vitamin analysis was performed in drained vegetable samples stored at -20°C before
315 analysis.

316 *Acids and alcohol analysis by high-performance liquid chromatography*

317 Supernatants were 2- to 4-fold diluted in a 0.005 mol-L⁻¹ H₂SO₄ and stored at -20 °C until
318 analysis. Lactic, acetic, citric, succinic, oxalic, and pyruvic acids, ethanol, and butanediol were
319 quantified by High-Performance Liquid Chromatography (HPLC, Ultimate 3000, Thermo Fisher
320 Scientific 91941 Courtaboeuf), using a Rezek ROA organic acid H + column (300*7.8 mm,

321 Phenomenex, California), with H₂SO₄ 0.005 M as the mobile phase at a flow rate of 0.4 mL/min
322 at 60 °C. Two detectors were used: UV detector (DIONEX-UVD 1704) operated at 210 nm and
323 refractometer (RI 2031 Plus Jasco).

324 Data was processed with Chromeleon™ software. Quantification was performed using multi-
325 standard external calibration. Standards of ethanol, butanediol, oxalic, lactic, citric, propionic,
326 butyric, succinic, and pyruvic acids were from Merck, St. Quentin Fallavier, France, and acetic
327 acid from PanReac, Lyon, France. Mannitol, fructose and glucose can also be analysed by this
328 method but in the present study were not quantified because the sucrose of vegetables
329 hydrolyses in glucose and fructose during analysis, and fructose is co-eluted with mannitol.

330 *Carbohydrate analysis by high-performance anion-exchange chromatography*

331 Supernatants were diluted by 400-fold in milli-Q® water (Merck, Darmstadt, Germany) and
332 kept frozen at -20°C until analysis. Carbohydrates (sucrose, glucose, fructose, galactose,
333 raffinose, xylose, arabinose, mannose, and mannitol) were quantified by high-performance
334 anion-exchange chromatography (HPAEC) and pulsed amperometric detection (PAD) on an ICS-
335 5000+ Dionex system (Thermo Electron SAS, Courtaboeuf France), as previously described
336 (Canon et al., 2020). The system was equipped with a Dionex CarboPac PA210-Fast-4 µm column
337 preceded by a CarboPac PA210-4 µm guard column (2*30 mm). Metabolites were eluted with
338 KOH as eluent, at a flow rate of 0.2 ml/min with the following gradient: 0 to 32 min 13 mM, 32
339 min to 55 min 100 mM then return to 13 mM from 55 to 65 min. Data were acquired and
340 processed by using the Chromeleon7™ software (Thermo Scientific). Metabolites were
341 quantified using multi-standard external calibration (prepared at 0.1 mg/L to 40 mg/L (Merck,
342 St. Quentin Fallavier, France).

343 *Minerals analysis using inductively coupled plasma-optical emission spectrometer (ICP-OES)*

344 Minerals were quantified in the initial brine and in juices during incubation using an
345 inductively coupled plasma-optical emission spectrometer (ICP-OES) (iCAP 7200, Thermo Fisher
346 Scientific, Courtaboeuf, France), as previously described (Martin et al., 2022). Sodium,
347 potassium, magnesium, phosphorus, and selenium were quantified using standard external
348 calibration. Na, Mg, K, and P standards were prepared from 100 ppm standard solutions
349 (Reagecon, Shannon, Ireland) at 0.5 to 10 ppm in a 2% v/v HNO₃ solution, and Se at 0.01 to 1
350 ppm in a 2% v/v HNO₃ solution. NaCl concentrations were calculated from Na concentrations.

351 *Volatiles analysis by headspace - gas chromatography - mass spectrometry*

352 Volatile compounds were extracted using a Turbomatrix HS-40 trap automatic headspace
353 sampler and analysed using a Clarus 680 gas chromatograph coupled to a Clarus 600T
354 quadrupole mass spectrometer, operated within a mass range of m/z 29 to m/z 206 and
355 ionisation impact of 70 eV (Perkin Elmer, Courtaboeuf, France) as previously detailed (Pogačić,
356 2015). Volatiles were eluted on an Elite WAX ETR column (30 m by 0.25 mm by 0.25 mm; Perkin
357 Elmer, Waltham, MA), with helium as the mobile phase, under the following conditions: initial
358 temperature 35°C maintained for 10 min, then increased t 5°C/min up to 230°C. Volatiles were
359 identified by comparing their mass spectra and retention index with data from the NIST 2008
360 Mass Spectral Library data (Scientific Instrument Services, Ringoes, NJ, USA), from literature
361 and from standard injection, when available. Volatiles were semi-quantified from the
362 abundance of one specific mass fragment (m/z), in arbitrary units. Mass spectrometry (MS) data

363 were processed using XCMS on R software (R Core Team. 2013. R: a language and environment
364 for statistical computing. R Foundation for Statistical Computing, Vienna, Austria). The full
365 width at half maximum was set to 5, the maximum number of peaks per ion to 1000, the interval
366 of m/z value for peak picking to 0.4, the signal-to-noise ratio threshold to 6, the group bandwidth
367 to 3, and the minimum to 0.4. The other parameters were those by default.

368 *Vitamins*

369 Vitamins C, K1, B9 and for carrot, beta-carotene, were quantified in vegetable samples
370 (without juice) sampled at T0 and T3, while vitamins K2 and B12, which are not present in raw
371 vegetables but potentially produced by bacteria, were analysed only in T3 samples. Vitamin C
372 was analysed at Vegenov laboratory (Saint-Pol-de-Léon, France), vitamins B9 et K1 by a
373 subcontractor laboratory, Labexia (Quimper, France), and beta-carotene and vitamins B12 and
374 K2 were determined by another subcontractor laboratory, Agrobio (Bruz, France), using HPLC
375 and LC-fluo internal methods.

376 Vitamin C was determined following NF V03-135 standard. Briefly, vitamin C was extracted
377 from samples using a 20 g/l metaphosphoric acid solution. L(+)-dehydroascorbic acid was
378 reduced in L(+)-ascorbic acid by using a 40 g/l L-cystein solution. L(+)-ascorbic acid was
379 quantified by HPLC (Agilent, Les Ulis, France) with photo diode array at 265 nm as detector.

380 Vitamin B9 was extracted from samples, and the diluted extracts and test broth medium
381 were put in the wells of a Vitafast B9 microplate kit, in the presence of a *Lacticaseibacillus*
382 *rhamnosus* strain, and incubated in the dark at 37°C for 44 to 48 h. The intensity of metabolism
383 of *L. rhamnosus* due to the vitamin B9 brought by the extract was measured by turbidity using a
384 microplate reader at 620 nm and compared to a standard curve.

385 Vitamin K1 was determined following the NF EN 14148 standard. Fat was first eliminated by
386 an enzymatic treatment, and vitamin K1 was measured by HPLC with fluorescent detection,
387 after post-column reduction.

388 **Statistical analyses**

389 In figures 2 and 4, means and 95% confidence intervals were calculated by using the excel
390 functions AVERAGE and CONFIDENCE.NORM, respectively.

391 Four-way ANOVAs were performed to determine whether the microbial and biochemical
392 variables differed according to the vegetable, the fermentation stage, the cutting type and the
393 NaCl concentration and the 2-way interactions, by using the R function *aov*. Means were then
394 compared using the sidak posthoc test from the R package *emmeans*. The factors and
395 interactions that were not significant (p -value > 0.05) were further removed from the model.
396 When the interactions were significant, the corresponding single effects were studied on a case-
397 by-case basis, for example the effect of the fermentation stage and the cutting type were
398 separately tested for each vegetable. The model was also adapted for the compounds detected
399 in only one of the two vegetables studied.

400 A Principal component analysis (PCA) was performed by using the PCA function of the
401 *FactoMineR* R package to illustrate the global biochemical and microbiological composition of
402 the fermented vegetables and the relationships between the different variables. A PCA was also
403 done on the volatile profile for each vegetable, using the *FactoMineR* R package. Hierarchical
404 clustering was performed on PCA data. The association of qualitative variables with sample

405 clusters was investigated by using v-tests and was considered significant for v-test values of <-2
406 or > 2.

407 A multi-block Partial Least Squares-Discriminant Analysis (PLS-DA) was performed to
408 determine if samples exhibited different signatures at T3 regarding metataxonomics (16S and
409 *gyrB*), metabolites (lactic acid, acetic acid, mannitol, ethanol, butanediol), volatiles and
410 enumeration results, given their cutting type or salt concentration. The relative abundance
411 values of a genus were retained only for the marker in which they were the highest. The function
412 *block.plsda* of the R package *mixOmics* was used with two components ($ncomp = 2$). Outputs
413 were visualised with the *plotIndiv* and *plotVar* R functions, and the discriminating power of the
414 model was interpreted thanks to the *auroc* R functions, giving the AUC and Wilcoxon test p-value
415 for each class comparison performed.

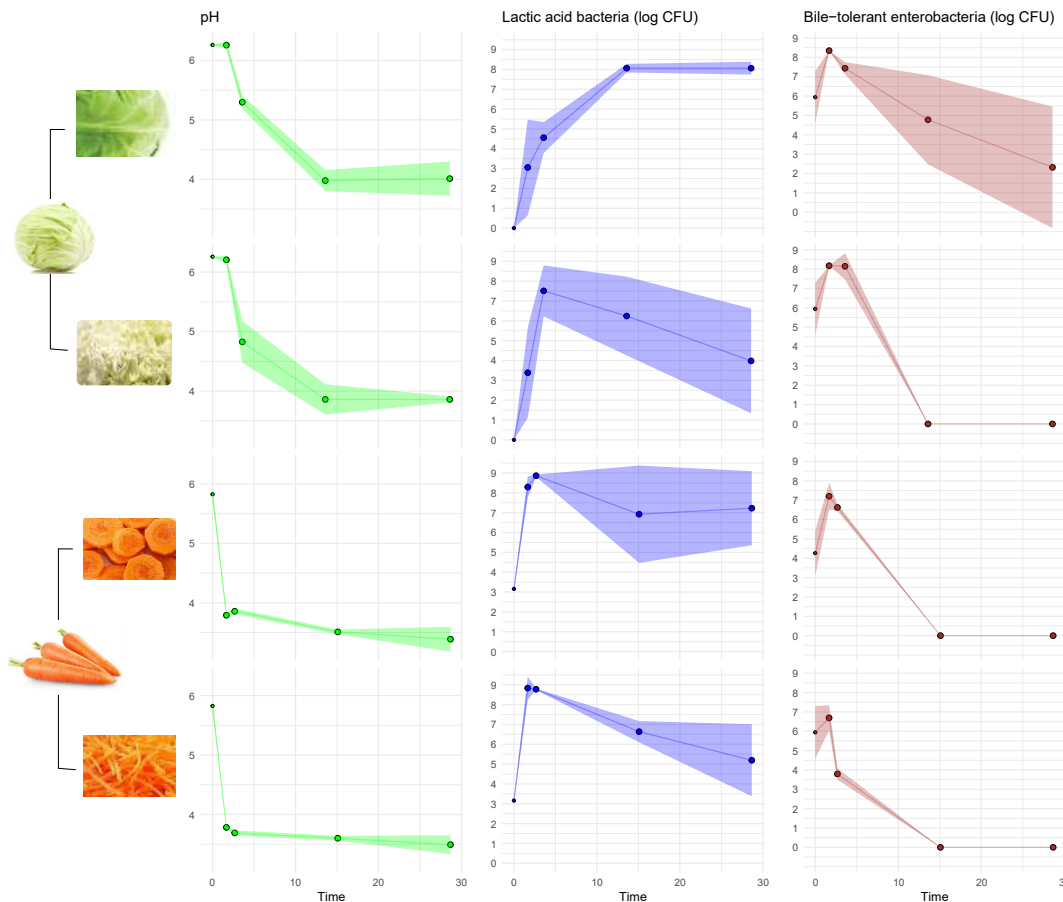
416 Results

417 Time course of microbial growth and acidification

418 The time-course of pH decrease and growth of the two main bacterial groups, i.e. bile-
419 tolerant *Enterobacteriaceae* and LAB, is depicted on **Figure 2**. These three variables, as well as
420 TTA, were significantly impacted by the vegetable studied, the fermentation stage, and, to a
421 lesser extent, the cutting type. In contrast, no effect of the NaCl content was observed at the
422 concentrations studied. Therefore, four replicates instead of two were available at each
423 sampling point for statistical analyses. Marked differences of microbial counts and pH values
424 were observed between the replicate jars sampled at each time point, but some significant
425 trends were however highlighted concerning the time-course of fermentation.

426 The first bacterial group that grew was bile-tolerant *Enterobacteriaceae*, enumerated on
427 VRBG, referred to as 'enterobacteria' below. Raw carrot and cabbage contained about 4.3 and
428 6.0 log enterobacteria CFU/g, respectively. Their number increased rapidly during the first days
429 of fermentation for both vegetables. They reached 6.9 +/- 0.7 log CFU/g within 40 h in carrot
430 samples and 8.3 log CFU/g in 40 h in cabbage samples (**Figure 2**). Then they decreased, at a
431 faster rate in carrot than in cabbage, and in thinly-cut vegetables than in roughly-cut ones. The
432 enterobacteria counts were 6.6 vs 3.8 log CFU/g at 64h in sliced and grated carrot, respectively,
433 and 8.1 vs 7.4 log CFU/g at 86h in leaf and shredded cabbage, respectively. For carrot and
434 shredded cabbage, no enterobacteria were detected after 14 days fermentation, while for leaf
435 cabbage, they were still detected in half samples after one-month fermentation, despite the pH
436 decrease to 3.2 to 4.4 (**Figure 2**). At that sampling point, 3 out of the 4 isolates from VRBG
437 medium were identified as *Hafnia alvei*. Enterobacteria were however no more enumerable in
438 7-month old cabbage, in which the pH was 3.1 to 3.7 (data not shown).

439 LAB were enumerated on MRS, on which the 58 isolates collected were effectively LAB. LAB
440 were present at low levels in raw carrot (3.16 +/- 0.06 log CFU/g), whereas they were below
441 detection level in cabbage. LAB counts significantly increased over time ($p\text{-value} < 0.005$). Like
442 for enterobacteria the number of LAB rapidly increased during the three first days of
443 fermentation and reached 8.8 log in 65 h-fermented carrot regardless of the cutting type. LAB
444 grew more slowly in cabbage than in carrot, with marked differences according to the cutting
445 type. LAB mean counts were 7.51 and 4.56 log CFU/g in 86 h in shredded and leaf cabbage,
446 respectively, in which they reached 8 log CFU/g only after ~5 and 13.6 days, respectively. At one



448

449 **Figure 2** Time-course of fermentation in cabbage and carrot for each cutting type,
 450 illustrated by the change in pH, and the viable counts of lactic acid bacteria enumerated
 451 on MRS and bile-tolerant *Enterobacteriaceae*, enumerated on VRBG, expressed as
 452 logCFU/g. Values are means of the results observed on four independent jars, and the size
 453 of symbols proportional to the number of biological replicates (n=4, except at T0 and 15
 454 days where n=2). The coloured areas show the 95% confidence intervals. Panels, from top
 455 to bottom: leaf cabbage, shredded cabbage, sliced carrot, grated carrot.

456 month (T3), LAB showed higher counts in roughly-cut vegetables than in thinly-cut ones (8.1 vs
 457 4.0 log CFU/g in leaf and shredded cabbage, and 7.2 vs 5.2 log CFU/g in sliced and grated carrot).
 458 After 7 months LAB were still viable both in all samples with mean value of 4.3 +/- 1.1 log CFU/g.
 459 Among BL, enterococci, selectively enumerated on KF medium, were detected at low counts (<
 460 4 log CFU/g, i.e. less than 0.04% of the total lactic acid bacteria) at the beginning of fermentation
 461 in both vegetables. They disappeared after 2 weeks fermentation, except in leaf cabbage
 462 samples, which all contained viable enterococci, ranging from 1.8 to 8.3 log CFU/g at one
 463 month. The 12 isolates collected from cabbage samples on KF were all identified as
 464 *Enterococcus faecalis*, while for carrot 7 of the 10 isolates collected were identified as
 465 *Enterococcus sp.* and 3 as other LAB genera (*Leuconostoc mesenteroides* and *Lactiplantibacillus*
 466 *sp.*).

467 The initial pH for raw material was 5.83 and 5.94 for carrot and cabbage, respectively. For
 468 carrot, the pH markedly decreased during the first two days of fermentation, with a mean value
 469 of 3.79 +/- 0.04 in 40 h regardless of the cutting type. TTA, in contrast, was highly significantly

470 ($p < 0.0001$) influenced by the stage and by the interaction stage*cutting ($p < 0.01$). TTA increased
471 faster in grated than in sliced carrot, with values of 0.30% vs 0.04%, respectively, at T1 (40h) and
472 76% vs 0.32% at T2 (64h). TTA was 1.06 +/- 0.35 % in carrot at T3 (1 month). Afterwards, the pH
473 only very slightly decreased, to reach 3.44 +/- 0.18 and 3.39 +/-0.30 after 1 and 7 months of
474 fermentation, respectively, in all carrot samples. For cabbage, the pH decreased faster in
475 shredded than in leaf cabbage during the first days of fermentation and reached 4.8 and 5.3 at
476 T2 (86 h) in shredded and leaf cabbage, respectively. However, at this stage TTA was still very
477 low ($< 0.08\%$) regardless the cutting type. TTA was 0.63 +/- 0.11 % in cabbage at T3. The pH
478 continued to decrease until about 15 days of fermentation, then stabilised to 3.94 +/- 0.21 and
479 3.55 +/-0.13 after 3 and 7 months, respectively, in all cabbage samples.

480 Regarding the other media used to enumerate bacteria, the counts enumerated on BHI-
481 YEnp, a medium used to enumerate Gram-negative aerotolerant bacteria, were very similar or a
482 bit lower compared to the counts on VRBG, suggesting that the same bacteria grew on both
483 these media. Accordingly, 28 out of the 30 collected isolates from BHI-YEnp medium at T1, T2 or
484 T2b were members of the *Enterobacteriales* order (*Enterobacteriaceae*, *Hafniaceae*, *Erwiniaceae*,
485 *Yersiniaceae* family) (**Supplementary Table S3**). Only a few carrot samples at the very beginning
486 of fermentation showed higher counts on BHI-YEnp than on VRBG. They probably corresponded
487 to the initial plant microbiota such as *Pseudomonadaceae* and *Erwiniaceae* members, the main
488 taxa isolated from raw carrot on this medium. On the BHI-YEn medium chosen to enumerate
489 total aerobic bacteria, *Pseudomonas sp.* and *Janthinobacterium sp.* isolates were identified at
490 T0, while only LAB were isolated from T2 (Supplementary Table S3). Likewise, on the TSA-NaCl
491 medium that targeted halophilic bacteria, 11 out of the 14 isolates collected at T3 were
492 identified as LAB, the major part belonging to the species *Leuconostoc mesenteroides*. On the
493 basis of the isolated and identified clones, the selectivity of KF, and VRBG media was confirmed
494 with, respectively, 19 enterococci out of the 22 collected isolates, and 4 bile-tolerant
495 *Enterobacteriaceae* out of the 4 collected isolates (Supplementary Table S3).

496 Yeasts were present on the raw vegetables, at counts ranging from 1.7 to 2.7 log CFU/g,
497 depending on the samples. Yeasts did not develop in cabbage and disappeared fairly quickly
498 after 4 days of fermentation. In contrast, for carrot, alive yeasts were enumerated after 7 months
499 regardless of the cutting type. Strong variations between replicate jars were observed, with, for
500 example at time T3 for sliced carrot, values ranging from 0 to 7.9 log CFU/g.

501 Regarding pathogenic and undesirable bacteria, none of the four pathogenic bacteria were
502 detected. Some spore-forming bacteria were present at low counts in carrot samples (median
503 value of 75 CFU/g enumerated on a rich medium, BHI-YE) and absent from cabbage except for
504 one sample, a one-month-old cabbage sample (331-a-T3). This specific sample was also the sole
505 that contained clostridia - 4 log CFU/g, enumerated on the selective TSN medium, and 2.44 log
506 CFU/g on BCA medium.

507 A total of 191 bacterial strains (126 from carrot and 65 from cabbage) were isolated and
508 identified to the species level by 16S rRNA gene sequencing. 97 strains were isolated during the
509 first stages of fermentation (from T0 to T2) and 94 strains were isolated after 2 to 4 weeks of
510 fermentation. Concerning LAB, the *Leuconostoc* genus was dominant and represented 52% of
511 the isolates collected during the first 15 days of fermentation, followed by the *Enterococcus*
512 (22%) and *Lactiplantibacillus* (10%) genera (Supplementary Table S3). Concerning non-lactic
513 acid bacteria, the *Bacillus* genus dominated, followed by *Hafnia*, *Pantoea*, *Rhanella*, and

514 *Pseudomonas* genera. Concerning yeasts, 12 strains (10 from carrot and 2 from cabbage) were
515 isolated and identified as members of the genera *Kazachstania*, *Rhodotorula*, *Saccharomyces*,
516 *Candida*, *Pichia*, and *Debaryomyces*(Supplementary Table S3).

517 **Changes in metabolite concentration**

518 The targeted compounds, which included carbohydrates, organic acids, and alcohols, were
519 analysed in sample juices. Concerning carbohydrates, saccharose, glucose, and fructose were
520 the main compounds detected at the beginning of fermentation (T0). After one-month
521 fermentation (at stage T3), the main vegetable carbohydrate detected in both vegetables was
522 glucose, with large variation in concentrations (0 to 4.8 g/kg juice), followed by saccharose in
523 carrot (0.5-1 g/kg juice) and fructose (0 to 0.4 and 0.1 to 1.6 g/kg juice in carrot and cabbage,
524 respectively). Low amounts of galactose (~250 mg/L) were also detected at T3 in both
525 vegetables and traces (< 30 mg/L) of xylose, mannose, and arabinose, and, in cabbage only, of
526 raffinose. Concerning bacterial metabolites, five organic acids (lactic, acetic, succinic, citric and
527 pyruvic acids) and mannitol, ethanol, and 2,3-butanediol were identified in vegetable juices, the
528 main ones being mannitol and lactic acid, which accounted for 67 to 80% of total metabolites
529 at T3, except in roughly-cut cabbage, which also contained high amounts of ethanol (**Figure 3**).
530 Two other, unidentified, compounds were detected by using HPLC-UV, at retention times 26 min
531 and 28 min, named RT26 and RT28. In addition, oxalic acid was also detected in carrot samples.
532 Its concentration increased from 30 mg/kg at T0 to 70 mg/kg juice at 3-month fermentation.

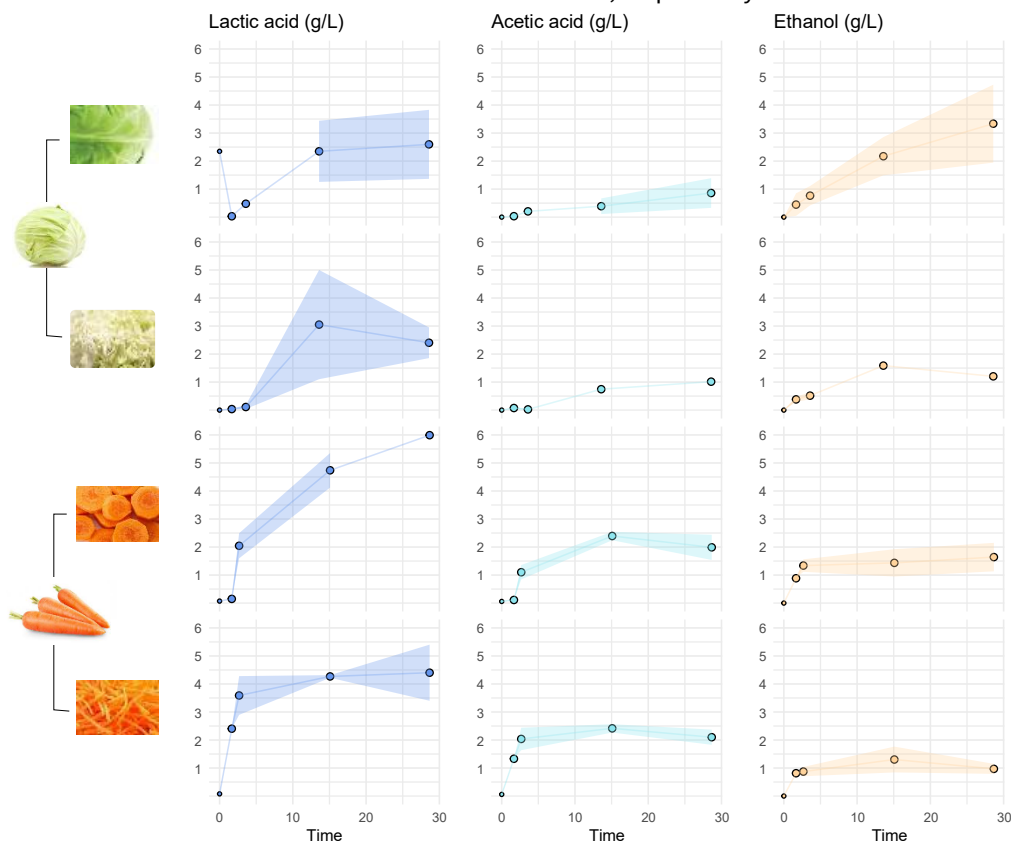
533 The concentrations of all metabolites except butanediol significantly (p -value < 0.001)
534 increased over time, with different rates depending on the vegetable and, for some metabolites,
535 on the cutting type. Their concentrations stabilised in juice after ~3 days in grated carrot, ~2
536 weeks in sliced carrot and shredded cabbage, and ~30 days in cabbage leaf, as illustrated in
537 **Figure 4** for lactic acid, acetic acid and ethanol. Lactic acid concentrations were globally 2.5-
538 fold higher in carrot compared to cabbage, and similar values about 2.8 g/kg were observed in
539 15 days-cabbage and 3-days-carrot juice samples (Figure 4). At T3 lactic acid concentrations
540 were 2.5-fold higher in carrot compared to cabbage (5.2 versus 2.5 g/kg, respectively). Similarly,
541 acetic acid concentration also increased over time and was higher in carrot than in cabbage
542 (Figure 4), but it showed complex variations with significant effects of the interactions between
543 the factors stage, vegetable (globally four-fold higher in carrot than in cabbage) and cutting type
544 (1.4-fold higher in thinly-cut vegetables). In contrast, ethanol concentration increased with
545 fermentation time but was mainly affected by the cutting type, with, globally 1.6-fold higher
546 values in roughly-cut than in thinly-cut vegetables (Figure 4). For example, at T3, ethanol was
547 two-fold more concentrated in leaf-cabbage than in shredded cabbage (3.0 vs 1.6 g/kg,
548 respectively), and threefold more concentrated in sliced carrot than in grated carrot (2.0 vs 0.6
549 g/kg, respectively) (Figure 3). Mannitol was quantified only after one month of fermentation (see
550 material and methods). At this stage, mannitol concentration was about two-fold higher in
551 carrot compared to cabbage (9.1 versus 3.9 g/kg, respectively) (Figure 3).



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Figure 3 Concentration of the metabolites in fermented cabbage and carrot juice, expressed in g/kg, after one month of fermentation (stage T3), for each cutting type, and two salt concentrations, for two replicate jars. Sample codes: 301 and 311 for shredded cabbage at 0.8% and 1.0% salt, respectively, 321 and 331 for cabbage leaf at 0.8% and 1.0% salt, respectively, 401 and 411 for grated carrot at 0.8% and 1.0% salt, respectively, and 421 and 431 for sliced carrot at 0.8% and 1.0% salt, respectively.



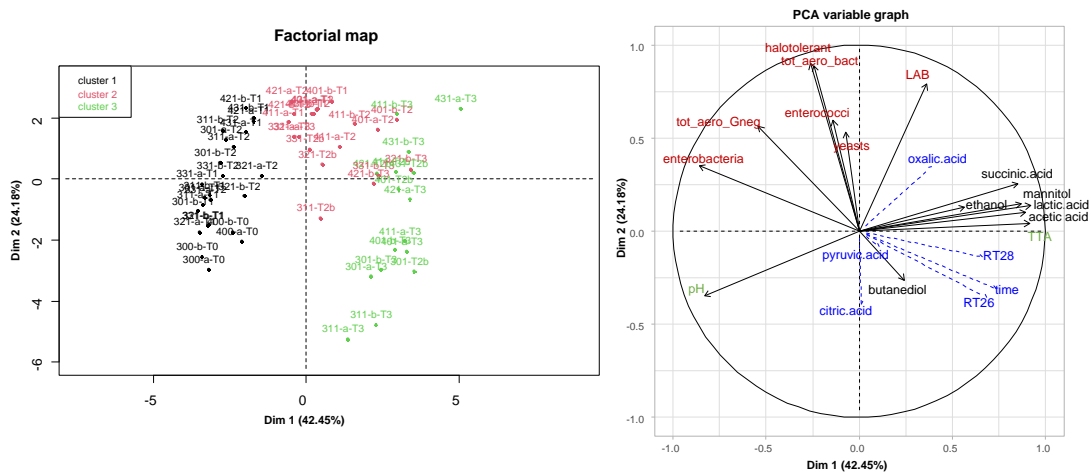
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Figure 4 Time-course (day) of fermentation in cabbage and carrot for each cutting type, illustrated by the change in concentrations in lactic acid, acetic acid and ethanol, in g/kg juice. Values are means of the results observed on four independent jars, and the size of symbols proportional to the number of biological replicates. The coloured areas show the 95% confidence intervals. Panels, from top to bottom: leaf cabbage, shredded cabbage, sliced carrot, grated carrot.

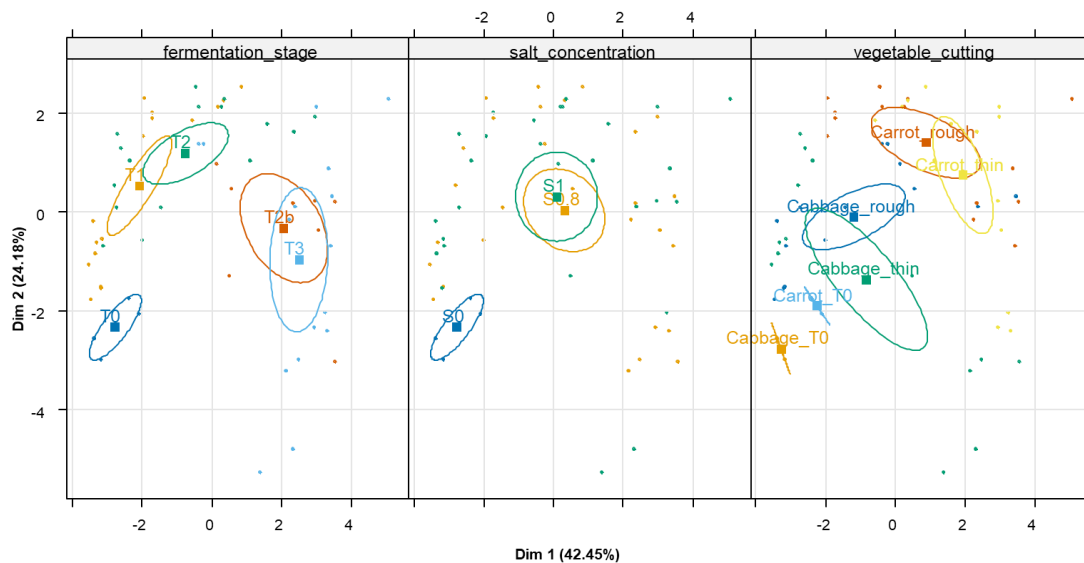
566 Global representation of microbial and biochemical changes using PCA

567 A PCA was done to draw a global picture of the changes during fermentation, using 14
568 variables, namely the viable counts of microorganisms (n=7), the amounts of the main
569 metabolites (n=6) and the pH values, for all cabbage and carrot samples analysed over time
570 **(Figure 5)**. The first axis, which explains 42.4% of total variability, separates samples on the
571 basis of pH value, negatively associated with PC1 and the concentrations in the three main
572 metabolites, mannitol, lactic acid and acetic acid, and of succinic acid, all positively associated
573 with PC1. PC1 was also negatively associated with enterobacteria counts. The second axis,
574 which explains 24.2% of total variability, separates samples on the basis of high viable counts in
575 Gram-positive bacteria, including LAB (Figure 5). Samples were clearly differentiated according
576 to the stage of fermentation (bottom 1st panel). They were also clearly differentiated according
577 to the vegetable and cutting type (bottom 3rd panel) but not to the salt concentration (bottom
578 middle panel). These results show that carrot fermentation was quicker than cabbage
579 fermentation.

580 Three clusters of samples were distinguished based on the hierarchical clustering performed
581 on PCA data (Figure 5). Cluster 1, shown in black, consisted of samples at the beginning of
582 fermentation. It was significantly ($v\text{-test} > 2$) associated with stages T0 and T1, a high pH, a low
583 titratable acidity, and high enterobacteria and Gram-negative bacteria counts. Cluster 2, shown
584 in red, characterised intermediary stage. It was significantly ($v\text{-test} > 2$) associated with high
585 microbial counts on varied culture media that targeted total anaerobic bacteria, halotolerant
586 bacteria, LAB, enterococci, and yeasts. It contained many thinly-cut carrot samples. Finally,
587 cluster 3, shown in green, consisted of samples at the end of fermentation. It was significantly
588 ($v\text{-test} > 2$) associated with stages T2b and T3, a low pH, a high titratable acidity and high
589 concentrations in metabolites, e.g. lactic and acetic acids and mannitol.



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592 **Figure 5** Principal component analysis made from the data of enumeration of viable
 593 microorganisms (n=7, shown in brown), the amounts of main metabolites (n=6, shown in
 594 black) and pH and total titratable acidity (TTA) (shown in green) for all samples (cabbage
 595 and carrot) analysed at five fermentation stages: T0, initial time, T1, 1.7 day, T2, 2.7
 596 (carrot) or 3.6 day (cabbage); T2b (2 weeks) and T3 (4 weeks). Some minor metabolites
 597 and unknown metabolites are projected as supplementary variables (blue, dashed lines).
 598 For culture media, see Table S1; LAB, lactic acid bacteria, enumerated on MRS,
 599 enterobacteria refers to the bile-tolerant *Enterobacteriaceae* enumerated on VRBG. The
 600 individual maps (bottom panels) show the 95% confidence ellipses according to the stage
 601 of fermentation (1st panel) the salt concentration (S0.8: 0.8% or S1:1%, 2nd panel), and the
 602 type of vegetable (carrot or cabbage) and its cutting (thin or rough, 3rd panel).

603 Volatile compounds

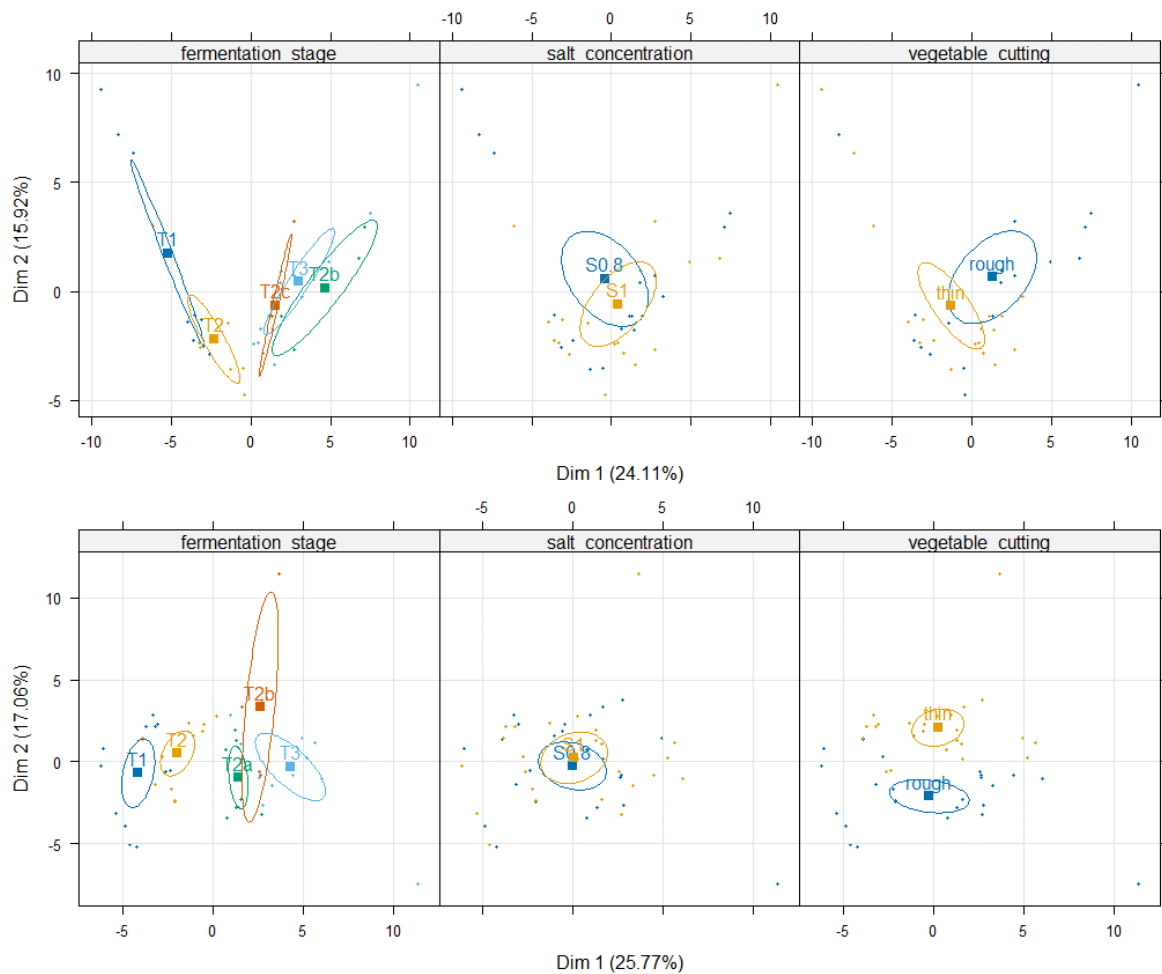
604 In fermented cabbage, 78 volatile compounds were identified. They contained 23 sulphur-
 605 containing compounds that included 9 (iso)thiocyanates and 4 nitriles, 23 esters, 8 acids, 7
 606 alcohols, 7 aldehydes, 6 ketones, and 4 other compounds (**Supplementary Table S4**). The
 607 abundance of 27, 15, and 10 volatiles were impacted by the stage of fermentation, the type of
 608 cutting, and the salt concentration, respectively, but in they were also interactions between
 609 these factors. The effect of the salt treatment, in particular, was always associated with
 610 interactions with the effect of stage and/or of cutting. The abundance of one third of cabbage
 611 volatiles significantly (p-value<0.01) varied during fermentation, with 27 that increased (fold
 612 change stage T3/stage T1 >2), and 9 that decreased (fold change stage T1/stage T3 >2). A PCA
 613 made to illustrate the global results on cabbage volatile profiles, showed that cabbage samples
 614 were separated on the first axis (24.1% of the total variability) according to the stage of
 615 fermentation, and on the 2nd axis (15.9% of the total variability) according to their cutting type
 616 and salt concentration (**Figure 6**). Four clusters of samples were distinguished based on the
 617 hierarchical clustering performed on PCA data (**Supplementary Figure S1**). Clusters 1, 2 and 3
 618 were significantly associated with stages T1, T1/T2, and T3, respectively, while cluster 4
 619 contained only one sample of roughly-cut cabbage (Supplementary Figure S1). Samples at the
 620 beginning of fermentation (cluster 1) showed high abundances of many esters, while one-month
 621 aged samples (cluster 3) contained more ethanol, butan-1-ol, acetic and butanoic acids, and

622 sulphur-containing compounds that originate from cabbage, such as isothiocyanates and
623 nitriles (Supplementary Figure S1).

624 In fermented carrot, 52 volatiles were identified (**Supplementary Table S5**). They included
625 9 ketones, 9 aldehydes, 8 alcohols, 7 esters, 5 acids, 8 terpenes, 2 sulphur-containing
626 compounds and 4 other compounds. In addition, many other terpenes and terpenoids were
627 tentatively identified, e.g. γ -terpinene, terpinolene, 1,3,8-p-menthatriene, α -bergamotene,
628 caryophyllene, terpinen-4-ol, β -cyclocitral, (E)- γ -bisabolene, zingiberene, cis- β -farnesene, β -
629 curcumene, and β -sesquiphellandrene. These compounds come from carrot and were not
630 further considered in this stud. The abundance of 32, 22, and 3 volatiles were significantly (p-
631 value<0.01) impacted by the stage of fermentation, the type of cutting, and the salt
632 concentration, respectively, but there were some interactions between these factors. One third
633 of the volatiles (18 of 52) increased in concentration (p-value< 0.01; fold change T3/T0 >2). The
634 compound with the highest fold-change was ethyl lactate (> 6000). Nine volatiles, decreased in
635 concentration over time (p-value< 0.01; fold change T0/T3 >2), of which four aldehydes. The type
636 of cutting also significantly (p-value< 0.01, fold-change >2) impacted the amount of 6 volatile
637 compounds, which were all more abundant in grated carrot compared to sliced carrot. The
638 greatest fold-changes were for two terpenes, beta-myrcene and D-limonene, suggesting that
639 grating facilitated their release in brine compared to slicing. A PCA made to illustrate the global
640 results on volatile profiles showed that, as observed in fermented cabbage, the samples were
641 first separated according to their stage of fermentation on the first axis (25.8% of the total
642 variability), and on the 2nd axis (17.1% of the total variability) according to the cutting type, and
643 not differentiated depending on their salt concentration (Figure 6). Five clusters of samples were
644 distinguished based on the hierarchical clustering performed on PCA data (**Supplementary**
645 **Figure S2**). Cluster 1 was significantly (v-test > 2) associated with stage T1, rough cutting, and
646 high abundance of diacetyl, cluster 2 with thin cutting and high abundance of several terpenes,
647 such as beta-myrcene and D-limonene, cluster 3 with last stages of fermentation (T2a and T3),
648 and many volatiles (e.g. ethyl lactate, benzaldehyde, hydroxypropanone, and dimethyl
649 trisulfide). Clusters 4 and 5 each contained only one sample (a grated carrot at stage T2b and a
650 sliced carrot at stage T3), characterized by peculiar volatile profiles (Supplementary Figure S2).

651 Only 21 volatiles were shared by the two vegetables, including 7 aldehydes (pentanal,
652 hexanal, heptanal, octanal, hepten-2-al(Z), nonanal, and benzaldehyde), 4 esters (methyl
653 acetate, ethyl acetate, ethyl butanoate, and ethyl hexanoate), 3 alcohols (ethanol,
654 methylbutanol, and hexan-1-ol), 3 ketones (pentan-2-one, diacetyl, and acetoin), 3 acids (acetic,
655 octanoic, and nonanoic acids) and one sulphur-containing compound (dimethyl trisulfide).

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659 **Figure 6** PCA of volatiles identified in fermented cabbage (upper row) and fermented
 660 carrot (bottom row). The three maps of individuals are coloured and show the 95%
 661 confidence ellipses according to, first panel, the fermentation stage: T1 (40 h), T2 (2.7 day
 662 for carrot or 3.6 day for cabbage), T2a (9.7 days), T2b (15 days), T2c (22 days), T3 (one
 663 month), 2nd panel, the salt concentration : S0.8: 0.8% or S1: 1%, and 3rd panel, the type
 664 of cutting: thin or rough

665

666 **Mineral and vitamin concentrations**

667 NaCl concentrations in juices, calculated from Na concentrations, significantly varied
 668 according to the amount of added salt with, on average, 9.06 g/l and 7.08 g/l in 1%-salted and
 669 0.8%-salted samples, respectively. The differences in salt concentrations between the salt
 670 concentrations observed in juices and the targeted concentrations (0.8 and 1%) results from the
 671 composition of the coarse grey salt used to prepare the brines. Our results are consistent with
 672 the composition of coarse grey salt (e.g. 34 +/- 3 g Na per 100 g of product, i.e. 86.4 g NaCl per
 673 100 g of product). The differences between targeted and observed salt concentrations could
 674 also result from Na migration from the brine to the vegetables during incubation, thus
 675 decreasing its concentration in the juice. Significant concentrations of Mg were also brought in
 676 the initial brine by the coarse salt: 1 g of Mg for 78 g of Na. By comparing the total concentrations
 677 in juice and the concentration brought by the salt added, we calculated that the proportion of
 678 Mg coming from salt accounted for more than half of the total Mg content in juices (59%, and

679 64% in thinly- and roughly-cut carrot, respectively, and 51% and 59% in thinly- and roughly-cut
680 cabbages, respectively). We thus calculated the Mg concentration that originated from
681 vegetables only, called 'Mg_veg'. In contrast, the coarse salt used did not bring P and K, and
682 their proportions coming from the salt in juice were negligible (< 0.01% and < 0.09%,
683 respectively).

684 The mineral content in P, K, and Mg_veg (Mg coming from the vegetable, see above)
685 significantly (p-value < 0.001) differ in the two vegetables. Carrot juice contained 1.9 times more
686 P, 1.7 times more K, and 20% less Mg_veg compared to cabbage juice, with average
687 concentrations of P, K, and Mg_veg of 1793, 146, and 27 mg/L, respectively, in carrot, and 1068,
688 78 and 34 mg/L, respectively, in cabbage (**Supplementary Table S6**). During fermentation, the
689 concentrations of P and Mg_veg significantly (p-value < 0.01) increased in cabbage and carrot
690 juice, with 32% more P and 52% more Mg_veg after a 1-month incubation (T3) than at the
691 beginning of fermentation (stages T1-T2), showing a gradual migration of minerals from the
692 vegetable tissue to the juice. The contents in P, K, and Mg_veg were significantly (p-value <
693 0.001) higher in the juice of thinly-cut vegetables, with a greater effect in cabbage than in carrot.
694 Juices from shredded cabbage contained, on average, 32%, 18% and 20% more P, K, and
695 Mg_veg, respectively, compared to juices from leaf cabbage, while grated carrot contained 16%,
696 10% and 13% more P, K, and Mg_veg, respectively, than sliced carrot. The contents in P and K
697 were also globally slightly but borderline significantly (p-value < 0.06) higher in the more salted
698 samples, with on average, 8% and 16% more P in 1% salted carrot and cabbage juice samples,
699 respectively, and 5% and 9% more K in 1% salted carrot and cabbage juice samples,
700 respectively. Trace amounts of Se were also detected in carrot only, at concentrations < 0.040
701 mg/L.

702 The concentrations of the six vitamins analysed, expressed in mg or µg per 100 g of fresh
703 drained vegetable, and the content in dry matter are given in **Table 1**.

704 Cabbage globally contained higher amounts of vitamins. Concentrations in vitamins C and
705 B9 were 12-fold and 2.8-fold higher in cabbage than in carrot, on average, while vitamin K1 was
706 detected at ~4 µg/100g in cabbage and was under the detection level (< 3 µg/100g) in carrot.
707 Compared to raw cabbage, fermented cabbage contained about twice more vitamin C after 1
708 month, while in carrot, a slight but not statistically significant increase of vitamin C was
709 observed. In contrast, vitamin B9 and beta-carotene tended (p-value = 0.010) to decrease over
710 time. Regarding vitamins B12 and K2, which are not present in raw vegetables, they were not
711 produced or at too low amounts to be detected in fermented vegetables. Concerning the impact
712 of cutting size, roughly-cut vegetables were slightly, but significantly (p-value<0.03) more
713 enriched in vitamin C than thinly-cut ones (+19% and +43% in cabbage and carrot, respectively).
714 As for the effect of salt concentration, the content in vitamin C was slightly higher (+20%) in the
715 less salty carrot samples, while it was not significantly impacted by salt in cabbage. The vitamin
716 B9 decreased more in the 0.8%-salted than in the 1%-salted samples.

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Table 1: concentrations of vitamins C, B9, B12, K1, K2, of beta-carotene and content in dry matter in vegetables before (T0) and after one-month fermentation (T3). Values are mean and standard deviation of duplicate analyses (except for vitamins K1, K2 and B12 for which one analysis was done)

Sample	Code	Vitamin C mg/100g		Vitamin B9 µg/100g		β-caroten mg/100g		Vit K1	Vit K2	Vit B12	Dry matter, %	
		mean	sd	mean	sd	mean	sd	µg /100g	mg /100g	µg /100g	mean	sd
cabbage T0	300-T0	10.17	0.39	16.5	2.12	nd		3.9			10.3	0.2
cabbage T3 thin salt 0.8%	301-T3	19.13	1.01	14.0	2.83	nd		<3.0	<5	<0.1	18.3	1.2
cabbage T3 thin salt 1%	311-T3	20.44	0.67	17.0	1.41	nd		3.4	<5	<0.1	17.0	1.6
cabbage T3 rough salt 0.8%	321-T3	22.25	0.53	11.5	0.71	nd		4.3	<5	<0.1	17.6	0.8
cabbage T3 rough salt 1%	331-T3	24.79	2.63	17.5	0.71	nd		6.7	<5	<0.1	17.7	1.9
carrot T0	400-T0	1.05	0.11	7.65	0.07	11.3	0.3	<3.0			9.2	0.1
carrot T3 thin salt 0.8%	401-T3	1.31	0.22	2.35	0.07	8.0	2.4	<3.0	<5	<0.1	12.6	0.5
carrot T3 thin salt 1%	411-T3	1.20	0.16	8.65	1.77	9.8	1.5	<3.0	<5	<0.1	12.9	0.1
carrot T3 rough salt 0.8%	421-T3	2.04	0.02	1.35	0.21	9.3	1.5	<3.0	<5	<0.1	13.8	0.1
carrot T3 rough salt 1%	431-T3	1.54	0.02	1.65	0.07	0.4	1.3	<3.0	<5	<0.1	12.6	0.3

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vitamin concentrations are expressed in mg or µg per 100 g of fresh drained vegetable; sd: standard deviation; nd: not determined;

728 Metataxonomics results

729 The read numbers of sequenced samples ranged from 2,617 to 186,755, with a median value
730 of 29,203 and a mean of 43,484. All samples sequenced after T0 had more than 10,000 reads. A
731 total of 314 ASVs were obtained after 16S rRNA gene sequencing, and 2,640 ASVs after gyrB
732 sequencing, each with an abundance exceeding 0.005% of the total. In total, ASVs belonged to
733 98 different genera, of which 62 detected using gyrB only, 12 using 16S only, and 24 common to
734 both markers. The ASVs derived from gyrB sequencing enabled a higher taxonomic resolution,
735 with 132 species identified.

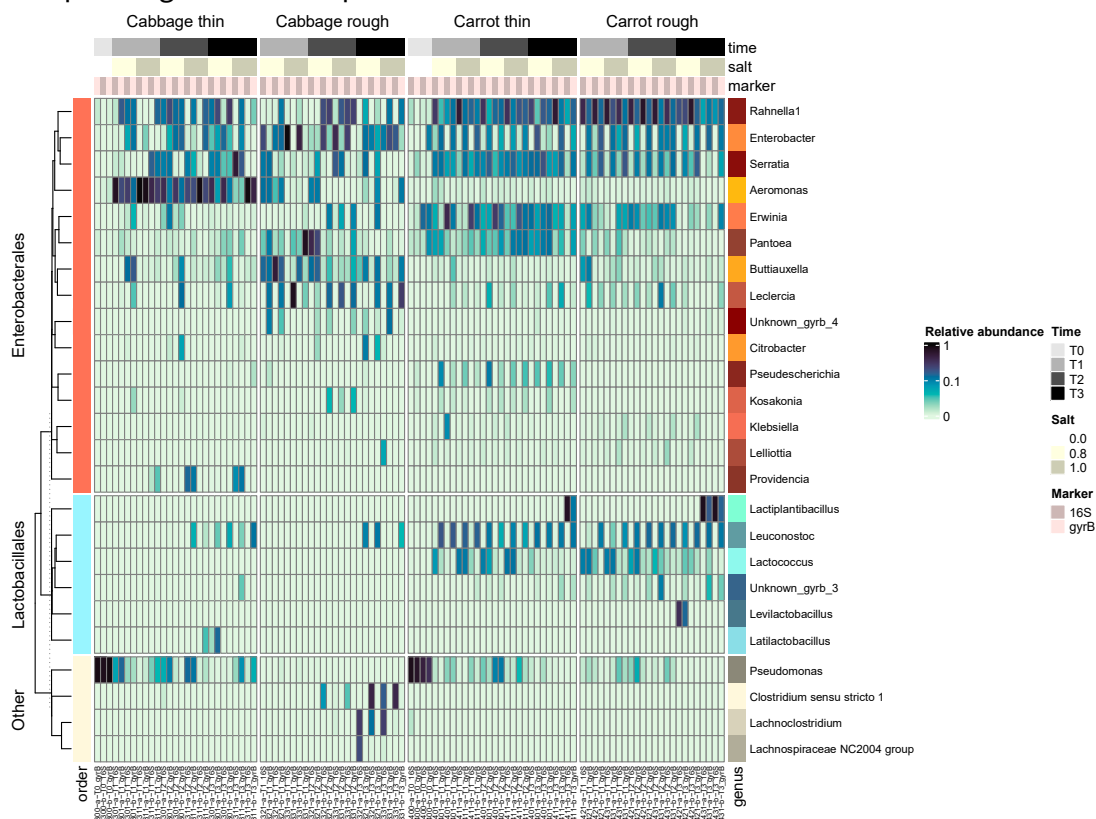
736 The two markers were used in parallel to define the taxonomic profile of the samples at the
737 genus level (**Figure 7**).

738 At T0, *Pseudomonas* largely dominated the bacterial community of both carrot and cabbage
739 samples. Then, taxonomic profiles shifted, and *Enterobacteriaceae* became predominant
740 (**Supplementary Figure S3**). Some genera were preferentially observed in shredded cabbage
741 (*Aeromonas*), leaf cabbage (*Buttiauxella*), or carrot (*Erwinia*) samples, while others were present
742 regardless of the vegetable (*Rahnella*, *Enterobacter*, *Serratia*). LAB appeared from T1
743 (*Leuconostoc*, *Lactococcus*) with *Lactiplantibacillus* or *Levilactobacillus* dominant at T3 in grated
744 and sliced carrot (except for sample 411-a-T3). In cabbage samples, the profile greatly differed,
745 depending on the type of cutting. *Leuconostoc* and *Latilactobacillus* were detected at T2 in
746 shredded cabbage, while *Clostridium* developed and became the main genus in leaf cabbage
747 (even if *Leuconostoc* was detected at T2). Therefore, the taxonomic profiles differed according
748 to the vegetable and the cutting type, especially for cabbage, but they did not appear as
749 impacted by the salt concentration.

750 The taxonomic profiles also varied according to the marker used (Figure 7, **Supplementary**
751 **Figure S3** and **Figure S4**). Some genera were similarly detected by both 16S and gyrB markers
752 (e.g., *Lactococcus*, *Aeromonas*, *Erwinia*, *Pseudomonas*), while others exhibited differential

753 detection patterns according to the marker. For example, the genus *Leuconostoc* was almost
 754 undetectable with the 16S marker but which was detected at a high abundance with the gyrB
 755 marker. Conversely, the genus *Clostridium* was scarcely detectable with the gyrB marker but
 756 detected with the 16S marker.

757 The gyrB marker higher resolution compared to the 16S marker made it possible to refine
 758 taxonomic profiles by identifying species (Figure 7), notably those relating to *Lactobacillales* and
 759 *Enterobacteriales*. Regarding *Enterobacteriales*, the species *Rahnella aquatilis*, *Enterobacter sp.*
 760 638, *Serratia sp. Leaf51* and *Pantoea agglomerans* were found in both cabbage and carrot
 761 samples. For LAB, *Leuconostoc mesenteroides*, *Lactococcus piscium*, and *Leuconostoc gelidum*
 762 were present in carrot samples from T1 onwards. At T3, *Lactiplantibacillus plantarum* and
 763 *Levilactobacillus brevis* were mainly observed. For shredded cabbage samples, *L. mesenteroides*
 764 and *Leuconostoc carnosum* were present from T2 onwards. *L. carnosum* and *Enterococcus*
 765 *faecalis* were observed for leaf cabbage samples at T3. Therefore, the taxonomic profiles at the
 766 species level also differed according to vegetable and cutting type, but they did not seem to be
 767 impacted by the salt concentration. Furthermore, it is worth noting that there were pronounced
 768 differences in taxonomic profiles between the duplicate jars of the carrot and cabbage samples
 769 at T0 (coded a and b). Among the 17 *Lactobacillales* species identified by gyrB sequencing, 10
 770 were common to the isolated bacterial strains: *L. mesenteroides*, *Lactiplantibacillus pentosus*,
 771 *Enterococcus faecium*, *L. brevis*, *L. carnosum*, *Latilactobacillus curvatus*, *E. faecalis*, *L. plantarum*,
 772 *Lactococcus lactis*, and *Enterococcus casseliflavus*. For instance, strains of *L. curvatus* were
 773 isolated from the samples 311-b-T2, 331-a-T2 and 301-a-T3 and were effectively detected with
 774 gyrB sequencing in those samples.



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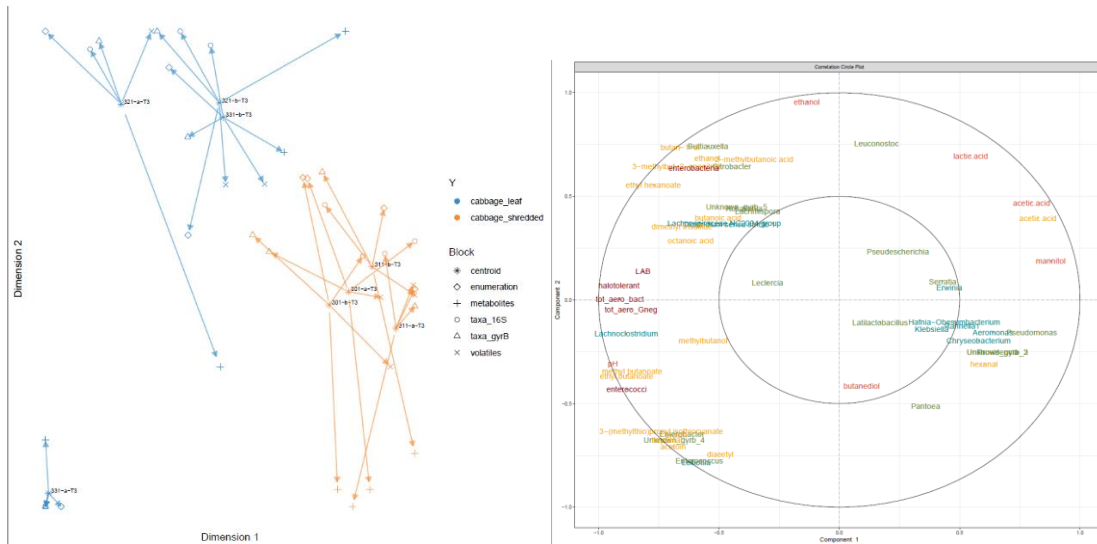
Figure 7: Heatmaps showing (A): the relative abundance of the 25 most frequently observed genera using both 16S rRNA and *gyrB* marker and (B) the relative abundance of the species detected with the *gyrB* marker. Taxa are coloured (*Lactobacillales* shown in different shades of blue, *Enterobacterales* in different shades of orange, and “other” in different shades of grey) and split according to their taxonomic order (*Lactobacillales*, *Enterobacterales* and “other”) and then clustered based on the Bray-Curtis dissimilarity. Samples are organised by vegetable and cutting types. Stage and salt level are indicated by an annotation at the side of the heatmap.

785 A multi-block Partial Least Squares-Discriminant Analysis (PLS-DA) was performed to
786 determine if samples exhibited different signatures after one-month fermentation (stage T3),
787 given their cutting type or salt concentration. The datasets included gyrB and 16S
788 metataxonomics profiles, concentration of the main metabolites from central metabolism
789 (lactic acid, ethanol, acetic acid, mannitol, butanediol), viable counts for six bacterial groups
790 and yeasts and some volatile compounds, selected because they result from different synthesis
791 pathways and showed marked changes in abundance during fermentation. Models based only
792 on cutting type did allow for the identification of a discriminant signature among the samples,
793 unlike the models based solely on salt concentration or on both salt concentration and cutting
794 type. The results of the PLS-DA on carrot and cabbage samples are shown in **Figure 8**. The model
795 discriminated the samples based on the cutting type according to variables belonging to the
796 different datasets (Figure 8).

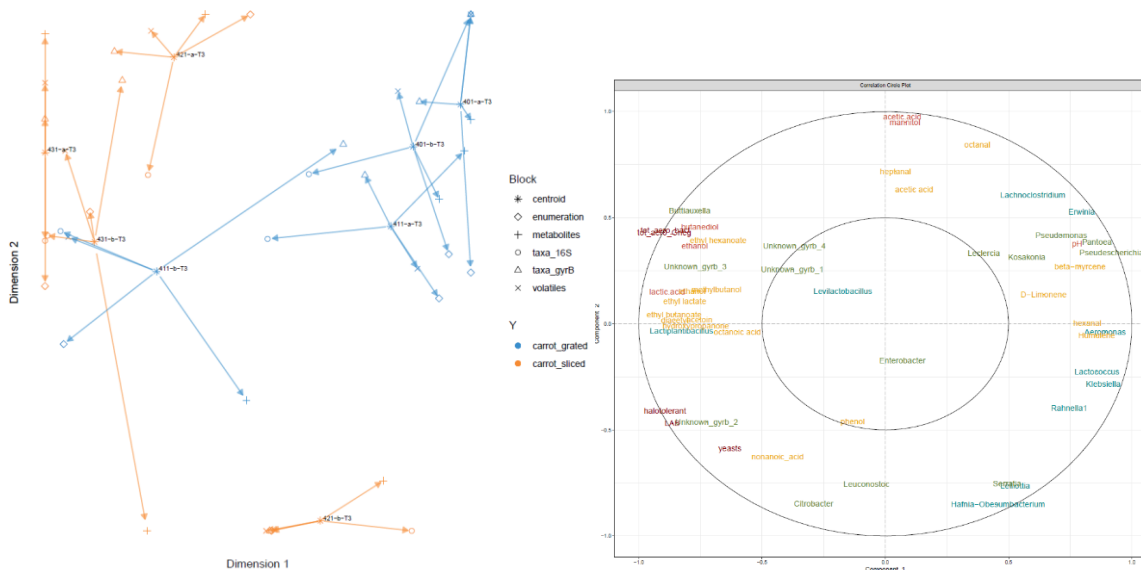
797 Regarding cabbage samples, the first dimension distinguishes the samples based on cutting
798 type across all datasets (p-value < 0.05 for all datasets, Wilcoxon test). Thinly-cut samples
799 exhibited a relatively homogeneous signature, characterised by high concentrations of acetic
800 acid, lactic acid and mannitol, a low pH, a higher abundance of *Leuconostoc*, and overall lower
801 bacterial viable counts. Roughly-cut cabbage samples showed a signature marked by high
802 ethanol concentrations, the presence of *Clostridium*, *Lachnoclostridium*, *Lachnospiraceae*, and
803 a higher abundance of *Buttiauxella*. One of the replicates of rough cabbage, 331-a-T3, is a
804 particular case with a higher abundance of *Enterococcus* and *Enterobacter*, and higher amounts
805 of acetoin and diacetyl compared with the three other roughly cut cabbage samples and lower
806 amounts of the main metabolites (mannitol, acetic and lactic acids).

807 For carrot, the first dimension distinguished samples based on cutting type only for the gyrB
808 and metabolite datasets, while the 16S, enumeration and volatile datasets failed in
809 discriminating the type of cutting of carrot samples at T3. Thinly-cut carrot samples had a
810 signature characterised by higher abundance of *Pseudodescherichia* while roughly-cut carrot
811 samples having a signature characterised by a higher abundance of *Buttiauxella* and higher
812 concentrations of lactic acid, ethanol and butanediol and a lower pH. The fermentation profiles
813 differed between carrot samples independently of their cutting type. For example, one thinly-
814 cut sample, 411-b-T3, showed a profile similar to that of two roughly cut samples (431-a-T3 and
815 431-b-T3) characterised by a lower pH, a higher abundance of *Lactiplantibacillus* and higher
816 concentrations of lactic acid, ethanol, acetoin, and diacetyl.

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821 **Figure 8:** Multiblock PLS-DA result for cabbage (upper) and carrot (bottom) samples at
 822 T3 (one-month fermentation). The left panels represent samples from multiple
 823 coordinates to assess the alignment in the latent space. The start of the arrow indicates
 824 the centroid between all data sets for a given sample and the tips of the arrows the
 825 location of that sample in each block. The right panels represent the correlation circle
 826 between each variable and the discriminant axes as a scatter plot. The variables
 827 corresponding to the microbial viable counts for the seven following targeted microbial
 828 groups are shown in brown: lactic acid bacteria (LAB), total aerotolerant bacteria
 829 (tot_aero_bact), halotolerant bacteria, aerotolerant Gram-negative bacteria
 830 (tot_aero_Gneg), yeasts, bile-tolerant *Enterobacteriaceae* (enterobacteria), and
 831 enterococci.

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Discussion

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836 **The experimental design allowed us to highlight a role of vegetable cutting despite a great**
837 **variability from jar-to-jar**

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The objective of the present study was to better understand the microbial dynamics and biochemical changes of spontaneous fermentation of vegetables by combining several omics approaches: culturomics, 16S rRNA gene and *gyrB* metataxonomics, and targeted metabolomics. More specifically, we aimed to investigate the effect of two factors, the type of cutting and a slight reduction of the amount of salt added, on the microbial and biochemical changes during fermentation. We chose both a root and a leafy vegetable, carrot and cabbage, which are commonly used for making fermented vegetables in France (Thierry, Madec, et al., 2023). However, the experiment was not designed to address the comparison of carrot and cabbage in itself, since the vegetable cultivar, culture conditions, harvest and storage conditions (time, temperature) can also impact their fermentation (Leff & Fierer, 2013). The impact of the cutting type or size has only been rarely addressed, although this factor can markedly vary, at least in domestic productions (Thierry, Madec, et al., 2023). Regarding the content of NaCl in food, the World Health Organisation has suggested reducing sodium intake by 30% to obtain the WHO guideline of 2 g day⁻¹ (i.e., 5 g of salt day⁻¹) by 2025 (World Health Organization. Regional Office for Europe, 2018). We chose to compare a salt concentration of 1%, which is the concentration of salt generally recommended, with a concentration of 0.8%, i.e. a 20% Na reduction. No significant differences in the microbial and biochemical changes were observed between these two salt concentrations, although mineral diffusion was slightly enhanced at the highest salt concentration (see below). As a direct consequence, quadruplicate samples instead of duplicate samples were available at each stage to investigate the effect of the other factors examined, i.e. the cutting and the fermentation stage. This high number of replicates was of great interest because we observed a large variability from jar-to-jar. Each jar exhibited its own fermentation path and showed some specificity regarding the microbial results, the profile of metabolites, and the acidification rate (Figures 2, 3, 4). Each jar was prepared by taking the required amount of cut vegetables from a large (~10 kg) bin, without previous mixing the bin content. Therefore, we hypothesise that the initial microbiota present in each jar differed from one another, in particular concerning LAB, which are highly sub-dominant or even under detection threshold in raw vegetables. Differences could also result from differences of composition between different carrots and different cabbages. The variations we observed were both quantitative, i.e. differences in the rate of fermentation, and qualitative, e.g. the nature of the dominant taxa that grew over time. For example, yeasts were detected in only 2 out of the 4 jars of leaf cabbage characterised at 40 h fermentation, metataxonomic profiles differed between replicates (Figure 7), and the metabolite profiles also showed quantitative and qualitative differences between replicates (Figure 3). In the industrial sauerkraut production, heterogeneity can occur in the tanks, and the juice is recirculated to avoid this source of potential defects (Pederson & Albury, 1969). Differences between replicates were also observed, but not discussed, in several studies, e.g. the results on 16S-based metataxonomics in fermented radish and carrot (Raghuvanshi et al., 2019), and in paocai (Wang et al., 2020; Wang, Chen, Tang, Ming, Huang, Li, Ye, Fan, Yin, et al., 2022). For example, the

877 abundance of *Enterobacteriaceae* according to the 16S rRNA gene metataxonomics ranged
878 between ~20% and ~80% in the triplicates of four-days fermented carrot and of one-day radish,
879 and high pH variations during the first two days of fermentation were also observed
880 (Raghuvanshi et al., 2019). These results stress the need to include a sufficient number of
881 replicates in studies on spontaneous vegetable fermentation, in particular for small-scale
882 fermentation.

883 **LAB quickly outcompeted bile-tolerant *Enterobacteriaceae* that dominate plant microbiota** 884 **at the beginning of fermentation**

885 For both studied vegetables, our culturomics as well as metataxonomic results confirm the
886 sequential establishment of the microbial community, with the presence of a large proportion
887 of *Pseudomonas* in raw carrot and the early development of bile-tolerant *Enterobacteriaceae*,
888 referred to as enterobacteria below. The dominance of *Pseudomonas* and enterobacteria during
889 the first hours of fermentation is consistent with the fact that these two groups constitute a large
890 part of plant surface microbiota (Lund, 1992; Leff & Fierer, 2013; Jackson et al., 2015).
891 *Pseudomonas* members are characterised by their great ability to colonise different ecological
892 niches and were recovered from a wide variety of 77 samples from 11 different vegetables (Ruiz-
893 Roldán et al., 2021). In the present study, viable enterobacteria were lower in raw carrot than in
894 raw cabbage, 4.3 and 6.0 log CFU/g, respectively, which may be due to the fact that carrots were
895 washed before use, in contrast to cabbages. Enterobacteria are largely represented in the
896 microbiota of fresh vegetables, e.g. at ~5.2 log CFU/g in 41 out of the 45 samples characterised,
897 which included carrot, cabbage, and five other fresh vegetables (Al-Kharousi et al., 2016). The
898 first shift conserved among different fermented vegetables was from the initial microbial
899 population of vegetables to *Enterobacteriales*, according to a recent integrative bioinformatics
900 approach used to perform a meta-analysis of 10 public amplicon data sets on fermented
901 vegetables (Junker et al., 2024). For example, members of the *Enterobacteriaceae* family that
902 included many non-affiliated taxa and *Erwinia* largely dominated on different vegetables,
903 according to a 16S-based metataxonomic analysis (Raghuvanshi et al., 2019).

904 Our results also confirm the early development of LAB, which manage to outcompete
905 *Pseudomonas* and enterobacteria notwithstanding their prevalence in raw vegetables. This is in
906 full agreement with the results of a bioinformatics meta-analysis on different fermented
907 vegetables, which showed that, after *Enterobacteriales* domination, a second shift led to an
908 assemblage dominated by *Lactobacillales*, i.e. LAB (Junker et al., 2024). This second shift was
909 observed for example in carrot juice (Wuyts et al., 2018), cucumber (Stoll et al., 2020), kimchi
910 (Song et al., 2020; Jung et al., 2022), and paocai (Wang et al., 2020). LAB are able to live as an
911 endophyte in a large variety of crop plants (Pontonio et al., 2018). In our study, viable LAB were
912 non-detectable in cabbage and their initial counts were 3 log CFU/g in carrot, in line with the
913 values of 2 to 4 CFU/g previously reported (Di Cagno et al., 2013). Plant endophytic communities
914 are dominated by *Gammaproteobacteria*, *Alphaproteobacteria* and *Actinobacteria*. *Firmicutes*
915 are sub-dominant and mainly represented by *Bacillales*, while *Lactobacillales* are generally
916 under 0.1% of relative abundance (Hacquard et al., 2015; Kõiv et al., 2019). LAB are often not
917 detected in the starting ingredients by metataxonomics, as shown in sauerkraut manufacture
918 (Zabat et al., 2018). The selective pressure of the environmental conditions that result from the
919 fermentation process applied, in particular the anaerobic conditions, indeed favours the growth

920 of LAB to the detriment of enterobacteria (Yu et al., 2020). LAB growth leads to a significant
921 acidification of the environment, thus inhibiting the growth of enterobacteria, which do not
922 withstand the acidic pH (Ostling & Lindgren, 1993). Concomitantly with acidification, we
923 effectively observed a drastic reduction in viable enterobacteria, which were no more detected
924 by plate counting after two weeks in 3 of the 4 conditions studied, i.e. in shredded cabbage and
925 both thinly and roughly-cut carrot, which were characterised by a pH < 4.0 and a titratable
926 acidity > 0.45. These results are in line with the safety threshold recommended by the Codex
927 Alimentarius standard for pickled fruits and vegetables, which stipulates that the product has
928 to be prepared and packed “to ensure an equilibrium pH of less than 4.6” (FAO, 2007). Our
929 results further illustrate the ubiquitous nature of LAB in food fermentation, thanks to their
930 ability to rapidly ferment different carbohydrates into lactic acid (Gänzle, 2015). Besides the
931 inhibitory activity of the organic acids they produce, LAB could also inhibit enterobacteria
932 through the synthesis of antimicrobial peptides, since many of the species found in our study
933 are known to potentially produce bacteriocins (Zacharof & Lovitt, 2012; Hernández-González et
934 al., 2021). A low proportion of LAB compared to that of *Enterobacteriaceae* was observed using
935 metataxonomics in the present study, even after one month of fermentation, in particular in
936 fermented cabbage. In a previous study using the same methods to characterise domestic
937 samples of fermented vegetables, metataxonomics results showed that LAB had a median
938 abundance of 90%, mainly represented by members of the *Lactobacillaceae* family, and that
939 *Enterobacterales* was the 2nd main taxon (Thierry, Madec, et al., 2023). Moreover, a negative
940 relationship was observed between the abundance of *Enterobacterales* and the age of the
941 samples. The lower LAB abundance observed in the present study could thus be explained by
942 the age of sample, one month maximum in the present study versus a median duration of 6
943 months (from 2 weeks to 4 years). Similarly, in a study on paocai fermented at 15°C and 25°C
944 during one year, LAB dominated, representing about 60% of the total abundance, with (former)
945 *Lactobacillus* as dominant genus (Wang et al., 2020).

946 The first LAB species that grew in both vegetables of the present study were
947 heterofermentative species, *Leuconostoc sp.* and *L. lactis*, in agreement with previous reports in
948 other fermented vegetables, such as paocai (Wang, Chen, Tang, Ming, Huang, Li, Ye, Fan, Chi, et
949 al., 2022). Heterofermentative LAB are capable of degrading a wide variety of carbohydrates
950 (Gänzle, 2015) and *Leuconostoc* efficiently metabolises sucrose (Cogan & Jordan, 1994).

951 The choice of the metataxonomics markers markedly impact the picture of the bacterial
952 community. Metataxonomics using both 16S rRNA and *gyrB* genes as markers helped us to
953 describe the changes in bacterial community during fermentation. The *gyrB* marker, although
954 rarely used in metataxonomics, provides species-level taxonomic resolution in food ecosystems
955 (Poirier et al., 2018), as effectively observed in the present study. For the 16S marker, the V3-V4
956 region is the most commonly used in the field of food microbiology (Parente et al., 2022), but we
957 chose the V5-V7 region in the present study to compare the results with that of our previous
958 study on fermented vegetables (Thierry, Madec, et al., 2023). Both markers confirmed the
959 succession of *Enterobacteriaceae* and LAB, except in some roughly-cut cabbage samples.
960 However, the *gyrB* marker uniquely detected *Leuconostoc* as the first LAB genus which
961 appeared, which is also confirmed by the results of the culture-dependent approach. In three
962 roughly-cut cabbage samples, the 16S marker uniquely detected *Clostridium* taxon. The
963 detection of this undesirable genus is important since some *Clostridium* can be responsible for

964 food poisoning. We however failed in finding reports on clostridia-related poisoning associated
965 with the consumption of fermented vegetables.

966 **Metabolites of fermented products as markers of microbial activity**

967 In the present study, the compounds analysed were carbohydrates, organic acids, alcohols
968 and volatile compounds. Among metabolites, mannitol, lactic and acetic acids were the main
969 metabolites produced, in agreement with previous reports on fermented carrot juice (Wuyts et
970 al., 2018) and on sauerkraut (Plengvidhya et al., 2007; Tlais et al., 2022). Mannitol, lactic acid,
971 and acetic acid respectively accounted for about 45-55%, 22-30%, and 10-12% of total
972 metabolites in carrot and shredded cabbage after one-month fermentation. These proportions
973 are similar to those reported in carrot juice (Wuyts et al., 2018), sauerkraut (Plengvidhya et al.,
974 2007), and other fermented vegetables as kimchi (Jung et al., 2011). These metabolites are
975 typical markers of LAB metabolism. Heterofermentative LAB, as the *Leuconostoc* members
976 identified in both cabbage and carrot, convert fructose into mannitol (Wisselink et al., 2002;
977 Martínez-Miranda et al., 2022). They also convert other carbohydrates into lactic acid, acetic
978 acid, and ethanol, while homofermentative LAB convert carbohydrates into lactic acid as the
979 main end-product. In our study, the ratio of lactic and acetic acids after one month of
980 fermentation varied from one jar to another, from 1.5 to 5 in fermented cabbage and 1.7 to 4.3
981 in carrot. Butanediol was also detected in fermented samples, at markedly variable
982 concentrations. Butanediol can be produced from acetoin by *L. mesenteroides* and
983 *Lactobacillus sakei*. For example, metatranscriptomic analyses in kimchi showed that genes
984 encoding the pathway from pyruvate to diacetyl/acetoin and butanediol were expressed during
985 kimchi fermentation (Chun et al., 2017; Kim et al., 2020). Concerning volatiles, most of them
986 cannot be used as specific markers of microbial activity, because their pathways of formation
987 are shared by many bacteria groups. For example, isothiocyanates, thiocyanates, and nitriles
988 were detected by GC-MS in fermented cabbage samples (Table S3). These sulphur-containing
989 compounds derive from the glucosinolates present in cabbage, which were completely
990 degraded after one month fermentation (results non shown), as previously reported (Wieczorek
991 & Drabińska, 2022). Even if some LAB strains can hydrolyse glucosinolates into nitriles, other
992 bacteria like enterobacteria also do it (Mullaney et al., 2013). Moreover, the activity of plant
993 myrosinase also results in glucosinolate hydrolysis, and is favoured by both the cutting of
994 vegetable, which releases glucosinolates and myrosinase from separated cell parts, and by the
995 pH decrease, favourable to myrosinase activity (Wieczorek & Drabińska, 2022). As for biogenic
996 amines, which are mainly produced by *Enterobacteriaceae* from amino acid decarboxylation
997 (Halász et al., 1994), they were not analysed in the present study. Total concentrations of
998 biogenic amines can reach from ~50 to ~600 mg/kg in different fermented vegetables (Świder et
999 al., 2020).

1000 **The fermentation rate of cabbage and carrot markedly differed in the present study**

1001 Carrot and cabbage fermentation exhibited a similar succession of the main bacterial
1002 groups, with *Enterobacteriaceae* quickly replacing the initial microbiota, further replaced within
1003 a few days by LAB, as detailed above. The main differences between the two vegetables used,
1004 in the present study, concerned the rate of fermentation. Despite a similar profile of metabolites

1005 in carrot and cabbage, with mannitol, lactic acid, and acetic acid as main products, the
1006 concentrations produced in carrot were two-fold higher than in cabbage (Figure 3).

1007 Many factors can be involved in the differences observed between carrot and cabbage,
1008 among which the specific microbiota of the vegetables used, the microbial changes during the
1009 processing steps. e.g. the washing of carrot vs only the removal of the external leaves of
1010 cabbage, and the composition of vegetables in macro- and micronutrients. Carrot generally
1011 contain 1.4-fold higher amounts of carbohydrates than cabbage (Anses, 2020), which likely
1012 explains why the concentrations in the main metabolites were higher in the juice of the former
1013 than in the latter one. Carrot and cabbage juice composition also differ in terms of
1014 micronutrients, which may also influence the development of micro-organisms. For example,
1015 our carrot juices contained more P and more K than cabbage, and similar amounts of Mg, while
1016 cabbage globally contained more vitamins. However, besides the type of vegetable, many other
1017 factors, such as the vegetable cultivar, its stage of harvest and storage time, and other factors,
1018 can influence their microbial and biochemical composition. As a result, the differences observed
1019 in the present study between carrot and cabbage fermentation should not be generalised.

1020 **A thin cutting favours the release of solutes and increases the fermentation rate**

1021 The cutting of vegetables before fermentation varies from thinly grated to large pieces of
1022 vegetables in domestic productions, as stated above, but the effect of cutting, to our best
1023 knowledge, has been scarcely studied. The “degree of disintegration” was cited, besides the
1024 temperature and the type of vegetable, among the factors that influence the fermentation
1025 (Buckenhueskes, 1993; Buckenhueskes, 2015). The nutrients present inside the vegetable cells
1026 must be released in the aqueous phase, i.e. juice, to be made available to the microorganisms
1027 via shredding, slicing, or only piercing, depending on vegetables (Buckenhueskes, 2015). The
1028 thinner the cutting, the higher the surface of cut plant tissue that can directly release vegetable
1029 solutes in brine, thus providing LAB with nutrients and increasing the buffering capacity of brine.
1030 Solutes can also diffuse from entire, free from injury, vegetables, as described in cucumber, but
1031 at a lower rate (Passos et al., 2005). In a study that aimed at modelling the equilibrium of solutes
1032 between the brine and entire cucumber, either peeled or not, it was shown that the diffusion
1033 coefficient of glucose was 9.2 times higher for peeled cucumber than for unpeeled one (Potts et
1034 al., 1986). The latter study suggests that the surface of cut tissue is an important factor to
1035 promote the diffusion of solutes into the brine. We therefore calculated the surface of cut
1036 vegetable, by estimating the mean dimension of the pieces of vegetables used in the present
1037 study, assimilated either to cylinders (entire, sliced and grated carrot), or to parallelepipeds
1038 (cabbage leaf pieces and shredded cabbage). Moreover, the experimental mass of vegetable
1039 and brine weighted per jar differed depending on the vegetable and the cutting, thus resulting
1040 in differences of the ratio of vegetable vs brine, which varied from 0.73 (leaf cabbage), 0.94
1041 (shredded cabbage), 1.24 (sliced carrot) to 1.33 (grated carrot). Based on these ratios and the
1042 estimations of the surface of cut tissue, we calculated the cut surfaces per g of initial brine,
1043 which were approximately 0.4 cm², 8 cm², 9 cm², and 19 cm², for leaf cabbage, sliced carrot,
1044 shredded cabbage, and grated carrot, respectively, as detailed in **Supplementary Table S7**. In
1045 other words, the cut surface of the thinly-cut cabbage was approximately 26-fold higher than
1046 that of roughly-cut cabbage, while it was only 2-fold for the thinly-cut carrot compared to
1047 roughly-cut one. We therefore hypothesised that these marked differences of the cut surface

1048 could, at least partly, explain why, in the present study, the two cutting types of cabbage
1049 markedly differed in the rates of acidification and viable enterobacteria decrease, in contrast to
1050 the slighter differences observed between sliced and grated carrots (Figure 2).

1051 The hypothesis of a greater diffusion of vegetable solutes into brine for thinly-cut vegetables
1052 is further supported by our results of the mineral composition of juices. First, juices contained
1053 18-32% more minerals (K, P, and Mg) coming from the vegetable tissue in shredded than in leaf
1054 cabbage, and 10-16% more in grated than in sliced carrot. Secondly, carrot juices contained
1055 more P and K than cabbage juice, although white cabbage is expected to be as rich in K and 1.5
1056 richer in P compared to carrot, according to Ciqual data (Anses, 2020), thus suggesting a higher
1057 global diffusion from vegetable into juice in the case of carrot, for which the cut surface was
1058 greater. As a result, we can hypothesise that the buffering capacity of the juice was higher for
1059 thinly-cut vegetables compared to roughly-cut ones. This assumption is consistent with the fact
1060 that, for a given pH, TTA was higher in thinly-cut vegetable. For example, TTA was twice as high
1061 in grated carrots at T1, compared to sliced carrots, despite a similar pH. The effect of cutting
1062 was previously studied to compare the survival of pathogenic strains during fermentation of
1063 cabbage either kept as whole heads or shredded (Niksic et al., 2005). The authors attributed the
1064 lower survival observed in shredded cabbage to the significantly higher total titratable acidity
1065 in shredded cabbage juice compared to the one of whole head cabbage, in relation to the higher
1066 buffering capacity of the juice. The importance of the buffer capacity of vegetable juice has been
1067 previously highlighted. A pioneer study showed that the composition of cucumbers depended
1068 on their size, the. Smaller fruit, however, contain lower levels of sugars and a higher natural
1069 buffering capacity than larger ones and achieved a complete sugar utilisation during
1070 fermentation (Lu et al., 2002). Buffer models were later developed in cucumber juice of different
1071 composition, so as to be capable of assessing the relationship between pH and the
1072 concentration of acids (Breidt & Skinner, 2022).

1073 The addition of salt is known to withdraw nutrients from the vegetable tissue towards the
1074 juice. We effectively observed, in the present study, a slight but significant effect of the amount
1075 of added NaCl on the release of P and K in the juice (+ 5-8% in carrot, and + 9-16% in cabbage).

1076 In the case of leaf cabbage, which had by far the smallest cut surface, we also observed faulty
1077 fermentation. For example, on the four jars of leaf cabbage characterised after one month
1078 fermentation, two still contained alive enterobacteria (321-a and 331-b), the third (321-b)
1079 contained lower viable LAB counts (7.6 log CFU/mL) and a high content in ethanol (5.2 g/mL vs
1080 1.6 g/mL in all other samples at that stage) and for the fourth one (331-a), the whole lactic
1081 population consisted of enterococci, associated with an atypical metabolite profile without
1082 mannitol (Figures 2, 3, and 4) and a distinct volatile profile, with for example the highest
1083 amounts of esters of butanoic acid. These four samples also contained *Clostridium* (321b, 331a,
1084 331b) and/or *Lachnoclostridium* (321a, 321b, 331a) taxa. The mean pH of these four samples was
1085 4.0, versus 3.6 at the same stage in all other samples. It is noteworthy to mention that many leaf
1086 cabbage samples had a very unpleasant and atypical smell. We therefore hypothesise that the
1087 cutting of cabbage into large leaf pieces was insufficient to provide LAB enough nutrients and
1088 that there could exist a threshold cut surface under which a rapid lactic fermentation is hardly
1089 achieved.

1090 In brief, a fine cutting, besides salting, favours the release of solutes towards the juice, thus
1091 providing microorganisms the nutrients they need to grow, and increasing the buffer capacity

1092 of brine. Consequently, a quicker acidification, a higher titratable acidity, and quicker decrease
1093 of the number of viable enterobacteria can be expected, as effectively observed in the present
1094 study in particular for cabbage, for which the surface generated by the cutting step was much
1095 greater (> 20-fold) in shredded cabbage than in leaf cabbage. The difference of salt
1096 concentration also intensified the release of solutes, as observed in the present study for some
1097 minerals, but the possible consequences on microbial growth were probably masked by the
1098 variability observed from jar-to-jar. In line with the importance of the buffer capacity, the
1099 targeted values of both the pH (< 4) and titratable acidity (1%) are given in the specifications for
1100 the protected geographical indication of “Sauerkraut of Alsace”, to satisfy safety and sensory
1101 property requirements (EU Commission implementing regulation, 2018).

1102 **Some health benefits and risks associated with fermented vegetables consumption**

1103 Besides the preservation of vitamins, discussed below, fermented foods have been
1104 associated with potential health benefits, which result from two main factors. The first is the
1105 microbial production of metabolites of interest for human nutrition, e.g. vitamins, bioactive
1106 peptides, or that can positively affect human health, e.g. mannitol, γ -aminobutyric acid (Lenhart
1107 & Chey, 2017). The second is the presence of live microorganisms that can interact with the
1108 intestinal microbiota (Rezac et al., 2018). Initially much explored for dairy-based fermented
1109 foods (Kok & Hutkins, 2018; Companys et al., 2020) and the Korean kimchi (Cha et al., 2023), this
1110 is now also well demonstrated for other non-dairy foods (Wuyts et al., 2020; Valero-Cases et al.,
1111 2020).

1112 On the other hand, in the case of poorly controlled production, the consumption of altered
1113 fermented products can lead to health risks. Concerning fermented vegetables, the high
1114 number of enterobacteria present at the beginning of fermentation is associated with the risk
1115 of toxin and biogenic amine production. The presence of spore-forming bacteria, among which
1116 toxin producers such as some *Clostridium* sp., has also been reported. In a recent South Korean
1117 quantitative risk assessment study for *Clostridium perfringens* foodborne illness via kimchi
1118 consumption, the authors conclude that the risk was “very low” (Choi et al., 2020).
1119 Enterobacteria disappear as soon as the pH is low enough for a period of time, and not all of
1120 them present hazards. For example, in the present study, we mainly identified *Hafnia alvei*
1121 among the clones isolated on the VRBG medium from the leaf cabbage samples in which
1122 enterobacteria were alive after one-month fermentation. *H. alvei* is commonly isolated from and
1123 even used as an adjunct culture in raw milk Camembert cheese. One of the leaf cabbage samples
1124 also contained clostridia. Fortunately, all these samples would not have been consumed
1125 because they had a very unpleasant odour.

1126 We focused in this study on the vitamin content in raw vegetables and after fermentation.
1127 According to literature, the final concentration in fermented vegetables of the vitamins first
1128 depends on their initial concentration in raw vegetables, even if fermentation can result in
1129 variations in their vitamin content. The vitamin concentration has been shown to decrease
1130 during fermentation in most of the reported cases, as stated in a recent literature review
1131 (Thierry, Baty, et al., 2023). The contents in vitamins C and K1 and beta-carotene in raw carrot
1132 and/or cabbage observed in the present study are in accordance with the expected values from
1133 nutritional food tables, while the vitamin B9 content was in the lower range of the reported
1134 values (Anses, 2020). We only observed an increase for the vitamin C content during

1135 fermentation, which may be due to microbial activity of ascorbigen degradation (Berger et al.,
1136 2020). In contrast, vitamin B9 content was not improved, in agreement with previous report
1137 (Jägerstad et al., 2004). Vitamins K2 and B12 are absent from raw vegetables and can result from
1138 microbial synthesis. Vitamin K2 is mainly present in fermented foods (Walther & Chollet, 2017)
1139 and can be synthesised by some LAB strains (Capozzi et al., 2012). Vitamin B12 is present in foods
1140 of animal origin (National Institutes of Health) and can also be synthesised by some bacteria as
1141 propionibacteria (Falentin et al, 2010). We did not observe the production of vitamins K2 and
1142 B12 in the present study. In the context of human nutrition, vitamin contents were expressed in
1143 the present study per quantity of fresh matter of fermented vegetables (without brine), i.e. as
1144 they are generally consumed. In our study, cabbage and carrot remained a good source of
1145 vitamin C and beta-carotene, respectively, after fermentation, since they bring 24 to 31% of
1146 nutritional value of reference in vitamin C for 100 g of fermented cabbage and 167 to 204 % of
1147 pro-vitamin A (in beta-carotene form) for 100 g fermented carrot.

1148

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1165

Conflict of interest disclosure

1166 The authors declare that they comply with the PCI rule of having no financial conflicts of
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1168

Data, scripts, code, and supplementary information availability

1169 The sequence data for this study have been deposited in the European Nucleotide Archive
1170 (ENA) at EMBL-EBI and are available online: PRJEB79032 on the webpage hosting the data
1171 <https://www.ebi.ac.uk/ena/browser/view/PRJEB79032>.
1172

1173 Supplementary information including data, and scripts is available online: DOI of the webpage
1174 hosting the supplementary information <https://doi.org/10.57745/MJWSJQ>; Thierry et al., 2024.

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