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Metabolic and functional paths of lactic acid bacteria in plant foods: get out of the labyrinth

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Even though lactic acid bacteria are only a small part of the plant autochthonous microbiota, they represent the most important microbes having the capability to promote significant changes in the health-promoting properties of plant foods. Owing to the variety of plant chemical components and the possible pathways for bioconversion, plant fermentation is like a metabolic labyrinth undertaken by bacteria. The winding metabolic pathways involve several secondary plant metabolites (e.g. phenolics). The success of these paths is connected to the adaptive growth and survival of lactic acid bacteria. A panel of various interacting omics approaches unraveled the specific traits of lactic acid bacteria to adapt to plants, which allow the optimal design of fermentation strategies for targeted raw matrices.

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Introduction

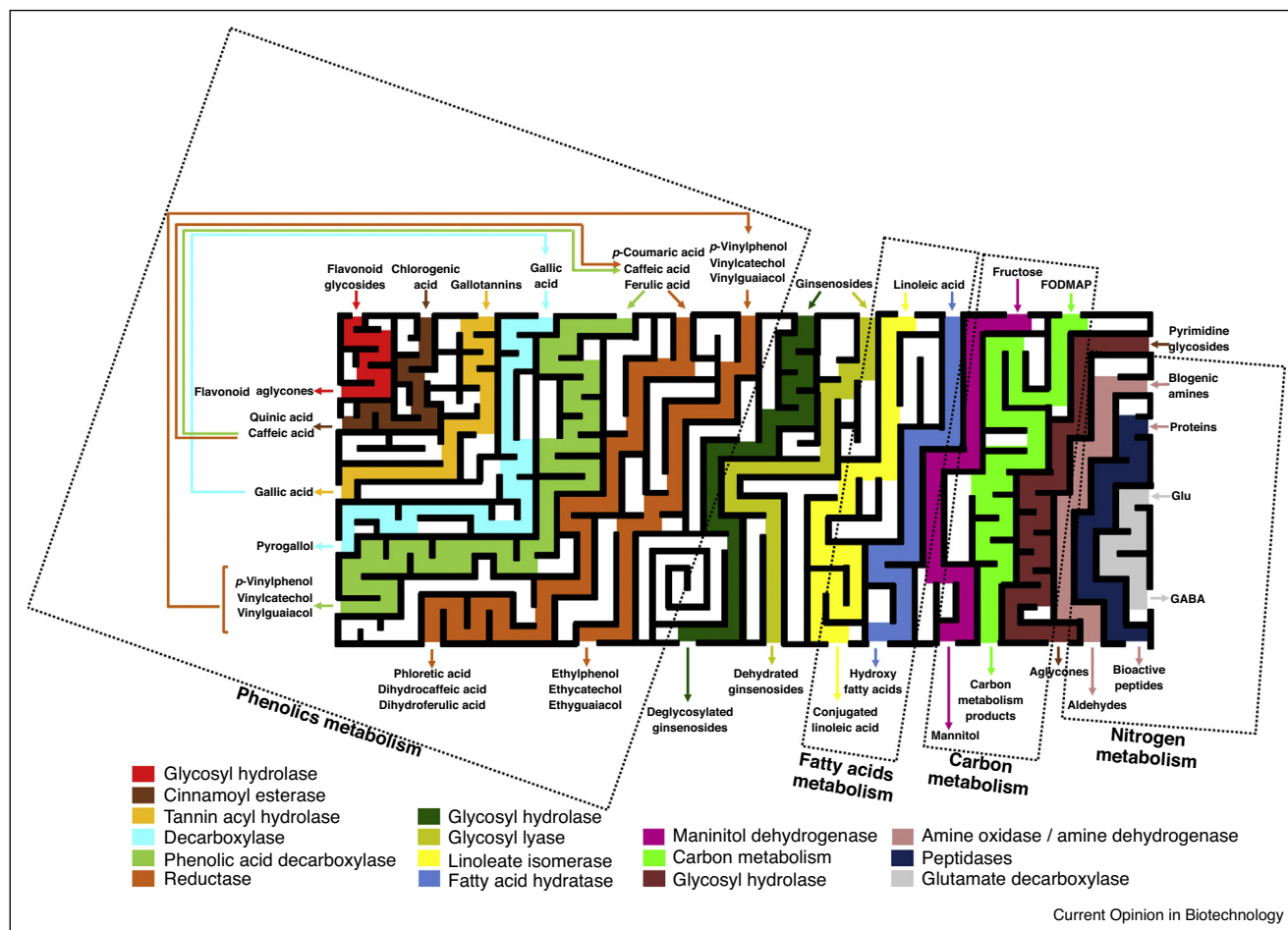
Fermentations may lead to significant changes to the health-promoting features to plant foods. The lactic acid fermentation is the most widespread. Nowadays, it is not an ancient method of food preservation, but a well-designed biotechnology for manufacturing functional foods [1]. The axis ‘fermented plant foods — human health’ is easily conceivable because of the inherent chemical composition of raw plant matrices, and the metabolic and functional versatility of lactic acid bacteria (LAB) [2]. Plants are excellent sources of health promoting components (e.g. vitamins, minerals, antioxidants, phenolics, and dietary fibers). They also contain various levels of anti-nutritional factors (e.g. oxalate, protease, and α -amylase inhibitors, lectins, condensed tannins, and

phytic acid). Such plant inherent reservoirs enable LAB to follow various metabolic routes, which figure as a complex labyrinth (Figure 1). Each plant labyrinth path involves specific bacterial enzymes for targeted substrates. The bacterial capability to follow the metabolic paths is species-specific or strains-specific and depends on their portfolio of enzymes. The way out of the labyrinth coincides with the success of those paths, resulting in fermented plant foods enriched with high bioavailable bioactive compounds and/or with weak amounts of anti-nutritional factors. This review will highlight how LAB may successfully drive the plant fermentation toward functional products with health-promoting features, and the metabolic labyrinth underlying the bacterial role within the biotechnology process. Despite the multitude of metabolic pathways that may potentially affect the health-promoting properties of plant foods, only the most innovative and relevant findings will be deepened.

Which lactic acid bacteria may perform metabolic labyrinth paths under plant-like conditions?

All plant-associated microenvironments contain a diversity of beneficial and pathogenic microbes, which are of pivotal importance for plant nutrition, health status and defense. Despite an immeasurable arsenal of microbes [3], each plant harbors a distinctive microbiota, where LAB represent only a small part ($2\text{--}4 \log \text{cfu g}^{-1}$) [4,5]. Hetero-fermentative and homo-fermentative species, belonging to *Leuconostoc*, *Lactobacillus*, *Weissella*, *Enterococcus* and *Pediococcus* genera, are those most frequently identified as epiphytes within the microbiota, depending on the plant species. Despite this diversity, *Weissella cibaria/confusa* and, especially, *Lactobacillus plantarum* are the species most frequently found [5]. Although reports on the endophyte populations of LAB are relatively scarce, advances on plant–microbe interactions have highlighted their importance as a new class of plant growth promoting microbes [6]. To date, *L. plantarum* was the only endophytic lactic acid bacterium identified throughout the life cycle of the oregano and wheat plants [7] [Pontonio *et al.*, unpublished data]. For manufacturing fermented plant-based foods having health-promoting properties, starter cultures must be equipped with a dedicated portfolio of enzymes, which enable them to undertake the paths successfully. Usually, these have to be selected among the LAB species that mainly dominate the spontaneous plant fermentation such as *Leuconostoc* spp., *L. plantarum*, *L. pentosus* and *W. cibaria* [5,8,9]. The capability to adapt to the intrinsic features of the raw plant

Figure 1



The metabolic and functional labyrinth followed by lactic acid bacteria during plant foods fermentation. Each colored pathway represents a potential route to release biogenic compounds or to remove antinutrients.

matrices and to persist stably as endophytes throughout plant phenological stages represent additional criterions for selecting robust LAB candidates. Within the LAB, fructophilic lactic acid bacteria (FLAB) represent novel potential sources of functional attributes [10]. FLAB belong to a special group that prefer fructose instead of glucose as a carbon source, and are mainly isolated from fructose-rich niches such as fruits, fruits-based and flowers-based fermented foods, and gastrointestinal tract of honeybees [11].

Molecular adaptation of lactic acid bacteria to plant niches

The fermentation of plant substrates relies on the capability of LAB to rapidly adapt and metabolize the available nutrients. Adaptation to vegetable and fruit ecosystems is species and strains-specific, and markedly varied depending on the plant niche. This is due to the diversity of the plant environments, and to the incidence of

inherent chemical and physical parameters such as the prevalence of inhibitory factors (e.g. phenolics), the lacking of fermentable carbohydrates, the induction of osmotic stress, and the acidic environment, that may lead to harsh conditions for bacterial growth. The importance of the adaptation responses as well the activation of specific metabolic pathways that affect the sensory, nutritional and functional features of fermented plant matrices has stimulated extensive research. The adaptive growth and survival strategies of LAB during plant fermentation, with the main focus on *L. plantarum*, have been recently investigated through a panel of various interacting omics approaches, including metabolomic, phenomic and transcriptomic profiling [12,13^{**},14^{**}]. In particular, a collection of transcriptional datasets has been generated under biologically relevant conditions reproducing the plant niches. The specific traits of LAB to adapt to plants have been unraveled, which allow the optimal design of fermentation strategies for targeted raw matrices (Table 1).

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