

Dynamics of Sourdough Microbiome Assembly: A Berlin-Specific Microbiological Framework for Culture Initiation and Stabilization

Introduction to Sourdough Microbial Ecology and Metagenomic Origins

The initiation and stabilization of a sourdough starter—technically defined as a Type I sourdough—represents one of the most complex, multi-species solid-state fermentations in human culinary history. Unlike commercial bread production, which relies entirely on the monocultural inoculation of highly adapted, industrial *Saccharomyces cerevisiae* strains, traditional sourdough is a spontaneous microbial ecosystem¹. The creation of this ecosystem from raw flour and water triggers a highly orchestrated sequence of microbiological succession, biochemical enzymatic degradation, and macroscopic rheological transformation. A pervasive culinary mythology attributes the origin of sourdough microorganisms to the "capture of wild yeast and bacteria from the air." However, rigorous quantitative metagenomic analyses and 16S rRNA amplicon sequencing unequivocally demonstrate that the primary inoculation vectors are the endophytic and epiphytic microbiota inherent to the cereal grain itself¹. While the localized "house microbiota" of the mixing environment and the baker's hands contribute to the overall diversity, the flour is the undisputed ecological driver³. The creation of a sourdough starter is therefore not a process of environmental capture, but rather an exercise in targeted ecological succession. The operator must manipulate abiotic parameters—specifically hydration, nutrient availability, and temperature—to suppress opportunistic spoilage organisms and select for a climax community of acid-tolerant Lactic Acid Bacteria (LAB) and wild yeasts⁶.

This analysis provides an exhaustive microbiological and biochemical framework for initiating and stabilizing a Type I sourdough culture, contextualized specifically within the geochemical and agronomic realities of Berlin, Germany. By examining the interplay of Berlin's unique hydrological chemistry, German flour typologies, microbial growth kinetics, and specific metabolic pathways, this report delineates the precise mechanisms required to cultivate a robust and predictable fermentative matrix.

The Geochemical and Agronomic Context of Berlin

The successful establishment of a resilient sourdough microbiome is inextricably linked to the raw substrates introduced into the matrix. In the context of Berlin, two primary variables exert profound selective pressures on the developing microbial community: the regional water chemistry and the highly standardized German flour typologies.

Hydrological Profile: The Buffering Capacity of Berlin Water

Berlin's municipal water supply, sourced primarily from groundwater and bank filtrate drawn from the River Spree and Havel, is geochemically classified as "hard" to "very hard"⁸. This mineralogical reality fundamentally alters the acidification kinetics of a developing sourdough starter.

Geochemical Parameter	Concentration / Value	Implications for Sourdough Fermentation Kinetics
Total Hardness	~250–303 mg/L CaCO ₃ (14–17 °dH)	Extremely high mineral content resists rapid pH shifts, stabilizing early microbial populations.
Calcium (Ca ²⁺)	110–116 mg/L	Enhances alpha-amylase stability and strengthens the developing gluten network via ionic bridging.
Hydrogen Carbonate	254–262 mg/L	Imparts a massive buffering capacity, necessitating greater organic acid production to lower macroscopic pH.
Sulfate (SO ₄ ²⁻)	105–113 mg/L	Influences yeast sulfur metabolism and potential trace aromatic compound formation during fermentation.
Chlorine (Cl ₂)	Trace / Not routinely added	Berlin water is unchlorinated, preventing halogen-induced oxidative stress and microbial inhibition during initiation.

Table 1: Key geochemical parameters of Berlin municipal water and their fermentative implications⁸.

The high concentration of hydrogen carbonate (HCO_3^-) in Berlin water serves as a powerful chemical buffer. When pioneer Lactic Acid Bacteria begin producing lactic and acetic acids, the dissociated protons are initially consumed by the bicarbonate buffer system, artificially delaying the drop in the dough's macroscopic pH¹¹. Consequently, starters initiated with Berlin tap water will require a significantly higher Total Titratable Acidity (TTA)—measured via titration with 0.1M NaOH—to achieve the critical pH threshold of 4.0 compared to starters initiated with soft water¹⁰. This delayed acidification prolongs the window of enzymatic activity for pH-sensitive cereal proteases and amylases, often resulting in a highly extensible, softer dough matrix before the acidity fully arrests gluten degradation¹⁴. Furthermore, because the Berliner Wasserbetriebe does not routinely chlorinate the municipal supply, the risk of oxidative stress inhibiting the fragile initial bacterial bloom is entirely mitigated, providing an optimal hydration medium for wild microbiology⁸.

Agronomic Substrates: German Flour Taxonomy and Polysaccharide Dynamics

German milling standards classify flour strictly based on its ash content (the mineral residue remaining after incineration at high temperatures), which serves as a highly accurate proxy for the extraction rate and total bran content¹⁶. The initiation of a wild starter absolutely requires whole-grain or high-extraction flours to maximize the initial microbial load and enzymatic potential.

The preferred substrate for culture initiation in Germany is *Roggenmehl Type 1150* (Rye Flour). Type 1150 is a dark, high-extraction rye flour containing approximately 1.15 g of ash per 100 g of dry matter¹⁷. Rye flour is vastly superior to wheat for initial microbial activation because its outer bran layers harbor immense populations of indigenous *Weissella* and *Lactobacillus* species, providing a massive microbiological head start¹. Furthermore, Type 1150 rye possesses a unique carbohydrate architecture. Unlike hexaploid bread wheat (*Triticum aestivum*), which relies on the hydration of gliadin and glutenin to form an elastic gluten network, rye relies heavily on arabinoxylans (pentosans) for structural integrity¹⁹. These pentosans, specifically water-extractable arabinoxylans (WEAX) and water-unextractable arabinoxylans (WUAX), possess an extreme water-binding capacity. They absorb massive quantities of hydration to create a highly viscous, mucilaginous slime that traps expanding carbon dioxide gases in the absence of a traditional protein network²⁰.

Following the successful capture and stabilization of the culture using rye, operators frequently transition the feeding regimen to *Weizenmehl Type 550* (Wheat Flour). As a standard strong bread flour, Type 550 possesses excellent gluten-forming proteins but lower indigenous microbial counts and lower micronutrient density compared to Type 1150¹⁷. This transition shifts the starter from a highly viscous, enzymatically aggressive rye matrix into a highly elastic maintenance matrix capable of leavening robust wheat breads without excessive proteolytic degradation¹⁷.

Microbiological Succession: The Three Phases of

Initiation

The transition from a raw flour-water slurry to a stabilized climax community is not instantaneous; it occurs over a period of 7 to 14 days and is governed by the strict principles of microbial ecology. This succession is driven entirely by competitive exclusion, where the continuous accumulation of metabolic waste (organic acids) selectively eliminates the initial generalist population in favor of highly adapted specialists¹.

Succession Phase	Timeline	Dominant Microbiology	Biochemical Environment	Macroscopic Observations
Phase 1: Lag & Opportunistic	Days 1–3	<i>Enterobacteriaceae</i> , environmental molds, <i>Bacillus</i> spp., <i>Weissella</i> spp.	pH 5.0–6.0; High free sugars; Abundant oxygen.	The "False Rise"; massive, unstable gas production; putrid or cheese-like aromas.
Phase 2: Competitive Acidification	Days 4–7	<i>Leuconostoc</i> spp., <i>Lactobacillus sakei</i> group, <i>Pediococcus</i> spp.	pH drops below 4.5; Oxygen depleted; Organic acids accumulate.	Volumetric expansion collapses; generalist organisms die off; dough becomes highly extensible.
Phase 3: Climax Community	Days 7–14+	<i>Fructilactobacillus sanfranciscensis</i> , <i>Kazachstania humilis</i> , <i>Saccharomyces cerevisiae</i> .	pH stabilizes at 3.8–4.1; High concentrations of lactic and acetic acid; Anaerobic.	Predictable, cyclical volumetric doubling; complex fruity, floral, and acidic aromas develop.

Table 2: The tri-phasic microbiological succession of a developing Type I sourdough culture¹.

Phase 1: The Lag and Opportunistic Bloom

Upon the initial hydration of Roggenmehl Type 1150 with Berlin tap water, the dormant

endophytic microbiota is activated. At this stage, the initial Lactic Acid Bacteria count is incredibly low, frequently hovering around 2.0 log CFU/g¹. Because the starting pH of the mixture is nearly neutral (typically pH 5.5 to 6.0), the environment is highly hospitable to a vast array of generalist microorganisms²⁵. This includes environmental molds, *Staphylococcus* species, *Bacillus* species (which pose the threat of ropy spoilage), and various members of the *Enterobacteriaceae* family¹.

During Day 2 or 3 of the initiation process, operators frequently observe a massive, rapid volumetric expansion of the dough matrix. This phenomenon is colloquially termed the "False Rise"²⁷. This hyper-activity is rarely caused by the target wild yeasts or climax LAB. Instead, it represents a catastrophic bloom of opportunistic, heterofermentative *Enterobacteriaceae* and aerobic generalists that aggressively metabolize the easily accessible free sugars⁶. They generate massive volumes of carbon dioxide alongside off-putting, putrid, or cheese-like aromas⁶. However, concurrently within this chaotic matrix, the limited cohort of indigenous LAB (such as *Weissella* spp. and *Lactococcus lactis*) also begin to reproduce and excrete lactic acid¹.

Phase 2: Competitive Acidification and the Biological Vacuum

By Day 4, the cumulative excretion of organic acids by the early LAB pioneers overcomes the strong bicarbonate buffering capacity of the Berlin water, finally driving the pH of the matrix below 4.5²⁵. This biochemical milestone triggers a mass extinction event within the starter. The *Enterobacteriaceae* and other opportunistic pathogens are completely intolerant of this acidic environment and undergo rapid cellular death¹.

Consequently, the starter visually appears to "die." The false rise collapses entirely, and macroscopic volumetric expansion ceases. However, microbiologically, this phase is exceptionally active. The death of the generalists creates a biological vacuum, allowing acid-tolerant heterofermentative LAB, primarily *Leuconostoc* species and members of the *Lactobacillus sakei* group, to proliferate rapidly without competition for the available maltose and glucose¹. During this phase, overall bacterial diversity peaks as the system transitions from generalist inputs to a highly specialized community⁶.

Phase 3: The Climax Community and Ratio Stabilization

As the operator maintains a regimen of continuous "backslopping"—the process of discarding a portion of the culture and re-feeding with fresh flour and water—the pH drops further, ultimately stabilizing in a tight band between 3.8 and 4.1²⁵. This extreme acidity, combined with the accumulation of ethanol, hydrogen peroxide, and antimicrobial peptides (bacteriocins), creates an exclusionary zone that only elite, highly specialized sourdough microorganisms can survive⁴.

By Day 14, the microbial community solidifies into a climax ecosystem. The bacterial load reaches immense densities exceeding 10⁸ CFU/g, overwhelmingly dominated by obligate heterofermentative LAB, most notably *Fructilactobacillus sanfranciscensis* (formerly *Lactobacillus sanfranciscensis*)²⁹. Simultaneously, acid-tolerant wild yeasts, which were outcompeted during the early phases, finally emerge from the lag phase and stabilize at population densities of 10⁶ to 10⁷ CFU/g²⁶. This dynamic equilibrium establishes the golden

stoichiometric ratio of a mature, stabilized sourdough starter: a strict 100:1 ratio of Lactic Acid Bacteria to Yeast³¹.

Metabolic Architecture: Bacterial Pathways and Antifungal Mechanics

The stability of the climax community is driven by complex metabolic interactions, resource partitioning, and biochemical specializations among the dominant bacterial strains. The bacterial cohort is broadly divided into homofermentative and heterofermentative species, a distinction that dictates the ultimate rheological and sensory profile of the sourdough matrix.

Homofermentative Metabolism

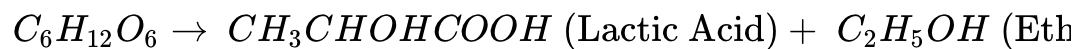
Homofermentative LAB (such as *Lactiplantibacillus plantarum*) metabolize hexoses, primarily glucose, via the standard Embden-Meyerhof-Parnas (EMP) glycolytic pathway. The critical enzyme aldolase cleaves fructose-1,6-bisphosphate into triose phosphates, which are ultimately converted to pyruvate³³. The terminal enzymes, L-lactate dehydrogenase and D-lactate dehydrogenase, subsequently reduce the pyruvate directly into lactic acid to regenerate NAD⁺³⁴. The EMP pathway is highly energy-efficient, yielding 2 moles of ATP and 2 moles of lactic acid per mole of glucose, but crucially, it generates zero carbon dioxide, providing no leavening power to the dough³⁴.



The precise ratio of L-lactic acid to D-lactic acid produced is strain-specific and heavily regulated by the genetic expression of the *ldhL* and *ldhD* genes, which encode for their respective lactate dehydrogenases³⁵. The optical type of lactic acid present in the dough can influence the final sensory perception of acidity, though both isomers contribute to the critical drop in pH required for stabilization³⁸.

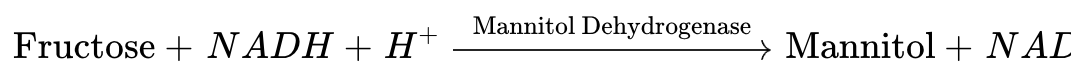
Heterofermentative Metabolism and the Phosphoketolase Pathway

The undisputed masters of the sourdough matrix are the obligate heterofermenters, including *Fructilactobacillus sanfranciscensis*, *Limosilactobacillus fermentum*, and *Weissella cibaria*. These species lack the critical aldolase enzyme and are therefore incapable of utilizing the EMP pathway. Instead, they catabolize sugars via the Phosphoketolase pathway, a branch of the Pentose Phosphate Pathway³⁴. The enzyme phosphoketolase cleaves xylulose-5-phosphate into glyceraldehyde-3-phosphate (which is subsequently reduced to lactic acid) and acetyl phosphate. Depending on the availability of electron acceptors, the acetyl phosphate is converted into either ethanol or acetic acid³⁴.



Strictly from a carbohydrate fermentation perspective, the phosphoketolase pathway is energetically disadvantaged, yielding only 1 mole of ATP per mole of glucose³⁶. However, heterofermentative LAB possess an elegant biochemical workaround to maximize energy yield. If alternative external electron acceptors—specifically fructose—are available in the flour matrix, these bacteria deploy the enzyme mannitol dehydrogenase⁴⁰. Mannitol dehydrogenase acts to reduce fructose directly into the sugar alcohol mannitol, simultaneously oxidizing NADH to NAD⁺.

This brilliant circumvention spares the acetyl phosphate pool from needing to be reduced to ethanol for redox balancing. Instead, the acetyl phosphate is converted to acetic acid via acetate kinase, generating an additional ATP molecule and doubling the energy yield of the pathway³⁶.



The Antimicrobial Physics of Undissociated Acids

The generation of acetic acid via the mannitol dehydrogenase bypass is technologically vital for the preservation of the final bread. Acetic acid possesses a higher pK_a (4.76) than lactic acid (3.86)⁴². In a mature sourdough matrix hovering at a pH of 4.0, only a small fraction of lactic acid remains undissociated. However, at this same pH, approximately 85% to 90% of the acetic acid remains in its undissociated, lipophilic form⁴³.

This undissociated molecular state is the primary mechanism of sourdough's legendary mold resistance. The lipophilic acetic acid molecules easily breach the lipid bilayers of competing fungal and bacterial cell membranes. Once inside the higher-pH cytoplasm of the invading pathogen, the acid dissociates, releasing protons that collapse the internal proton motive force, acidify the cytoplasm, and inhibit active transport⁴³. This mechanism acts as a lethal, natural antifungal preservative, massively extending the mold-free shelf life of the final baked product without the need for synthetic chemical preservatives⁴³.

Yeast Dynamics, Aroma Synthesis, and the Symbiosis Debate

While the bacterial population governs the acidity and rheology of the dough, the yeast population is fundamentally responsible for leavening power (via immense carbon dioxide production) and complex aroma generation. While wild strains of *Saccharomyces cerevisiae* are frequently isolated from mature starters, non-conventional yeasts such as *Kazachstania*

humilis (formerly *Candida humilis*) and *Kazachstania exigua* are highly prized and prevalent⁴⁵.

The Ehrlich Pathway and Fusel Alcohols

These yeasts contribute profoundly to the sensory architecture of the bread primarily through the catabolism of flour proteins. As indigenous cereal proteases degrade flour proteins into free amino acids during the long fermentation, the yeast cells internalize these amino acids and deploy the Ehrlich Pathway⁴⁷. The Ehrlich Pathway is a biochemical cascade wherein branched-chain amino acids (leucine, isoleucine, valine) and aromatic amino acids

(phenylalanine, tyrosine, tryptophan) undergo three sequential steps: transamination to an α -keto acid, decarboxylation to an aldehyde, and final reduction to a "fusel alcohol" by alcohol dehydrogenase⁴⁸.

The specific amino acid catabolized strictly dictates the resulting volatile organic compound (VOC). For example, the catabolism of leucine yields isoamyl alcohol (imparting distinct fruity or banana notes), while the degradation of phenylalanine yields 2-phenylethanol (imparting intense rose and floral notes)⁴⁷. Following their synthesis, the esterification of these higher alcohols with acetyl-CoA produces potent acetate esters (e.g., isoamyl acetate and phenylethyl acetate)⁴⁷. These esters possess extremely low odor thresholds and are the defining olfactory fingerprints that distinguish a premium, long-fermented sourdough from a rapidly manufactured commercial loaf⁴⁷.

The Collapse of the Glucose Cross-Feeding Hypothesis

For decades, the dominant ecological theory explaining the extreme stability of the 100:1 LAB-to-Yeast ratio in Type I sourdoughs posited a mutualistic "glucose cross-feeding" relationship⁵². *Fructilactobacillus sanfranciscensis* possesses a highly specific, energy-efficient enzyme called maltose phosphorylase. This enzyme allows the bacterium to import maltose (the most abundant fermentable sugar in wheat and rye dough) and cleave it directly into glucose and glucose-1-phosphate without expending ATP⁵⁴. The prevailing theory suggested that *F. sanfranciscensis* metabolized the glucose-1-phosphate while expelling the free glucose into the extracellular matrix. This expelled glucose theoretically "fed" the maltose-negative yeast *Kazachstania humilis*, forging a perfect symbiotic dependency⁵².

However, cutting-edge metabolomic and flow-cytometry assays have recently drawn this elegant theory into severe question. Recent in vitro co-culture studies reveal that *K. humilis* fitness is actually impaired when co-cultured with *F. sanfranciscensis* compared to when grown in a monoculture⁵². Advanced spent-medium analyses suggest that *F. sanfranciscensis* consumes significantly less maltose in co-culture and does not excrete sufficient glucose to support mutualistic yeast growth. Consequently, modern microbiological consensus is shifting. The stability of the sourdough microbiome is no longer viewed as a cooperative mutualism, but rather as an asymmetric, neutral, or actively competitive environment where extreme physical stress tolerances (specifically to high acidity and ethanol concentrations) enforce coexistence⁵².

Enzymatic Transformations in the Bioreactor Matrix

While the microorganisms drive the metabolic outputs of the system, the sourdough matrix is

fundamentally a massive enzymatic bioreactor. The continuous drop in pH orchestrated by the Lactic Acid Bacteria dramatically alters the activity of endogenous cereal enzymes present in the flour, leading to massive structural, rheological, and nutritional modifications.

Enzyme Type	Origin	Target Substrate	Action	Technological Outcome
α -Amylase	Cereal	Damaged Starch	Cleaves internal α -(1,4) bonds.	Liquefies starch; provides substrate for β -amylase.
β -Amylase	Cereal	Starch Dextrins	Cleaves maltose from non-reducing ends.	Generates maltose to fuel LAB and yeast fermentation.
Aspartic Protease	Cereal	Glutenin & Gliadin	Cleaves peptide bonds in low pH.	Depolymerizes gluten network; increases dough extensibility.
Phytase	Cereal	Phytic Acid (IP6)	Dephosphorylates IP6 to lower-order inositols.	Unlocks bound Ca^{2+} , Mg^{2+} , Fe^{2+} , Zn^{2+} , increasing bioavailability.
Invertase & Fructanase	Yeast & LAB	Fructans (FODMAPs)	Hydrolyzes fructosyl-fructose bonds.	Degrades IBS-triggering carbohydrates up to 90%.
Dextranase	LAB (<i>Weissella</i>)	Sucrose	Polymerizes glucose into dextran.	Synthesizes hydrocolloidal EPS; retards staling.

Table 3: The primary enzymatic activities driving the physical and nutritional transformation of the sourdough matrix⁵⁷.

Amylolysis and Starch Degradation Kinetics

Sound wheat and rye flours contain dormant α -amylase and β -amylase enzymes. As the flour hydrates, these enzymes activate. α -amylase acts as an endo-enzyme, randomly cleaving the internal α -(1,4) glycosidic bonds of mechanically damaged starch granules, effectively liquefying the starch into smaller dextrans⁶⁰. β -amylase subsequently acts as an exo-enzyme, attacking the non-reducing ends of these newly formed dextrans and systematically cleaving off molecules of maltose⁶⁰.

This continuous enzymatic generation of maltose is absolutely critical; it provides the inexhaustible carbohydrate fuel source required to sustain the *F. sanfranciscensis* population

during prolonged 24- to 48-hour fermentation cycles⁴⁵. However, excessive α -amylase activity—often caused by Pre-Harvest Sprouting (PHS) or Late Maturity Alpha-Amylase (LMA) in the field—results in a low Hagberg Falling Number. If the starch is liquefied too rapidly, the dough loses its structural capacity to hold water, resulting in a sticky, gummy crumb that collapses in the oven⁵².

Proteolysis, Glutenin Depolymerization, and Rheology

As the bacterial population drives the pH of the matrix below 4.5, the solubility of the gluten proteins increases due to an accumulation of positive net charges, which causes electrostatic repulsion between the protein strands²¹. Simultaneously, this highly acidic environment optimally activates endogenous cereal aspartic proteases⁵⁷. These proteases aggressively attack the complex, highly polymerized high-molecular-weight glutenin subunits (HMW-GS) and monomeric gliadins¹⁵.

This enzymatic depolymerization of the glutenin macropolymer (GMP) has profound rheological consequences, measurable via advanced rheofermentometer analytics. The structural integrity of the dough is deliberately weakened, forcing a transition from a highly elastic, Hookean solid to a highly extensible, viscous fluid⁶⁵. If fermentation proceeds too long, or if the pH drops below 3.8, catastrophic gluten liquefaction occurs, resulting in a sticky, un-shapeable dough matrix²³. However, when carefully controlled by the baker, this mild proteolytic degradation increases dough extensibility, allowing the expanding gas bubbles to stretch the matrix without rupturing, directly resulting in massive oven spring. Furthermore, the degradation of gliadin proteins can partially detoxify the flour, though not to levels universally safe for celiacs unless specific fungal proteases are introduced alongside the sourdough¹⁴.

Phytase Activation and the Liberation of Mineral Wealth

From a nutritional perspective, the most critical enzymatic event in the sourdough process is the activation of phytase. Whole grain flours, such as Type 1150 rye, are incredibly rich in

essential minerals, including calcium, magnesium, zinc, and iron. However, in raw flour, these positively charged mineral cations are tightly chelated by phytic acid (myo-inositol hexakisphosphate, or IP6), a powerful anti-nutritional compound bearing six highly electronegative phosphate groups⁵⁸. The human gastrointestinal tract lacks the endogenous phytase required to cleave these bonds, rendering the minerals biologically unavailable and causing them to be excreted⁷¹.

Endogenous cereal phytase possesses a strict optimal pH range of 5.0 to 5.5⁵⁸. In standard commercial breadmaking utilizing fast-acting baker's yeast, the pH rarely drops below 5.5, and the fermentation time (1–2 hours) is far too brief for significant enzymatic action. Therefore, commercial whole wheat bread retains roughly 60% to 70% of its intact phytic acid, trapping the nutritional value⁵⁸. Conversely, the lactic acid bacteria in a sourdough starter drive the dough directly through this critical pH 5.0 window and hold it in an acidic state for 12 to 24 hours. Under these prolonged conditions, the cereal phytase systematically dephosphorylates IP6 down to lower-order inositol phosphates (IP5 through IP1)⁵⁸. This unzips the molecular lock, freeing the bound magnesium, calcium, and iron into the dough matrix in highly soluble, bioavailable forms, reducing the total phytic acid content of the final loaf by up to 90%⁷¹.

Exopolysaccharide (EPS) Synthesis and Hydrocolloidal Stabilization

Specific heterofermentative LAB, notably *Weissella cibaria*, *Weissella confusa*, and *Leuconostoc mesenteroides*, possess extracellular enzymes known as glucansucrases (or dextransucrases, EC 2.4.1.5)⁵⁹. When sucrose is present in the matrix, dextransucrase utilizes the thermodynamic energy of the sucrose glycosidic bond to cleave the molecule into glucose and fructose. The enzyme then rapidly polymerizes the glucose monomers into massive,

high-molecular-weight homopolysaccharides called dextrans (primarily α -(1→6) linked

glucans with some α -(1→3) branching)⁷⁶. Kinetic studies of *Weissella confusa* dextransucrase

reveal exceptional efficiency, with a K_m of 14.7 mM and a V_{max} of 8.2 μ mol/(mg·min) at an optimum pH of 5.4⁷⁹.

These exopolysaccharides act as powerful, biologically synthesized hydrocolloids within the dough⁸¹. Dextrans bind massive amounts of water, significantly increasing the viscosity of the matrix. In rye breads, or in wheat doughs that have suffered severe proteolytic degradation, these EPS molecules effectively mimic the viscoelastic properties of the missing or degraded gluten network⁸¹. They improve gas retention, increase final loaf specific volume, and most critically, retard starch retrogradation (staling) by restricting water mobility and preventing starch recrystallization within the baked crumb⁵⁹.

FODMAP Degradation and Digestive Tolerability

Fermentable Oligosaccharides, Disaccharides, Monosaccharides, and Polyols (FODMAPs)—specifically fructans—are abundant in wheat and rye flours and are primary dietary triggers for Irritable Bowel Syndrome (IBS)⁶¹. Sourdough fermentation facilitates the rapid and extensive degradation of these compounds. Both the wild yeast and specific LAB

deploy invertase (β -fructofuranosidase) and fructanase (exo- β -fructosidase) enzymes. These enzymes hydrolyze the fructosyl-fructose bonds of the long-chain fructans, reducing them to simple fructose monomers that are easily digested or further fermented⁸⁵. Extended sourdough fermentation (24 to 48 hours) has been shown to reduce fructan levels by up to 90%, physically transitioning a high-FODMAP wheat flour into a biologically distinct, highly digestible, low-FODMAP bread matrix⁸⁶.

Operational Controls for Culture Stabilization

To transition a volatile, developing microbial community into a highly stable, predictable commercial leavening agent, the operator must exert precise control over three primary variables: feeding ratios (backslopping), hydration, and temperature.

Feeding Ratios and Bacterial Growth Kinetics

Bacteria in a sourdough starter follow a strict, predictable growth curve: Lag phase, Exponential (Logarithmic) phase, Stationary phase, and Death phase²⁴.

- **Lag Phase:** Microorganisms synthesize necessary enzymes and adapt to the fresh flour and water. No cellular division occurs²⁴.
- **Exponential Phase:** Nutrients are abundant; binary fission occurs at maximum velocity, generating massive amounts of CO₂ and organic acids²⁴.
- **Stationary Phase:** Nutrients deplete, and acid accumulation reaches toxic levels, inhibiting further cellular division. The culture "peaks"²⁴.

The act of "backslopping" is fundamentally the act of resetting this growth curve²⁴. If a starter is fed too infrequently (e.g., once every 48 hours at room temperature), the bacteria enter an extended stationary and death phase. Acidity plummets below pH 3.5, triggering severe proteolytic degradation of the flour proteins and fatally damaging the yeast population, which is sensitive to extreme acetic acid concentrations²⁴. Conversely, if a starter is fed too frequently (e.g., before it has doubled in volume), the bacteria are perpetually trapped in the lag phase. They never achieve the exponential growth necessary to outcompete pathogens, leading to a weak, highly susceptible culture²⁴.

To stabilize a Berlin-based starter, backslopping must occur precisely at the apex of the exponential phase—typically when the culture has doubled or tripled in volume but has not yet begun to collapse²⁴. A standard maintenance ratio is 1:2:2 (one part mature starter, two parts flour, two parts water by weight). This dilution rate forces a moderate lag phase, ensuring that the heavy buffering capacity of the Berlin water is adequately overcome by a healthy, vigorously multiplying LAB population.

Hydration: Dough Yield (DY) Dynamics

The hydration of the starter is quantified using the Dough Yield (DY) metric, where $DY = [(flour\ weight + water\ weight) / flour\ weight] \times 100^{91}$.

- **Liquid Starters (DY 200–300):** A 100% hydration starter (equal parts water and flour by weight, DY 200) features high water activity (a_w). High free-water mobility facilitates rapid enzymatic action, accelerated starch hydrolysis, and swift cellular multiplication.

Liquid starters favor homofermentative pathways and the rapid production of lactic acid, yielding a mild, yogurt-like aroma profile⁷.

- **Stiff Starters (DY 150):** A 50% hydration starter (e.g., the traditional French *levain* or Italian *Pasta Madre*) restricts water mobility²⁸. The high osmotic stress and limited diffusion of metabolic waste inhibit rapid bacterial division. However, this environment heavily selects for robust wild yeasts, promoting exceptional leavening power²⁸. Stiff starters generally accumulate higher concentrations of acetic acid due to the restricted environment, yielding a more pungent, complex aromatic profile²⁸.

Temperature and the Fermentation Quotient (FQ)

Temperature is the ultimate master variable in sourdough management, primarily because it dictates the **Fermentation Quotient (FQ)**—the molar ratio of lactic acid to acetic acid³¹. The FQ is the most critical determinant of a bread's final sensory profile; an optimal FQ typically resides between 4:1 and 10:1 (lactic to acetic)⁹³.

Incubation Temperature	Dominant Metabolic Pathway	Dominant End-Product	Fermentation Quotient (Lactic:Acetic)	Sensory Result
Warm (25°C–30°C)	Homofermentative (EMP Pathway)	Lactic Acid	High (>10:1)	Mild, sweet, dairy-like acidity; preserves delicate wheat flavors.
Cool (15°C–21°C)	Heterofermentative (Phosphoketolase)	Lactic + Acetic Acid	Low (<4:1)	Sharp, pungent, vinegar-like tang; robust flavor profile.

Table 4: The influence of temperature on the Fermentation Quotient and sensory profile⁷. The metabolic pathways of heterofermentative and homofermentative LAB possess divergent thermal optima⁷. Warm fermentation heavily favors the growth kinetics of homofermentative LAB and accelerates the enzymatic release of maltose⁷. The rapid accumulation of lactic acid drives the FQ higher, resulting in a "sweet," mild acidity desirable for artisanal wheat breads²⁸. Conversely, lower temperatures suppress homofermentative growth and favor heterofermentative LAB. The lower thermal energy also increases the solubility of oxygen in the dough matrix. The presence of oxygen provides an additional external electron acceptor for

heterofermenters, driving the biochemical conversion of acetyl phosphate into acetic acid rather than ethanol⁷. This drops the FQ, resulting in a sharp, pungent acidity characteristic of traditional rye and San Francisco-style sourdoughs⁹⁵.

If a Berlin baker's starter becomes excessively acidic and "vinegary" (indicating a dangerously low FQ), stabilization is achieved by simultaneously increasing the hydration (acting as a diluent for accumulated acids) and raising the ambient incubation temperature to 28°C–29°C²⁸.

Performing three to four consecutive backslapping cycles under these parameters will systematically suppress the heterofermentative acetic output, favoring a homofermentative bloom, and ultimately restoring the starter to a sweet, lactic-dominant equilibrium²⁸.

Works cited

1. Microbial Ecology Dynamics during Rye and Wheat Sourdough, <https://pmc.ncbi.nlm.nih.gov/articles/PMC3837820/>
2. Role of lactic acid bacteria and yeasts in sourdough fermentation, <https://www.frontiersin.org/journals/microbiology/articles/10.3389/fmicb.2022.969460/full>
3. Diverse Microbial Composition of Sourdoughs From Different Origins, <https://www.frontiersin.org/journals/microbiology/articles/10.3389/fmicb.2020.01212/full>
4. Sourdough Microbiota for Improving Bread Preservation and Safety, <https://pmc.ncbi.nlm.nih.gov/articles/PMC12542873/>
5. The hidden microbes that decide how sourdough tastes - ScienceDaily, <https://www.sciencedaily.com/releases/2026/01/260121034132.htm>
6. Sourdough starters exhibit similar succession patterns but develop, <https://pmc.ncbi.nlm.nih.gov/articles/PMC10559884/>
7. How Sourdough Fermentation Works: 6 Stages Explained, <https://www.bakingsubs.com/blog/how-sourdough-fermentation-works>
8. Water Quality - Berliner Wasserbetriebe, <https://www.bwb.de/en/2471.php>
9. Capillary Nanofiltration under Anoxic Conditions as Post-Treatment, <https://www.mdpi.com/2073-4441/10/11/1599>
10. What Is Hard Water? A Simple Guide | PICKI NIKI, <https://www.pickiniki.com/blogs/learn/what-is-hard-water>
11. Wasserqualität - Berliner Wasserbetriebe, <https://www.bwb.de/de/wasserqualitaet.php>
12. Every Shower Filter Technology, Explained | PICKI NIKI, <https://www.pickiniki.com/pages/filtered-shower-head-technology-explained>
13. Effects of sourdough and enzymes on staling of high-fibre wheat bread, https://www.researchgate.net/publication/223261782_Effects_of_sourdough_and_enzymes_on_staling_of_high-fibre_wheat_bread
14. [PDF] Prolamin degradation in sourdoughs - Semantic Scholar, <https://www.semanticscholar.org/paper/Prolamin-degradation-in-sourdoughs-Lo-ponen/06d6343949e858817ac045e263270761d49b3682>
15. Prolamin degradation in sourdoughs - Helda - University of Helsinki,

<https://helda.helsinki.fi/bitstreams/fce78ed4-e7bc-4002-ad73-7943784ed766/download>

16. Ash Content in Flour: What Does It Mean For Sourdough Baking?,
<https://somebodyfeedseeb.com/ash-content-in-flour/>
17. Identification and Population Dynamics of Yeasts in Sourdough,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC309968/>
18. Type 1150 Rye Flour - Heimatsmühle,
<https://www.heimatsmuehle.com/en/commercial-customers/products/type-1150-rye-flour>
19. 26 Wheat Cultivation and Processing Methods.pdf
20. Use of transglutaminase for preparing bakery products,
<https://patents.google.com/patent/EP1190624A2/en>
21. Sourdough production: fermentation strategies, microbial ecology,
<https://www.tandfonline.com/doi/full/10.1080/10408398.2021.1976100>
22. Enzymatic Solubilization of Arabinoxylans from Isolated Rye,
<https://pubs.acs.org/jafcau/article/50/22/6473/3578006/Enzymatic-Solubilization-of-Arabinosylans-from>
23. Gluten Hydrolysis and Depolymerization during Sourdough,
<http://microsour.com/pdf/gluten-hydrolysis.pdf>
24. The science of your sourdough starter - All you knead is bread,
<https://allyoukneadisbread.com/the-science-of-your-sourdough-starter/>
25. On pH and sourdough breads - wordloaf - Andrew Janjigian,
<https://newsletter.wordloaf.org/on-ph-and-sourdough-breads/>
26. Identification of Predominant Lactic Acid Bacteria and Yeasts of,
<https://journal.pan.olsztyn.pl/pdf-98447-31200?filename=31200.pdf>
27. How to Make a Sourdough Starter From Scratch (And Set Yourself,
<https://www.nordicware.com/how-to-make-a-sourdough-starter-from-scratch/>
28. Sourdough Starter Science: pH & Acidity Control - Katia Oldani,
<https://katiaoldani.com/2025/12/09/sourdough-starter-science-acidity/>
29. Fructilactobacillus sanfranciscensis - Wikipedia,
https://en.wikipedia.org/wiki/Fructilactobacillus_sanfranciscensis
30. Lactic Acid Bacterium and Yeast Microbiotas of 19 Sourdoughs,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC3273004/>
31. Volatile Organic Compounds in Breads Prepared with Different,
<https://www.mdpi.com/2076-3417/11/3/1330>
32. Universidade Federal do Rio de Janeiro - PPGCAL,
https://ppgcal.iq.ufrj.br/wp-content/uploads/A-theoretical-practical-approach-to-sourdough-starter-microbiology-and-drying-process_DISSERTA%C3%87%C3%83O-2022_GABRIEL-ALBAGLI.pdf
33. A metabolic reconstruction of Lactobacillus reuteri JCM 1112 and,
<https://www.biorxiv.org/content/10.1101/708875v1.full-text>
34. Classical Food Fermentations as Modern Biotechnological Platforms,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC12844091/>
35. Major role of lactate dehydrogenase D-LDH1 for the synthesis of,
https://www.researchgate.net/publication/342937693_Major_role_of_lactate_dehy

[drogenase_D-LDH1_for_the_synthesis_of_lactic_acid_in_Fructobacillus_tropaeoli_CRL_2034](#)

36. *Leuconostoc citreum*: A Promising Sourdough Fermenting Starter for, <https://www.mdpi.com/2304-8158/13/1/96>
37. Unexpected complexity in the lactate racemization system of lactic, https://academic.oup.com/femsre/article/41/Supp_1/S71/3894113
38. Metabolism Characteristics of Lactic Acid Bacteria and the ... - Frontiers, <https://www.frontiersin.org/journals/bioengineering-and-biotechnology/articles/10.3389/fbioe.2021.612285/full>
39. Sourdough Bread Fermentation and Probiotics - Encyclopedia.pub, <https://encyclopedia.pub/entry/41568>
40. Sourdough Fermentation with *Leuconostoc citreum* DSM 5577 for, <https://www.mdpi.com/2076-3417/16/8/3697>
41. Global Analysis of Mannitol 2-Dehydrogenase in *Lactobacillus*, <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0169441>
42. Sourdough Microbiota for Improving Bread Preservation and Safety, <https://www.mdpi.com/2304-8158/14/14/2443>
43. Comparison of the antifungal effect of undissociated lactic and acetic, https://www.researchgate.net/publication/339127229_Comparison_of_the_antifungal_effect_of_undissociated_lactic_and_acetic_acid_in_sourdough_bread_and_in_chemically_acidified_wheat_bread
44. 6 Microbial Fermentation for Food Preservation - CABI Digital Library, <https://www.cabidigitallibrary.org/doi/pdf/10.5555/20113333887>
45. Sourdough Bacteria: The Complete Guide, <https://doughdoughathome.com/blogs/news/sourdough-bacteria-complete-guide-lactobacillus-wild-yeast>
46. (PDF) Three novel ascomycetous yeast species of the Kazachstania, https://www.researchgate.net/publication/311349039_Three_novel_ascomycetous_yeast_species_of_the_Kazachstania_clade_Kazachstania_saulgeensis_sp_nov_Kazachstania_serrabonitensis_sp_nov_and_Kazachstania_australis_sp_nov_Reassignment_of_Candida_humilis_t
47. Reviewing the Source, Physiological Characteristics, and Aroma, <https://pmc.ncbi.nlm.nih.gov/articles/PMC10529235/>
48. The Ehrlich Pathway for Fusel Alcohol Production - ResearchGate, https://www.researchgate.net/publication/27343438_The_Ehrlich_Pathway_for_Fusel_Alcohol_Production_a_Century_of_Research_on_Saccharomyces_cerevisiae_Metabolism
49. Quantitation and Enantiomeric Ratios of Aroma Compounds Formed, <https://pubs.acs.org/doi/10.1021/acs.jafc.5b05427>
50. Adding Flavor to Beverages with Non-Conventional Yeasts, https://pure.uva.nl/ws/files/35265487/fermentation_04_00015.pdf
51. Volatile organic compounds and their generation in sourdough, <https://www.cabidigitallibrary.org/doi/pdf/10.5555/20230316342>
52. Lactic acid bacterium *Fructilactobacillus sanfranciscensis* impairs, <https://www.biorxiv.org/content/10.64898/2026.04.01.716005v1.full-text>

53. Lactic acid bacterium *Fructilactobacillus sanfranciscensis* impairs, https://www.researchgate.net/publication/403472185_Lactic_acid_bacterium_Fructilactobacillus_sanfranciscensis_impairs_fitness_of_yeast_Maudiozyma_humilis_in_synthetic_wheat_sourdough
54. overview of the metabolism of heterofermentative laB species in a, https://www.researchgate.net/figure/overview-of-the-metabolism-of-heterofermentative-laB-species-in-a-sourdough-matrix-only_fig4_354617014
55. Lactic acid bacterium *F. sanfranciscensis* impairs fitness of yeast *M.*, <https://www.biorxiv.org/content/10.64898/2026.04.01.716005v2.full>
56. Interactions between *Kazachstania humilis* Yeast Species ... - PMC, <https://pmc.ncbi.nlm.nih.gov/articles/PMC7074792/>
57. (PDF) Degradation of HMW Glutenins During Wheat Sourdough, https://www.researchgate.net/publication/228737845_Degradation_of_HMW_Glutenins_During_Wheat_Sourdough_Fermentations
58. Moderate Decrease of pH by Sourdough Fermentation Is Sufficient, <https://pubs.acs.org/jafcau/article/53/1/98/3557707/Moderate-Decrease-of-pH-by-Sourdough-Fermentation>
59. Comparison of the Functionality of Exopolysaccharides Produced by, <https://pubs.acs.org/doi/abs/10.1021/acs.jafc.0c02703>
60. Variation in quality of grains used in malting and brewing - PMC, <https://pmc.ncbi.nlm.nih.gov/articles/PMC10291334/>
61. Low-FODMAP Sourdough: What the Fermentation Research Shows, <https://jayarrbread.com/blog/low-fodmap-bread-sourdough-science/>
62. pre-harvest sprouting and late maturity alpha-amylase in triticum, https://rex.libraries.wsu.edu/view/pdfCoverPage?instCode=01ALLIANCE_WSU&filePid=13465571860001842&download=true
63. Best Bread Production Handbook - European Union, <https://ec.europa.eu/programmes/erasmus-plus/project-result-content/615f0f23-9ea5-4bc9-b154-fb72b36fdd68/Best%20Bread%20Production%20Handbook%20OEN.pdf>
64. Impact of Long-Fermented Sourdough on the Technological and, https://www.researchgate.net/publication/359040549_Impact_of_Long-Fermented_Sourdough_on_the_Technological_and_Prebiotic_Properties_of_Rye_Bread
65. Comparative Study of Rheology and Steamed Bread Quality of, https://www.researchgate.net/publication/347309113_Comparative_Study_of_Rheology_and_Steamed_Bread_Quality_of_Wheat_Dough_and_Gluten_Starch_Doughs
66. Review: Rheology and the breadmaking process - ResearchGate, https://www.researchgate.net/publication/343106627_Review_Rheology_and_the_breadmaking_process
67. (PDF) A comprehensive review on wheat flour dough rheology, https://www.researchgate.net/publication/260310001_A_comprehensive_review_on_wheat_flour_dough_rheology
68. Proteolysis by Sourdough Lactic Acid Bacteria, <https://thesourdoughschool.com/research/4-proteolysis-sourdough-lactic-acid->

[bacteria-effects/](#)

69. Sourdough Fermentation and Gluten Reduction - MDPI,
<https://www.mdpi.com/2036-7481/16/7/161>
70. Sourdough and cereal fermentation in a nutritional perspective,
https://sites.evergreen.edu/townhalls/wp-content/uploads/sites/28/2015/02/Food-Microbiology_Nutritional-Perspective.pdf
71. Bioavailability: How Acidity Neutralises Phytic Acid to Unlock Iron,
<https://www.thepact.com.au/science-of-sourdough/bioavailability-how-acidity-neutralises-phytic-acid-to-unlock-iron-and-zinc>
72. Does Sourdough Reduce Phytic Acid? What the Evidence Says,
<https://jayarrbread.com/blog/sourdough-fermentation-phytic-acid-bioavailability/>
73. Effect of acidification or fermentation of barley grain ... - WUR eDepot,
<https://edepot.wur.nl/648922>
74. Understanding Phytic Acid in Sourdough and Whole Grains,
<https://thenourishinghearthfire.com/2025/11/04/understanding-phytic-acid-in-sourdough-and-whole-grains/>
75. Lactic Acid Bacteria-Derived Exopolysaccharides: Dual Roles as,
<https://www.mdpi.com/2311-5637/11/9/538>
76. Characterization of a novel dextransucrase from *Weissella confusa*,
https://www.researchgate.net/publication/232229783_Characterization_of_a_novel_dextransucrase_from_Weissella_confusa_isolated_from_sourdough
77. Structure–function relationships of family GH70 glucansucrase and,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC4919382/>
78. Functional food applications of dextran from *Weissella cibaria*,
https://www.researchgate.net/publication/310050720_Functional_food_applications_of_dextran_from_Weissella_cibaria_RBA12_from_pummelo_Citrus_maxima
79. Cloning and characterization of a *Weissella confusa* dextransucrase,
<https://helda.helsinki.fi/bitstreams/821efcde-d2b9-4030-a2ab-515f12edea24/download>
80. (PDF) Cloning and Characterization of a *Weissella confusa*,
https://www.researchgate.net/publication/271333697_Cloning_and_Characterization_of_a_Weissella_confusa_Dextransucrase_and_Its_Application_in_High_Fibre_Baking
81. Effects of Extracted Exopolysaccharides from *Weissella confusa*,
<https://pubs.acs.org/afsth/article/6/2/473/5082803/Effects-of-Extracted-Exopolysaccharides-from>
82. Challenges and opportunities for wheat alternative grains in ... - Helda,
<https://helda.helsinki.fi/bitstreams/79684011-1f8a-499e-b662-6996029f0704/download>
83. Evaluating the Properties of Gluten-Free Bread Produced Using,
<https://iem.modares.ac.ir/article-4-32433-en.pdf>
84. Physico-Chemical Properties of Sourdough Bread Production Using,
https://www.researchgate.net/publication/264467656_Physico-Chemical_Properties_of_Sourdough_Bread_Production_Using_Selected_Lactobacilli_Starter_Cultures

85. Effects of Sourdough on FODMAPs in Bread and Potential ... - Frontiers,
<https://www.frontiersin.org/journals/microbiology/articles/10.3389/fmicb.2018.01972/full>
86. FODMAPs & Fermentation: Navigating IBS and the 48h Degradation,
<https://www.thepact.com.au/science-of-sourdough/fodmaps-and-fermentation-navigating-ibs-and-the-48h-degradation-curve>
87. FODMAP (fructans and mannitol) content of bread and sourdough,
https://www.auri.org/wp-content/uploads/2022/03/Handout_Ver4.pdf
88. The FODMAP-Reducing Potential of Sourdough-Derived ... - PMC,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC12045933/>
89. Coculture fermentation processes in wheat sourdough simulation,
<https://journals.asm.org/doi/10.1128/aem.01325-25>
90. Guide to quick sourdough starter with minimum discard,
<https://theflavorbells.com/quick-sourdough-starter/>
91. Diversity of the Lactic Acid Bacterium and Yeast Microbiota in ... - PMC,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC4018931/>
92. What is sourdough? An in-depth guide to sourdough technology for,
<https://www.mygermantable.com/what-is-sourdough-an-in-depth-guide-to-sourdough-technology-for-bakers/>
93. Determination of Lactic and Acetic Acids and Estimation of Their,
https://www.researchgate.net/publication/378323920_Determination_of_Lactic_and_Acetic_Acids_and_Estimation_of_Their_Molar_Ratio
94. Optimizing Lactic Acid Bacteria Proportions in Sourdough to ... - PMC,
<https://pmc.ncbi.nlm.nih.gov/articles/PMC11311496/>
95. The Science of Sourdough Fermentation, Simply Explained,
<https://atomebakery.com/blogs/atome-bakery-blog/sourdough-fermentation-science-explained>
96. Effects of process parameters on growth and metabolism of,
https://www.researchgate.net/publication/225455590_Effects_of_process_parameters_on_growth_and_metabolism_of_Lactobacillus_sanfranciscensis_and_Candida_humilis_during_rye_sourdough_fermentation