

THE SCOVILLE SPLICE LIBRARY · VOLUME XIV · ORGANISM MONOGRAPHS

The Tomato

Grown back, gene by gene. *Like a tomato should.*

The one organism where the loss is most visible and the restoration most complete. A receptor-level account of the fruit a century of shipping emptied — the pathway we reopened, the flux model that made it hold, the flagship we named for a cooled volcano, and the two dishes you need to understand it with your mouth. 2,040 constructs, every number grown rather than added.

SCOVILLE SPLICE · GROWN BY OUR FAMILY. ENGINEERED FROM SCRATCH.

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Opening essay · The tomato that tastes like a tomato should

Everyone who has grown a tomato knows the moment, and no one who has only bought one does. The fruit comes off the vine still warm, heavier than it looks, and when your thumb breaks the skin the smell arrives first — green and sweet and faintly electric, the scent of the cut stem and the ripe flesh at once — and then the taste goes round and savory and a little wild, and you stop talking. Everyone who has bought a tomato in January knows the other thing: the pale, firm, obedient object that looks like the memory under a grocery light and tastes like water that was told about tomatoes. Same plant. Same name on the sticker. Somewhere between the vine and the shelf, something was taken out.

We can tell you how much, because we measured it. On the long road from the heirloom vine to the supermarket pallet, a century of breeding selected the tomato for everything except the way it tastes — for the firm wall that survives a bruise, for the uniform red that reads as ripe before the fruit is ripe, for the shelf life that lets a truck cross a continent. Flavor was never on the breeder's form, so flavor was never protected, and it drained away one rational decision at a time. The fruit quietly surrendered something near **ninety-three percent** of its peak umami — the savory depth that was the whole reason the plant was worth eating — traded a fraction at a harvest for a tomato that could take a thousand miles without complaint.



The restored fruit. Everything in this book begins and ends with the object in the hand — a tomato grown back to the savor a century of shipping-first breeding bred out of it.

This is the monograph for that organism, because the tomato is where the loss is loudest and the repair is cleanest. It is also, for us, the easy case and the proud one. *Solanum lycopersicum* is the plant our family understands most completely — native engineering difficulty **Easy**, a genome read down to its last locule — and **2,040 constructs** into the work it is the fruit we are gladdest to hand across a table. We did not make it taste like *more* than a tomato. We grew it back until it finally tasted like *all* of one. Nothing in this book is added to the fruit that the fruit did not already evolve to make; the compounds were always written in its own genome, and a hundred

years of breeding only turned the volume down. We turned it back up, at the source, and then — because a gain you cannot measure is a gain you cannot keep — we put a number on every part of it.

A word about the *we* in these pages, because it carries the whole book. Scoville Splice is a family's work. The computing — the protein models, the sequence scans, the flux mathematics that fill the chapters ahead — came from one pair of hands; the reverence for the plant, the table it is grown for, and the long argument about what a tomato is *supposed* to taste like belong to all of us, and always did. When we write *we grew it back*, we mean a family that could not stop talking about a fruit. The tomato was the argument we kept having at dinner — somebody's grandmother's vine, the one no store has sold in forty years, the one that made a child go quiet — until the tools finally caught up with the longing, and we could answer it with a pathway and a number instead of a sigh. This monograph is that answer, worked all the way out.

And of all the organisms in the library, the tomato is the right one to begin the monographs with, because it is where every thread of the project crosses in a single fruit. It carries the clearest umami biology of any plant we grow, so the method is legible in it. It is the easiest to engineer, genome in hand since 2012, so the restoration is clean. It is the most eaten vegetable on Earth — technically a berry, universally a staple — so the stakes are ordinary and enormous at once; a better tomato is not a novelty, it is a better Tuesday for several billion people. And it is the fruit whose loss anyone can confirm with their own mouth, in any supermarket, in January. We did not choose the tomato because it was easy, though it was. We chose it because it is where the whole argument of this company becomes a thing you can hold in your hand and taste.

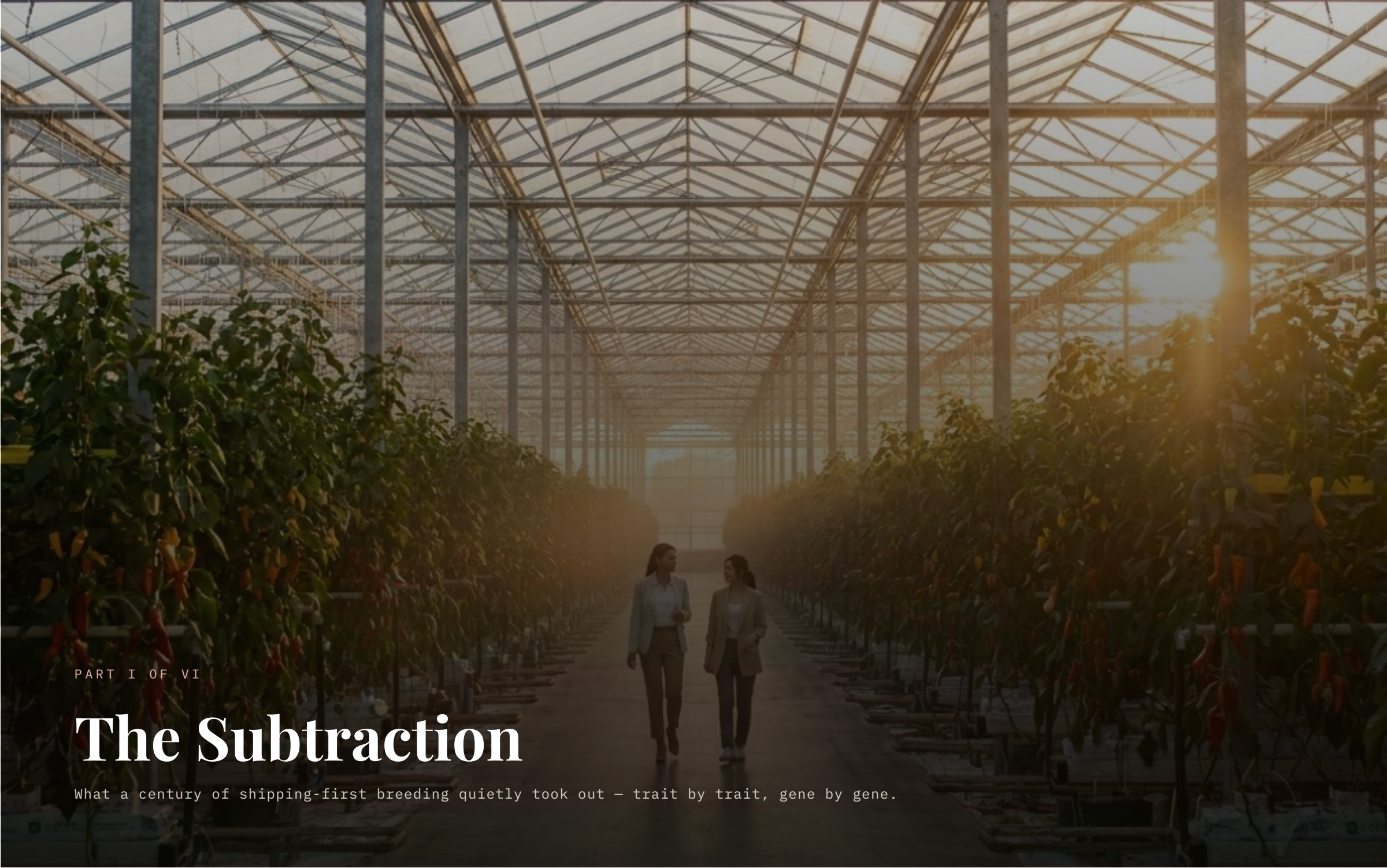
The number is the quiet spine of everything here, so it is worth meeting at the start. Every axis of flavor in this library is anchored to the half-maximal activation of a receptor. Not how much of a compound a fruit holds, but how *loudly* that compound speaks to the tongue:

> **IFI(candidate) = 1,000 × EC_{50}(reference) ÷ EC_{50}(candidate)**

EC_{50} is the concentration at which a stimulus drives its receptor to half of its full response. Invert it against a fixed reference, scale by a thousand, and loudness becomes a score a hollow January tomato and a vine-warm August one can be read against on a single page. On that line the whole story of this fruit fits between two figures: the commodity tomato sits near **IFI-U 300**, and our model predicts the tomato we restored reaches approximately **2,600**, designed to hold within a few percent in February as in August. Between those two numbers lies the entire difference between a sauce you have to rescue with salt and long cooking and meat, and a sauce that was already complete when it left the pan.

What follows is the whole fruit, in order. First what the century took, and the exact genes it took it through. Then umami itself — the receptor, the synergy that multiplies it, the pathway we reopened, and the flux model that keeps the gain from collapsing. Then the rest

of the chord: the sweetness returned, the savory floor beneath a kitchen, the bright dry edge that keeps depth from going heavy. Then the flagship, **Caldera**, named for the cooled, collapsed heart at the center of a volcano, which is exactly what it is — pure restored depth with no heat at all. Then the shelf, the spec, and the law; then the family and the frontier of fire the fruit could become; and at the end, two dishes, good oil, and flaky salt, in front of the people we love. Everything is scored, because a number held with care is how we keep a promise. The tomato that tastes like a tomato should is not a nostalgia. It is an instruction now, and it is measurable.



PART I OF VI

The Subtraction

What a century of shipping-first breeding quietly took out — trait by trait, gene by gene.

Chapter 1 · The Great Subtraction — *what the truck took.*

THE FRUIT · Solanum lycopersicum · Solanaceae · 2,040 constructs

To understand what we restored you have to sit, without blame, with what was lost — because the commodity tomato is not a failure of nature. It is a triumph of logistics. Every trait that makes a modern tomato survive the supply chain was selected *for*, on purpose, generation after generation, by breeders doing exactly their job. The thick, lignified pericarp that shrugs off a bruise in a bin forty fruit deep. The reluctance to soften that buys another week on a shelf. The uniform set and the uniform ripening that let a mechanical harvester take a whole field in one pass instead of a crew taking it over three. Each of these was a small, defensible trade. Taken together, compounded across a hundred years, they emptied the fruit.

It helps to see the scale of the engineering that preceded us, because our work is only the latest chapter of a very long one. The tomato humans eat today is one of the most heavily redesigned organisms on the planet, and almost none of that redesign was molecular. The wild ancestor, *Solanum pimpinellifolium*, bears fruit the size of a blueberry — one to two grams, two seed chambers, a thin skin over a little sour pulp. The beefsteak on a summer counter can run past a thousand grams. That is a **hundred- to thousand-fold** increase in fruit mass, achieved entirely by selection, and we can now name the handful of genes that carried most of it: **fw2.2**, a cell-number regulator that alone accounts for roughly a third of the size difference between wild and domesticated fruit; **fw3.2** (*SlKLUH*, a cytochrome P450) and **fw11.3** (a cell-size regulator) stacking on more; and the locule-number genes **lc** and **fas**, mutations near the *WUS* and *CLV3* stem-cell regulators that multiply the fruit's internal chambers from two to the many-chambered cross-section of a modern slicer. None of these touches flavor directly. But every one of them changed the ratio of flesh to gel, of wall to chamber, of water to everything else — and flavor lives in those ratios.



The commodity fruit and the restored one are the same species and nearly the same picture. The difference a century made is almost entirely invisible from the outside — which is precisely why it went unprotected.

The sharpest single loss is umami. Free L-glutamate — the molecule the tongue reads as savory depth, loose in the watery flesh rather than locked inside protein — accumulates in a ripening tomato to levels that, at their best, make the fruit taste almost like a broth. A vine-ripened heritage tomato can carry free glutamate in the low hundreds of milligrams per hundred grams of flesh, enough that cooks have reached for the tomato as a savory base for as long as there have been cooks. The modern commodity tomato sits far below that, near an **IFI-U of 300** on our index — a pale whisper of what the fruit can do. Put the two on the same line and the arithmetic is brutal and plain: the commodity tomato retains barely one part in fourteen of a true vine-ripe peak. The other thirteen parts — call it **ninety-three percent** of the fruit's savor — were bred out, never once chosen against on purpose, simply never chosen *for* while everything else was.

TRAIT SELECTED FOR	WHAT IT BOUGHT THE SUPPLY CHAIN	WHAT IT QUIETLY COST THE EATER
Thick, firm pericarp	Bruise resistance, stacking depth	Less gel and locule — where savor is highest
Delayed softening	A week more of shelf life	Flavor that never fully finishes developing
Uniform ripening (*u*)	One-pass mechanical harvest	~10–12% of sugars and carotenoids (Ch. 2)
Large, many-loculed fruit	Yield, pack-out, slicing uniformity	More water per gram of everything else
Picked mature-green	Survives transit; gassed red on arrival	Volatiles and sugars left unwritten on the vine

The strangest part of the subtraction is how *reasonable* each step was in isolation. Consider the harvest alone. A tomato bred for machine harvest needs far more than uniform color: it needs a **jointless** pedicel (the *j-2* trait) so the fruit snaps off without a woody stem that would puncture its neighbors forty-deep in a bin; a **determinate** growth habit so the whole plant sets and ripens in one window a harvester can take in a single pass; and a skin tough enough to survive a fall onto a steel conveyor. The entire processing-tomato industry — the rivers of fruit that become paste, sauce, and ketchup, most of it grown in a few hot valleys and taken by machine — was built on exactly these traits, and it feeds a continent cheaply and reliably, which is no small gift and no villain. We do not sneer at that system. We only observe, flatly, that flavor was never once on its ledger, and that a ledger with no line for a thing will spend that thing freely, generation after generation, without anyone deciding to.

It is worth being precise about the magnitude, because "it tastes worse" is an impression and the loss is a number. On our index the commodity fruit sits near **IFI-U 300** and a true vine-ripe peak runs toward the low thousands — call the retained fraction roughly one part in fourteen, the famous **ninety-three percent**. But the subtraction compounds across more than umami: the sugars are down perhaps ten to fifteen percent (Chapter 2), the fresh-green aroma is in most varieties genetically gone (Chapter 3), and the fruit is picked before it can finish writing either (Chapter 15). No single decision did this. It is the sum of a hundred small optimizations, each

one correct for the truck and silent about the tongue — which is precisely why the fix cannot be a single decision either, and why this book is 2,040 constructs long.

We think of our whole program on this fruit as a single act of subtraction, reversed. Not addition — we are emphatic about that, and we will be emphatic about it in every chapter, because it is the part that matters most to anyone who cares what they put in their body. We do not dust the tomato with a savory powder, do not spray it, do not fold glutamate into it the way a factory folds it into a snack. We reopen the fruit's own metabolism and let it make, on the vine, in the right tissue and at the right ripeness, as much of its native flavor as it once did. **Restoration**, not fortification. The honest word is *grown*. A tomato that reads IFI-U 2,600 at the receptor got there the way a wild one would have — by being a better tomato — and that is a thing you can taste, and, as the rest of this book will show, a thing you can also prove.

Chapter 2 · Uniform Ripening — *the gene that greyed the fruit.*

MECHANISM · the u locus · SlGLK2 · GOLDEN 2-LIKE

If you want one gene to stand for the whole century of subtraction, it is the one behind *uniform ripening*, and its story is almost too neat to be true. Look at a good heirloom before it ripens and you will see a dark green collar around the shoulders, near the stem — the "green shoulder," a band of deeper color the rest of the fruit lacks. Growers disliked it. The dark shoulder ripens unevenly, holds a stubborn yellow-green patch when the rest of the fruit has gone red, and reads as a defect on a uniform-red commodity grade. So, sometime around the 1920s and 1930s, breeders fixed a naturally occurring mutation called **u**, for uniform ripening, that erased the green shoulder and gave a fruit that was an even pale green unripe and an even red ripe — perfect for a machine that cannot tell a ripe tomato from an unripe one and simply takes the whole field at once.

For eighty years no one knew what *u* actually was. Then, in 2012, a team led by Ann Powell and Alan Bennett reported it in *Science*: the *u* mutation is a loss-of-function in **SlGLK2**, a **GOLDEN 2-LIKE** transcription factor, one of a small family of master regulators of chloroplast development. The dark green shoulder was not a cosmetic quirk. It was a window. It marked the region of the unripe fruit richest in chloroplasts — the fruit's own little solar factories — and chloroplasts in a developing tomato do real work: they fix carbon and build the sugars and the carotenoid precursors that the fruit will carry, as stored capital, into ripeness. Breed out GLK2 and you breed out the chloroplasts; breed out the chloroplasts and you breed out the factory that was quietly funding the flavor.



Cut a tomato at its equator and the architecture of its flavor is laid open: the firm outer wall, the radial arms of flesh, and the seed-filled locular gel where free glutamate runs highest. Much of what the *u* mutation greyed out was the fruit's own capital for building this.

The cost is measurable, and it is worse than a single number suggests, because the loss compounds down two pathways at once. The direct hit is sugar: a GLK2-deficient fruit ripens with roughly **ten to twelve percent less sugar** than its green-shouldered equivalent — a flat tax on sweetness levied before the fruit has even begun to ripen. The second hit is subtler and, to a flavor scientist, more

painful. Carotenoids are not only pigment; they are the raw stock from which the tomato cleaves some of its most important aroma molecules. Fewer chloroplasts and plastids mean less lycopene and β-carotene, and less lycopene and β-carotene mean less substrate for **carotenoid cleavage dioxygenase (CCD1)**, the enzyme that snips those long pigment chains into **6-methyl-5-hepten-2-one**, **geranylacetone**, and **β-ionone** — floral, fruity, haylike volatiles that sit near the very top of every consumer-preference study ever run on tomato. The greyed fruit loses the sugar and the aroma precursors in the same stroke. It was never a fair trade; it was simply an invisible one, because you cannot see sugar or smell a chloroplast, and a uniform red fruit photographs beautifully.

The deeper biology rewards a second look, because it explains why the lever is so clean to pull back. Plants carry two **GOLDEN 2-LIKE** genes: **GLK1**, expressed mainly in the leaves, and **GLK2**, which in the tomato does the work in the fruit. Both govern the development of **chloroplasts**, and here is the elegant part — in a ripening tomato those chloroplasts do not die but *convert*, into **chromoplasts**, the organelles that manufacture and store lycopene and β-carotene. So a green fruit rich in chloroplasts becomes a red fruit rich in chromoplasts, rich in pigment, rich in the carotenoid stock that Chapter 3 will show is also the raw material for a whole class of aroma. The dark green shoulder was never cosmetic. It was the fruit's factory *and* its warehouse, visible as a darker band simply because that was where the machinery stood densest. The *u* mutation dimmed the factory everywhere at once, and the warehouse emptied in step.

What makes GLK2 the right gene to open with is that the dimmer turns back up. Drive GLK2 under a **fruit-specific** promoter and the ripe fruit regains chloroplast-then-chromoplast capacity — more sugar, more lycopene, more aroma precursor — while the leaves and the plant's whole field behaviour stay exactly as the grower knows them. The surgery is confined to the fruit, which is the recurring shape of nearly all our tomato work and a genuinely hopeful one: the century did not *break* the machinery, it only switched pieces of it off, one silent transcription factor at a time. Much of restoration is reading the breeding record backward — finding the regulators selection quietly silenced, and handing the plant its own permission back.

What is quietly thrilling about the GLK2 story — and what makes it the right gene to open the restoration with — is that it runs *both ways*. The same group showed that driving GLK2 expression back up, especially under a fruit-specific promoter, raises chloroplast number, and with it sugars and lycopene, in the ripe fruit. The capital can be refunded. This is the shape of nearly all our tomato work, and it is a hopeful shape: the century did not break the machinery. It only switched pieces of it off. Much of restoration is reading the breeding record backward — finding the regulators that selection quietly silenced, and giving the plant its permission back.

	GREEN-SHOULDERED (GLK2 ACTIVE)	UNIFORM (U / GLK2 OFF)
Fruit chloroplasts (developing)	High, concentrated at shoulder	Low, uniform
Ripe sugars (Brix)	Baseline	~10–12% lower
Carotenoids (lycopene, β-carotene)	Higher	Lower
Carotenoid-derived volatiles	Higher (more CCD1 substrate)	Lower
Harvest	Reads uneven; hand-grade	Uniform; machine-harvestable

We restore GLK2-type function carefully, under fruit-specific control, so the leaves and the plant's architecture are untouched and only the fruit regains its factory. It is one node among the 2,040, but it is the one we point to first when someone asks how a tomato could possibly have *lost* flavor without anyone noticing. A breeder in 1930 did not decide to make tomatoes worse. He decided to make them pickable by a machine, and a transcription factor he had never heard of paid the bill.

Chapter 3 · The Chemistry of a Great Tomato — *sugars, acids, and four hundred volatiles.*

COMPOSITION · Brix · titratable acidity · the volatilome

Before we can grow a tomato back, we have to say precisely what a great one is made of, because "it just tastes better" is not something you can build toward. Tomato flavor resolves, under instruments, into three contributions that the brain fuses into a single impression: **sugars**, **acids**, and **aroma volatiles**, with free glutamate and the kokumi peptides threading savory depth and body underneath. Get the ratios right and the fruit sings; get any one of them wrong and the whole thing goes flat, sour, or oddly artificial, no matter how good the others are.

The sugars are simple to name and hard to earn: almost entirely **glucose** and **fructose**, in near-equal measure, accumulated as the fruit ripens and measured on a refractometer as degrees **Brix**. A watery commodity tomato might limp in at 4° Brix; a concentrated heritage fruit or a good cooking tomato can reach 8–10°. The acids are **citric** (dominant) and **malic** (secondary), which set the fruit's pH down around 4.3–4.5 and give it the bright backbone that keeps sweetness from cloying. Neither sugar nor acid alone is flavor. What the tongue and the kitchen both actually track is the **ratio** between them — the sugar-to-acid balance — which is why a tomato can be sweet and lifeless (sugar high, acid gone), or bright and thin (acid high, sugar gone), and why the fruit at its best holds both high at once, in tension. A tomato is a chord before it is a note.

The numbers behind that chord are worth carrying, because they are what we actually formulate against. A good fresh-market tomato runs around **5–7° Brix** of total soluble solids and a titratable acidity near **0.4–0.5%** as citric acid, which puts the sugar-to-acid ratio most tasters prefer somewhere between about **8 and 12**. Below that window the acid dominates and the fruit reads green and sharp; above it the sugar runs unopposed and the fruit goes flat and juvenile, sweet in the dull way a watery melon is sweet. Processing tomatoes push the solids higher still — every extra degree of Brix is roughly a few percent less water a factory must boil off, which is why paste varieties are bred toward 8–10° and why a cook reducing a sauce is, in effect, climbing the Brix scale by evaporation. The acid is not a flaw to be bred away; it is the backbone the whole structure hangs on, and a tomato that loses it does not become better, it becomes soup.

The aromas ride on top of all of this at almost unbelievable dilutions, and that is both the difficulty and the opportunity. Many of the fifteen-to-thirty compounds that actually matter are active at **parts per billion** — a few micrograms per kilogram of fruit — so the signal

a breeder was never measuring is carried by quantities a kitchen scale cannot see. Take the first row of the table, the fresh-green C6 volatiles, which are the smell of a tomato being cut: they are made in *seconds*, the instant the knife ruptures a cell. Intact, the fruit keeps its membrane fatty acids (linolenic, linoleic) and the enzymes **TomLoxC** and **HPL** apart; break the cell and they meet, the lipoxygenase oxygenates the fatty acid and the lyase cleaves it, and **cis-3-hexenal** and **hexanal** bloom off the cut surface before you have finished slicing. That burst *is* the smell of freshness, and it is enzymatic, instantaneous, and — in most modern tomatoes, their favorable **TomLoxC** promoter allele lost — a reaction with the gene at its head all but deleted. The fruit still has the membrane. It has mislaid the match.

Then there is the aroma, which is where the fruit becomes strange and wonderful and nearly inexhaustible. A ripe tomato releases on the order of **four hundred** distinct volatile organic compounds. Almost all of them are present at concentrations far too low to matter; the fruit's actual signature is carried by perhaps **fifteen to thirty** that sit above their odor threshold and reach the nose retronasally as you chew. And the quietly astonishing thing, established by the chemistry, is how *little* of that aroma is random: the important volatiles descend from just a few precursor pools, by named enzymatic routes the plant runs on purpose.

VOLATILE CLASS	SMELLS LIKE	BUILT FROM	KEY ENZYMES
C6 "green" (cis-3-hexenal, hexanal, cis-3-hexenol)	Fresh cut tomato, grass	Membrane fatty acids (linolenic/linoleic)	13-lipoxygenase **TomLoxC**, hydroperoxide lyase **HPL**
Carotenoid-derived (6-methyl-5-hepten-2-one, geranylacetone, β-ionone)	Floral, fruity, hay	Lycopene, β-carotene	Cleavage dioxygenase **CCD1**
Phenylalanine-derived (phenylacetaldehyde, 2-phenylethanol)	Rosy, honeyed	Phenylalanine	Aromatic aminotransferase, decarboxylase **SlAADC1/2**
Branched-chain (3-methylbutanal, 3-methylbutanol, 2-methylbutanal)	Malty, savory	Leucine, isoleucine, valine	Branched-chain aminotransferase **BCAT**
Sulfur / phenolic (dimethyl sulfide, guaiacol, methylsalicylate)	Cooked-tomato, smoky, wintergreen	Methionine, lignin precursors	Various methyltransferases / esterases

This table is, in a sense, the whole fruit's flavor written as a wiring diagram — and it is also a map of what breeding dismantled. The single most consequential loss science has traced belongs in the first row. In 2019, a landmark tomato pan-genome study reported that a favorable version of the **TomLoxC** promoter — the gene at the head of the fresh-green C6 pathway, the smell of a tomato being cut — is present in about **ninety-one percent** of wild *S. pimpinellifolium* accessions but survives in only around **two percent** of modern cultivated tomatoes. A flavor allele that was nearly universal in the

wild was all but selected out of the crop, not because anyone was breeding against fresh-tomato smell, but because it happened to sit near something a breeder *was* selecting for, and it went over the side as cargo. The green top note of a tomato, the part that makes your whole mouth believe the fruit is ripe, is in most supermarket tomatoes a genetic ghost.



We photograph the cut fruit more than the whole one, and not only because it is beautiful. A halved tomato is a tomato being honest — the chambers, the gel, the seeds, and the architecture of its sweetness and savor all laid open at once.

The capstone of the modern understanding arrived in 2017, when Denise Tieman, Harry Klee, and their colleagues published in *Science* a chemical-genetic roadmap built from chemistry on hundreds of tomato varieties, consumer taste panels, and a genome-wide association study tying the two together. Their finding was both damning and hopeful. Modern varieties were, on average, measurably lower in sugars *and* in roughly **thirteen flavor-critical volatiles** than older ones — and in many cases the better-tasting alleles still existed, scattered across heirlooms and wild relatives, lost from the elite lines only through decades of selection that never scored for flavor. The flavor was not extinct. It was dispersed, and un-scored, and waiting for someone to measure it back into one fruit. That is the sentence our whole company grew out of.

Chapter 4 · The Volatiles That Taste Like Sweetness — *sugar without sugar.*

AXIS 02 · IFI-S · TAS1R2·TAS1R3 · retronasal integration

Here is a result that sounds like a magic trick and is in fact careful science: you can make a tomato taste sweeter without adding a single gram of sugar. It comes from the same Florida group, reported by Tieman and colleagues in 2012, and it is one of the most useful facts in this entire library, because it changes what "sweetness" even means and hands us a second, cheaper lever for restoring it.

The experiment was simple to state and hard to do. Give trained tasters tomato samples and solutions; hold the actual sugar concentration fixed; vary the aroma volatiles; and ask people how *sweet* the sample is. If sweetness were purely a sugar signal — purely glucose and fructose clasping the **TAS1R2·TAS1R3** receptor pair on the tongue — then varying the smell should do nothing to the sweetness rating. It did something large. A handful of specific volatiles — among them **6-methyl-5-hepten-2-one**, **geranial**, and **1-nitro-2-phenylethane** — reliably **raised** a taster's rating of sweetness, at identical sugar. The nose was voting in the sweetness election, and its vote counted.

The mechanism is the brain, not the tongue, and understanding it is worth a paragraph because it governs how we design. Taste (sweet, sour, salty, bitter, umami) is transduced on the tongue; aroma is transduced in the olfactory epithelium, most of it reaching the receptors **retronasally**, up the back of the throat, as you chew and swallow. The brain does not keep these two channels in separate rooms. It fuses them, early and automatically, into a single unified percept it then labels "flavor" — and through a lifetime of eating sweet things that also smell a particular way, it learns to treat certain aromas as *evidence* of sweetness. Present the aroma and the brain pre-commits to the expectation; the sugar that arrives then reads as more sweetness than it is. This is learned, cross-modal, and completely real — not a trick of suggestion but the ordinary way perception works.

The Florida group quantified this precisely enough to design against, which is what lifts it from curiosity to tool. Across hundreds of tasters rating dozens of varieties, with the actual sugar held statistically constant, they could still watch perceived sweetness rise and fall with the volatile profile — and they could name the molecules doing the lifting. Beyond the three already named, the sweetness-linked set includes **(Z)-2-heptenal**, **isovaleraldehyde** (3-methylbutanal), **β-damascenone**, and **β-ionone** — and notice what several of those are: the very **carotenoid-derived** volatiles that the *u* mutation starved of substrate back in Chapter 2. The phenomenon has a name in the sensory literature, **odor-induced taste**

enhancement, and the tomato is its textbook case. The nose is not merely accompanying the sweetness; it is *contributing* to it, and the contribution is large enough to measure and specific enough to attribute to named compounds.

For a designer this is a second, cheaper budget for sweetness, and the discovery of it changes the whole economics of the sweet axis. We can raise perceived sweetness by restoring aroma the fruit used to make, without raising a single gram of sugar — which matters because sugar is metabolically expensive for the plant to accumulate and bluntly caloric for the eater, while a microgram of the right volatile is nearly free on both counts. It also, quietly, lets a fruit read as generous and ripe while carrying less of the thing the modern diet already oversupplies. We say that exactly that carefully and claim nothing past it: it is not a health benefit, it is a design fact — that the brain will accept aroma as evidence of sweetness, and that a century of breeding spent that evidence down without ever noticing sweetness was the bill it was paying.



Restoring sweetness is not only a sugar problem. A handful of carotenoid- and amino-acid-derived volatiles raise perceived sweetness independent of sugar — the nose voting in the tongue's election — which lets us lift the ripe-afternoon impression without loading the fruit.

For us this is a design gift with two edges. The obvious edge is efficiency: restoring the carotenoid-derived volatiles (the very ones the *u* mutation starved of substrate, back in Chapter 2) pays out *twice* — once as aroma in its own right, and once as perceived sweetness it donates to the sugar already present. Lift 6-methyl-5-hepten-2-one and you have made the fruit smell more like itself *and* taste sweeter, without touching Brix. On our index, this is why the restored fruit's **IFI-S** climbs toward **900** on the strength of two contributions working together — native sugars raised modestly, and perceived sweetness enhanced by volatiles — rather than on sugar alone, which is a blunt and metabolically expensive instrument. A tomato is not candy and must never become it; the goal is the sunlit

sweetness of a fruit that got one more afternoon on the vine, not the flat sweetness of a dessert. Volatiles let us reach that impression with a lighter hand.

The subtler edge is restraint, and it is the kind of restraint that separates a designed fruit from a gimmicked one. Because aroma donates sweetness, the sweetness axis cannot be tuned in isolation from the aroma axis; push a volatile for its sweetness contribution and you have also changed the fruit's smell, which the taster will notice and judge. So we do not chase IFI-S as a solo number. We compose it against the aroma profile and against the acid, holding the whole chord, which is the recurring discipline of this book and the reason the next Part is about method before it is about any single axis. The headline — *you can taste sweetness that isn't sugar* — is true, and it is one of the quietly nourishing facts in our work, because it means a fruit can read as sweet and generous while carrying less of what the body already gets too much of. We state it exactly that carefully, and claim nothing past it. It is simply a better tomato, built to be read the way the brain actually reads.



PART II OF VI

Umami, Exactly

The receptor, the multiplier, the pathway, and the flux model that makes the gain hold.

Chapter 5 · Umami, Exactly — *the taste of being fed.*

AXIS 03 · IFI-U · mGluR1 · TAS1R1·TAS1R3

Umami is the savory round that makes a broth feel like being cared for, and it is not a metaphor or a mood — it is a receptor event, as concrete as a key in a lock. Free glutamate, loose in the flesh of a ripe tomato, settles onto two kinds of receptor on the surface of the tongue: **mGluR1**, a metabotropic glutamate receptor borrowed, in evolutionary terms, straight from the brain's own glutamate-sensing machinery, and the **TAS1R1·TAS1R3** heterodimer, a two-part receptor whose large "Venus flytrap" domain closes around a glutamate molecule like a hand around a coin. When they fire, the body hears a specific and very old sentence: *here is protein, here is nourishment, eat and be fed.* That is why a tomato at its savory peak satisfies the way a merely bright or merely sweet fruit never does. It is speaking the language the body uses for sustenance itself.

To design toward that, we have to measure it, and the honest unit of measure is **EC_{50}** — the concentration of a stimulus at which it drives its receptor to half of full response. A low EC_{50} means a molecule that shouts at a whisper's concentration; a high one means a molecule the receptor can barely hear. The full relationship between concentration and response is the **Hill equation**, and it is worth writing once because every axis in this library stands on it:

$$R([L]) = R_{max} \cdot [L]^n \,/\, (EC_{50}^n + [L]^n)$$

Here R is the receptor's response, [L] the ligand concentration, R_max the saturating maximum, and **n** the Hill coefficient that sets how steeply the response climbs. Set [L] equal to EC_{50} and the equation collapses to R = R_max⁄2 — half-maximal, the half-way point, the single most information-rich number on the whole curve, because it is where the receptor is most sensitive to a change in concentration and therefore where design has the most leverage. Glutamate's EC_{50} at the umami heterodimer sits in the low **millimolar** range; the fruit's job, and ours, is to present enough free glutamate, in the right place, to push well up that curve.

The two umami receptors are worth telling apart, because they listen differently and the fruit speaks to both. **mGluR1** (with its cousin mGluR4) is a *metabotropic* glutamate receptor — the same class the brain uses for its own fast glutamate signalling — and a truncated "taste" variant sits on the tongue, exquisitely sensitive, answering glutamate down in the **micromolar** range. The **TAS1R1·TAS1R3** heterodimer is less sensitive on its own, responding in the **low millimolar** range, but it is the one that carries the synergy of the next chapter, because its large Venus-flytrap domain holds both the glutamate site and the allosteric site where the nucleotides bind. So a ripe tomato addresses two listeners at once: a sensitive one that catches the first whisper of savor, and a louder, synergy-capable one that the kitchen's oldest pairings were built, blindly, to exploit. The Hill coefficient **n** sets how steeply each climbs — above one, the

response is cooperative and switch-like; and because design has the most leverage exactly at the steep middle of the curve, around EC_{50}, that is where we aim the fruit.



The savory heart of a tomato is literally its wettest, most overlooked part — the loose locular gel a careless cook spoons into the bin. This is where free glutamate runs highest, and where much of our restoration work lives.

From EC_{50}, the index follows in one step. Fix a reference stimulus, invert the candidate's EC_{50} against it, scale by a thousand, and you have a score where *louder* means *higher*:

> **$IFI(candidate) = 1{,}000 \times EC_{50}(reference) \div EC_{50}(candidate)$**

A candidate that activates its receptor at a tenth the concentration of the reference is ten times as loud and scores ten times as high. The per-axis scorecard is normalized to a maximum of **5,000**, so every number in this book is a fraction of a known ceiling rather than a figure floating in the dark. On that line, the tomato's whole arc fits between two values. The commodity fruit sits near **IFI-U 300** — technically savory, practically silent. Our model predicts the restored fruit reaches approximately **2,600**, roughly the depth of the vine your grandmother kept seed from, except that hers depended on a good year and the right afternoon, and ours is designed to hold within that range, every lot — the harder and less romantic commitment. Between 300 and 2,600 lies everything a kitchen is built on.

THE TOMATO, MEASURED	IFI-U	WHAT IT MEANS AT THE MOUTH
Commodity / shipping-bred	~300	Savory in name; a base that needs rescuing
Vine-ripe heritage peak	~4,300	The fruit at its wild best — rare, unrepeatable
Restored (Caldera)	2,600	Held savory depth, balanced on purpose, every lot
Per-axis scorecard maximum	*5,000*	The ceiling every score is read against

It is worth taking apart the jump from 300 to 2,600, because it is not one lever but two multiplied, and the decomposition is honest about where the savor actually comes from. Roughly, the restored fruit presents on the order of **three to four times** more free glutamate in the ripe locular tissue than a commodity fruit — the direct work of Chapter 7's pathway. The way that glutamate is held and delivered, concentrated in the gel where the tongue meets it rather than diluted through the flesh, pushes its *effective* potency further still.

Compound a few-fold gain in concentration with a more favourable presentation and you arrive at the roughly eight-to-nine-fold gain in loudness that 300 → 2,600 represents (a factor of about 8.7). Every step of that is biology we can name and measure. That is the whole difference between a designed fruit and a flavored one: you can take the score apart and find a gene behind each piece of it, which means you can also *hold* each piece — the subject, eventually, of Chapter 13.

Notice what we did and did not target. We restore to 2,600, not to the 4,300 of a theoretical vine-ripe peak and emphatically not to the 5,000 ceiling, because a tomato that is only umami is as wrong as one that is only sweet — it reads as a bouillon cube, not a fruit. The number we chose is a *balanced* number, held against the sweetness and the acid and the bright edge, and choosing it was a judgment about deliciousness, not a race to the top of a scale. That restraint is the whole ethos of the index: the number is a servant of the chord, never the point of it. We measured umami exactly so that we could put exactly the right amount of it back.

Chapter 6 · The Synergy — *glutamate and the nucleotide multiplier.*

MECHANISM · IFI-U × nucleotides · the Venus flytrap

There is a second fact about umami, discovered in a Japanese kitchen long before anyone could explain it, and it is so large that no honest account of the savory tomato can skip it: umami **multiplies**. Glutamate alone is savory. Glutamate in the presence of a tiny amount of a **5′-ribonucleotide** — **IMP** (inosinate), **GMP** (guanylate), or to a lesser degree **AMP** (adenylate) — is savory far out of proportion to the sum of its parts. This is the synergy that underlies dashi (kombu's glutamate meeting bonito's inosinate), the long marriage of tomato and parmesan, the depth of a mushroom-and-tomato ragù. It is not addition. It is amplification, and it has a molecular mechanism and an equation.

The mechanism lives in that Venus flytrap domain of the **TAS1R1·TAS1R3** receptor. Glutamate binds inside the cleft of the flytrap and nudges it toward its closed, active conformation. The ribonucleotide does not compete for that site; it binds nearby, at the lip of the flytrap, and acts like a clasp — it **stabilizes the closed, glutamate-bound state**, lowering the energy of the active conformation so that the same amount of glutamate holds the receptor shut far more effectively. In the language of Chapter 5, the nucleotide drops glutamate's **apparent EC_{50}**: the fruit's savor becomes louder without a single additional molecule of glutamate. Structural and mutational studies have mapped this allosteric site; it is one of the cleaner stories in taste biology, and it is the reason a pinch of one thing can transform a pot of another.

Put numbers to Yamaguchi's equation and the multiplication stops being abstract. Work in her units, grams per deciliter, and take a restored tomato presenting the equivalent of **0.1 g/dL** of free glutamate. Alone, that is an umami intensity of 0.1. Now add just **0.02 g/dL** of guanylate from a few grams of dried mushroom, and the cross-term contributes `1218 × 0.1 × 0.02 ≈ 2.4` — so the perceived umami leaps from 0.1 to roughly **2.5**, a more than twentyfold jump in savor bought with a trace of a nucleotide that has almost no taste of its own. The exact coefficient depends on the pair of molecules, and the equation is empirical rather than fundamental, but the shape of it is universal and a little violent: synergy is not a seasoning, it is a **multiplier**, and it multiplies whatever glutamate is actually there.

That last clause is the entire design consequence for the tomato, so we state it plainly. The synergy acts on the *u*, and a hollow commodity tomato brings almost no *u* to be multiplied — throw all the mushrooms you like at IFI-U 300 and there is little there to amplify. Caldera brings a loud, generous glutamate, so a small and honest amount of a culinary nucleotide — dried porcini or shiitake (GMP), a spoon of miso or soy, and yes, for those who eat it, cured anchovy or bonito (IMP), each written with equal respect — lifts the

whole dish into a register a flat tomato could never reach. We grow the glutamate back, in part, so that the kitchen's oldest trick finally has something worth multiplying.

The quantitative form was worked out empirically by Shizuko Yamaguchi in 1967, and it is worth seeing because it shows how violent the multiplication can be. For a mixture of glutamate (fraction *u*) and inosinate (fraction *v*), the perceived umami intensity *y*, expressed as the equivalent concentration of glutamate alone, follows:

```
y = u + 1218 · u · v
```

Read that coefficient again. The cross-term carries a multiplier of **1218**. When *v* is zero — no nucleotide — you simply get *u*, the glutamate on its own. But introduce even a small *v* and the product term *u·v*, scaled by 1218, can dwarf the linear term. In the classic result, a 1:1 mixture of glutamate and inosinate tastes roughly **eight times** as intense as the same total weight of glutamate alone, and well-chosen ratios push the apparent intensity far higher. A whisper of the right nucleotide does not add to the savor; it multiplies it.



Umami synergy is vegetarian at its heart: the tomato brings the glutamate, a dried mushroom or a spoon of miso brings the guanylate, and the receptor multiplies the two. A restored tomato is the ideal glutamate partner in that equation — loud enough that a little nucleotide goes a very long way.

For the tomato, the synergy cuts two ways, and we design around both. First, the tomato is one of nature's great **glutamate** donors but a modest nucleotide donor — it carries some free AMP and GMP, but it is fundamentally the *u* in the equation, not the *v*. That is precisely why the tomato has always wanted a partner: cured anchovy or bonito (IMP), aged cheese (free glutamate plus some nucleotide), and — the vegetarian-first pairing we reach for first at our own table — **dried mushrooms**, which concentrate GMP as they dry, or a spoon of miso or soy, which ferment both glutamate and nucleotides into being. Write the respect plainly in both directions: the anchovy earns its place in a sauce by exactly this chemistry, and so does the dried porcini; neither is an apology for the other. Second, and this is

the design consequence, a *restored* tomato is a better synergy partner than a hollow one, because the multiplier acts on the glutamate that is actually there. A commodity tomato at IFI-U 300 brings little for the nucleotide to multiply; Caldera at 2,600 brings a loud, generous *u*, so a small, honest amount of dried-mushroom GMP lifts the whole dish into a register that a flat tomato could never reach no matter how much mushroom you threw at it. The synergy is free savor the fruit was built to accept. We grow the glutamate back in part so the kitchen's oldest trick finally has something to work with.

Chapter 7 · Grown Back In — *the glutamate pathway.*

METHOD · GAD · GDH1 · GS·GOGAT · the GABA shunt

Now the crucial word: *grown*. The savor in a restored tomato is not sprayed, dusted, or injected; it is manufactured by the fruit, in the fruit, out of the fruit's own carbon and nitrogen, along routes the plant has run since long before we arrived. Our entire intervention is to adjust how much the plant makes and how much of it it holds as free glutamate in the ripe flesh, rather than shunting it away. To do that honestly you have to know the pipes, so here are the pipes.

Glutamate sits at the busiest intersection in all of plant nitrogen metabolism. It is made and consumed by four reversible or near-reversible reactions that the cell uses to move nitrogen between amino acids and keep its carbon-skeleton budget balanced. **GDH** (glutamate dehydrogenase; the fruit's workhorse isoform is **GDH1**) condenses ammonium with **2-oxoglutarate** — a carbon skeleton pulled straight from the TCA cycle — to make glutamate, and runs the reaction the other way when the cell needs that skeleton back. The **GS·GOGAT** cycle (glutamine synthetase paired with glutamate synthase) is the main highway for assimilating nitrogen into glutamine and then glutamate. And crucially, draining the pool from the side, **GAD** (glutamate decarboxylase) converts glutamate into **GABA**, feeding the so-called **GABA shunt**, a bypass around part of the TCA cycle that the fruit ramps up under stress and during ripening.

This is where the design becomes interesting, and where a cautionary piece of real-world prior art makes the point better than any diagram. In 2021, Japan's Sanatech Seed brought to market the world's first commercialized CRISPR-edited food: a tomato, "Sicilian Rouge High GABA," engineered to accumulate high **GABA** by knocking out the autoinhibitory domain of **SlGAD** so the enzyme runs harder. It is an elegant, approved, shelf-ready product — and it edits the *exact* gene at the heart of our pathway. But look at the direction. GABA is made *from* glutamate, by GAD. To pile up GABA you pull glutamate *down* the shunt and *out* of the free pool. The GABA tomato and the umami tomato push on the very same valve — in opposite directions. For us, chasing free glutamate for umami, the lesson is precise: it is not enough to make more glutamate; you have to make more *and* keep GAD from quietly carrying it off to GABA at the ripe stage, all without starving the fruit of the GABA shunt it needs for normal ripening. That is a balance problem, not a single-gene problem, and it is exactly why the next chapter exists.

The GABA shunt itself deserves a word of respect, because the naive move is to simply shut it off and keep all the glutamate, and that move is wrong. The shunt — glutamate to GABA by **GAD**, then GABA onward by **GABA-T** and **SSADH** back into the TCA cycle as succinate — is one of the fruit's main tools for buffering cytoplasmic pH, balancing carbon against nitrogen, and weathering the oxidative stress of ripening. Green tomatoes are, by fresh weight, startlingly

rich in GABA for exactly these reasons, and a healthy fruit spends that GABA down as it ripens. Abolish GAD and you get more glutamate *and* a fruit that ripens badly and stores poorly. So our design is a dimmer, not a switch, and it is stage-specific: let the shunt run in the green fruit, where the plant needs it, and restrain it late, at the ripe stage, in the locular tissue, where we want the glutamate to stay free and savory. It is the difference between taking the fruit's tool away and asking it, politely and at the right moment, to set the tool down.

It also helps to ask where the glutamate's atoms even come from, because "make more glutamate" is only free if the fruit has the raw material. The carbon skeleton is **2-oxoglutarate**, pulled from the TCA cycle; the nitrogen is ammonium, assimilated through GS·GOGAT. A ripening fruit is, usefully, a fruit that has *stopped growing* — it is no longer spending its carbon and nitrogen on cell division and expansion — so there is slack in the budget exactly when we want to spend it on savor. That timing is not a coincidence we exploit so much as a door the fruit opens on its own; ripening is when a tomato turns from building itself to presenting itself, and glutamate is part of the presentation. We are, in a real sense, asking the fruit to present a little harder.



Restoration happens at the source — in the fruit, on the vine, in the living plant — not at the shaker. The glutamate a Caldera carries was condensed from the tomato's own carbon and nitrogen by enzymes it already owned; we only adjusted how much it makes and how much it keeps.

So the intervention is a set of coordinated nudges, not a hammer. We tune expression so the ripening fruit (i) feeds the glutamate pool more generously through GDH1 and GS·GOGAT, drawing on the 2-oxoglutarate the fruit can spare as it stops growing and starts ripening; (ii) holds more of that glutamate as *free acid in the locular gel*, the wet chambered tissue where Chapter 2 showed the savor naturally concentrates and where a cook will actually meet it; and (iii) restrains, without abolishing, the GAD draw to GABA at the ripe stage, so the fruit still ripens correctly but keeps its savor in the free pool. Every one of these is a native reaction under a tuned promoter; we add no foreign flavor and no foreign metabolism. The tomato

ends up doing what a wild, vine-ripe, unhurried tomato does — building and keeping its own glutamate — just reliably, and in February.

ENZYME / ROUTE	NATIVE JOB	OUR RESTORATION NUDGE
GDH1 (glutamate dehydrogenase)	2-oxoglutarate + $NH_4^+ \rightleftharpoons$ glutamate	Feed the free-glutamate pool during ripening
GS · GOGAT	Primary N assimilation into glutamate	Sustain supply without nitrogen stress
GAD (glutamate decarboxylase)	Glutamate → GABA (the shunt)	Restrain at ripe stage; keep glutamate free
Locular partitioning	Where free acids pool	Hold glutamate in the gel, where it's tasted

This is the difference that matters to anyone who cares what they put in their body, and we will not stop saying it: a tomato designed to reach **IFI-U 2,600** at the receptor gets there by being a better tomato, not a dressed-up one. When you taste the depth, you are tasting *Solanum lycopersicum*, concentrated back toward itself. Nothing stands between the plant and the pleasure.

Chapter 8 · The Flux-Balance Argument — *why the pathway, not the gene.*

METHOD · FBA · S·v = 0 · 2,040 constructs

The single most common way to fail at engineering flavor is to find the gene that makes the molecule you want and simply turn it up. It feels like it should work. It almost never does, and the reason is the subject of this chapter, because it is the reason our tomato work is 2,040 constructs and not one.

Metabolism is not a line of genes; it is a network of shared intermediates, and every intermediate is being pulled on from several directions at once. Overexpress one enzyme in the middle of that network and you do not get more product — you get a traffic jam. The enzyme starves for its substrate because the step feeding it cannot keep up; or it floods the next step, which backs up; or it drains a shared pool, like 2-oxoglutarate or ammonium, that four other reactions were counting on, and the cell, which is very good at defending its own balance, quietly compensates until your intervention nets to almost nothing. Glutamate, sitting at the busiest intersection in nitrogen metabolism (Chapter 7), is the worst possible place to apply a single-gene hammer, because *everything* touches it. Push GDH1 alone and the GABA shunt or the GS·GOGAT cycle will rebalance around you. The pool is defended.

The tool built for exactly this problem is **flux-balance analysis (FBA)**, and its central assumption is both humble and powerful. Write down every reaction in the network as a column in a great stoichiometric matrix **S**, with a row for every metabolite, and let the vector **v** hold the rate (flux) of each reaction. At metabolic steady state — which a ripening fruit approximates over the hours and days that matter — nothing accumulates unboundedly, so production and consumption of each internal metabolite must balance:

> $\mathbf{S} \cdot \mathbf{v} = 0$

This single equation, over a genome-scale network with thousands of reactions, defines the entire space of flux distributions the cell *could* run without violating mass balance. It is underdetermined — many flux patterns satisfy it — so you add the constraints you know (nutrient uptake limits, irreversibilities, measured maxima) and then ask a linear-programming solver to find, within that feasible space, the flux distribution that **maximizes an objective** you choose: here, free-glutamate accumulation in ripe locular tissue, subject to the fruit still ripening normally. The solver does not tell you to turn up one gene. It tells you which *combination* of steps, nudged together,

actually moves product — and, just as valuable, which beloved candidate genes do nothing because the network routes around them.



The 2,040 constructs are a designed search, not a brute-force spray. A genome-scale flux model nominates the handful of coordinated nudges worth testing; the bench confirms which actually move free glutamate without breaking ripening. This is the compute-then-grow loop the whole platform runs on.

For the tomato, the flux model's verdict matched the biology of Chapter 7 and sharpened it: the lever is not any one enzyme but the **branch point** — the balance between feeding the glutamate pool (GDH1, GS·GOGAT) and draining it to GABA (GAD), governed under ripening-stage control so the fruit keeps its shunt but keeps its savor. That is a multi-gene, multi-promoter proposition by its nature, and it is why "the tomato" is 2,040 constructs. A **construct**, in our shorthand, is one testable combination — a particular gene or edit, under a particular promoter, in a particular genetic background. The 2,040 is the designed search space the platform actually walked, most of it nominated in silico and pruned hard before anything was grown, because growing a tomato takes a season and compute takes an afternoon.

It is fair to ask what two thousand constructs could possibly consist of, and the answer is a combinatorial grid, not two thousand unrelated ideas. A handful of **target nodes** — GDH1, GS·GOGAT, GAD, GLK2, LIN5 and their regulators — times a palette of **promoters** (constitutive, fruit-specific, ripening-stage-specific, each setting *how much* and *when*) times several **genetic backgrounds** times the **edit types** themselves (up-regulation, knock-down, point substitution, domain removal) generates a design space in the thousands before anyone has had a genuinely new idea. The flux model and the sequence models prune that grid savagely — most combinations are predicted to do nothing, or to break ripening, and are never planted — so the 2,040 that reach soil are the survivors of a far larger in-silico tournament. That is the real meaning of the word *platform*: the slow, expensive step (a growing season) is rationed by the fast, cheap step (an afternoon of compute), and the living plant is only ever asked a question worth a season to answer.

The objective function matters as much as the search, and choosing it is a judgment, not a default. We do not maximize free glutamate; we maximize it **subject to constraints** — the fruit must still ripen on schedule, still set a normal crop, still hold its sweetness and acid in the window of Chapter 9, still land its umami at a *balanced* 2,600 rather than a bludgeoning 5,000. A solver handed "maximize

glutamate" with no constraints will happily propose a fruit that is a savory brick and a horticultural failure. The art is in the constraints, and the constraints are where a family that cares how a tomato should taste gets to put its thumb on the scale — not against the math, but inside it.

FROM ONE FRUIT, BY THE NUMBERS	VALUE
Constructs designed and screened	**2,040**
Native engineering difficulty	Easy
Primary axes expressed	S · U · F · M
Free-glutamate restoration (IFI-U)	300 → 2,600
Batch coefficient of variation	**≤ 7%**

The method is not ours alone and it is not ours first; it is the same **ESM2-plus-flux-balance** loop that the platform proved on the pepper, where a protein language model scores sequence variants and a genome-scale flux model confirms where the true rate limit lives (we will meet that machinery again, in its native pepper form, when we carry heat *into* the tomato in Chapter 18). Five of the platform's seven modules transfer unchanged to any organism with a sequenced genome, and the tomato — genome in hand since 2012, difficulty Easy — was the obvious place to prove the transfer. The point to carry out of this chapter is a philosophy as much as a technique: we do not turn up a gene and hope. We model the whole network, find the combination the network cannot route around, test it, measure it, and keep only what holds to CV ≤ 7%. Deliciousness, done this way, stops being luck and becomes a specification.



PART III OF VI

The Whole Chord

Umami is the depth. Sweetness, kokumi, and the bright dry edge are the notes it needs to hear.

Chapter 9 · Sweetness, Returned — *the ripe afternoon.*

AXIS 02 · IFI-S · TAS1R2·TAS1R3 · LIN5 · the sink

Umami is the depth; sweetness is the light, and the memory tomato tasted like both at once. Sweetness is a duet on the tongue — **TAS1R2** and **TAS1R3** clasp together, and only when both are moved does the brain register *sweet* — and a great tomato plays that duet not with the flat sugar of candy but with the specific, sunlit sweetness of a fruit that was allowed one more afternoon on the vine. We have already met the brain's half of this, the volatiles that donate perceived sweetness independent of sugar (Chapter 4). Here is the tongue's half, and the genetics beneath it, because a restored tomato lifts both.

The sugars themselves, glucose and fructose, are the end of a supply chain that runs from the leaf to the fruit, and the single most studied control point on that chain is an enzyme called **LIN5**, a cell-wall (apoplastic) **invertase** that sits at the fruit's doorstep. Sucrose arrives from the leaves through the plant's plumbing; LIN5, anchored in the cell wall of the fruit, cleaves it into glucose and fructose right at the point of unloading, and that cleavage is a big part of what makes the fruit a strong **sink** — a tissue that pulls sugar toward itself. The gene sits under a famous flavor QTL, **Brix9-2-5**, which was mapped to a single amino-acid difference in LIN5 inherited from the wild green-fruited relative *Solanum pennellii*; carry the wild allele and the fruit accumulates measurably more sugar. This is one of the clearest cases in all of crop science of a single, nameable molecular difference moving a trait people can taste, and it tells us exactly where to work: sink strength, set at the fruit's own wall, is a lever on sweetness as surely as photosynthesis is.

Downstream of LIN5 the fruit keeps more dials, and naming them shows how much room there is to work without ever touching the leaf. **SWEET** transporters move sugar across membranes into the fruit's storage cells; a small protein called **INVINH1** inhibits the cell-wall invertase, so tuning *it* changes how much of LIN5's own capacity actually gets used; **sucrose synthase** and **fructokinase** set whether incoming sugar is burned or banked. Each is a native gene with a known effect on the final sweetness, and each compounds with the restored chloroplasts upstream. The picture to hold is of a supply chain — leaves make sucrose, the plant's plumbing carries it, the fruit's wall unloads and cleaves it, transporters bank it — where a century of breeding happened to weaken several links at once. Restoration here is not forcing sugar in; it is strengthening the links back toward a fruit that *pulls hard for its own sweetness*, the way a wild vine-ripe one does when nothing is rushing it.

And still we do not simply maximize Brix, because sweetness is not the goal — *balance* is. A tomato bred only for solids, with its acid left behind, is the flat, over-sweet, strangely lifeless fruit that tells you something is wrong without telling you what. The missing thing is the

acid's argument against the sugar. So the sweetness axis is always tuned *against* the citric backbone of Chapter 3, landing near **IFI-S 900** not because 900 is a maximum but because 900 is where the sweetness meets the acid and the savor and resolves. The ripe afternoon is a ratio. We restore the sugar only until the ratio is right, and then — this is the hardest instruction in flavor design and the one a machine will not give you — we stop.



The ripe afternoon is a ratio, not a sugar. We lift the fruit's native sweetness — through sink strength and perceived-sweetness volatiles together — only until it meets the savor and the acid, and then we stop. A tomato that is only sweet is as wrong as one that is only sour.

But — and this is the discipline the whole Part is built to teach — we do not chase sugar as a solo number either. The afternoon the truck steals is not just missing sweetness; it is missing *balance*. A tomato is a running conversation between its sweetness, its acid (the citric and malic backbone of Chapter 3), and its umami, and the gift of a measured axis is that we can raise one voice precisely without flattening the others. We lift the native sugars, through sink strength and the GLK2-restored photosynthetic capital of Chapter 2, and we lift *perceived* sweetness through the carotenoid-derived volatiles, and we raise both only until the sweetness **meets** the savor and the acid — landing the restored fruit near **IFI-S 900**. Not dessert-sweet. August-sweet: just enough to hold the acid and the glutamate in tension, the way the fruit does on its own when no one is rushing it.

CONTRIBUTION TO IFI-S	LEVER	CAPS ON
Native sugars (glucose, fructose)	Sink strength (**LIN5**), restored chloroplasts (**GLK2**)	The acid balance — sugar must meet, not bury, the citric backbone
Perceived sweetness (no sugar)	Carotenoid-derived volatiles (6-methyl-5-hepten-2-one, geranial)	The aroma profile — a volatile pushed too far reads artificial

The number 900 is, like the 2,600 of umami, a *chosen* number — a balance point, not a maximum. The sweetness exists to serve the chord. Raise it past where it meets the acid and the fruit goes slack and juvenile; leave it too low and all that restored umami turns heavy and savory-flat, a broth with no light in it. Between those failures is the ripe afternoon, and a measured axis is simply how we put every fruit at that afternoon on purpose, instead of once a summer, by luck, in a good year.

Chapter 10 · The Savory Floor — *kokumi and the body of a sauce.*

AXIS 05 · IFI-K · CaSR · γ-glutamyl peptides

Umami is a taste. **Kokumi** is something stranger and, in the tomato, inseparable from it — and no account of why a restored tomato *anchors a kitchen* is complete without it. Kokumi has no flavor of its own. You cannot point to a "kokumi taste" the way you can point to sweet or sour. It is mouthfeel made molecular: the sensations of **richness, continuity, and mouthfulness** — the feeling that a dish fills the whole mouth and *stays*, that it is complete rather than merely correct. It is the difference between a quick tomato sauce that tastes right and a long-simmered one that tastes finished, and until recently it had no mechanism. Now it has one.

The receptor is **CaSR**, the calcium-sensing receptor, the same molecule your parathyroid uses to monitor blood calcium, expressed also on the tongue. Its agonists for taste are **γ-glutamyl peptides** — small peptides with a glutamate joined through its side-chain (the γ-carbon) rather than the usual backbone linkage. The most studied is **glutathione** (γ-Glu-Cys-Gly), but a whole family of γ-glutamyl di- and tri-peptides does the work, and they are produced and accumulated exactly where you would hope: in ripening fruit, in alliums, in aged cheeses, in long ferments, and generated continuously during slow cooking as proteins break down and glutamate gets re-ligated.

Two facts about kokumi make it unusually powerful in a kitchen. The first is structural: **CaSR** is a *class C* G-protein-coupled receptor — the very same family as the umami and sweet receptors, with the same Venus-flytrap architecture — which is part of why kokumi and umami feel so intertwined on the tongue. Related machinery, adjacent cells, overlapping glutamate chemistry; the body built its savor-sensing as a neighborhood, not a set of islands. The second fact is temporal, and it is the one cooks have always felt without naming: the kokumi peptides are *manufactured by cooking itself*. Every hour a pot simmers, proteins hydrolyze and free glutamate re-ligates through its γ-carbon into new γ-glutamyl peptides, so a long braise literally builds its own mouthfeel as it goes. "Depth from time," measured, is largely this reaction running.

A restored tomato short-cuts that clock, and that is its quiet gift to a weeknight. It arrives already carrying the peptides a long simmer would have had to make, so a twenty-minute sauce built on it tastes like it cooked for an afternoon. We did not invent kokumi — the sensation was characterized in Japan, and the γ-glutamyl peptides behind it catalogued, over decades of careful work — but we grew into the fruit the thing a Sunday at the stove used to be the only way to get. The measurement matters here too: because kokumi has no taste of its own, it was for a long time the hardest axis to pin down, describable only by what it did to *other* tastes. Anchoring it to CaSR activation gave it a number, **IFI-K**, and a number is what let us put

exactly 1,400 of it into Caldera on purpose instead of hoping a long cook would deliver some. When these peptides move CaSR, they do not add a flavor; they **modulate** the others — they round the umami, extend its finish, and lend the whole mouthful a physical body. Kokumi is the floor the rest of the dish stands on.



Kokumi is why a long-simmered thing tastes complete and a quick one only tastes correct. A clove of slow-cooked garlic brings a wave of γ-glutamyl peptides to a tomato's own — two sources of CaSR agonist rounding the savor into a body you feel before you can name it.

In the tomato we grow kokumi in beside the glutamate, lifting the fruit's native γ-glutamyl peptides so that **Caldera** carries **IFI-K 1,400** — enough that the restored fruit arrives already round, already bodied, before a cook has done anything to it. This is the tomato's deepest structural gift to cuisine, and the reason it is the savory foundation of so many of them: it is not an ingredient so much as a *base layer*. Lay a restored tomato under a dish and it does the work a cook used to need a stockpot and a Sunday for — the depth, the body, the continuity — so that everything built on top of it has a floor to stand on. Umami gives the depth; kokumi makes the depth belong to the whole mouth instead of the tip of the tongue.

Composing the two axes is the subtle part, and it is pure Chapter 8 thinking applied at the receptor instead of the pathway. Umami (mGluR1, TAS1R1·TAS1R3) and kokumi (CaSR) are different receptors reading different molecules, but they share the same glutamate chemistry upstream — free glutamate for one, γ-glutamyl peptides for the other — so a naïve attempt to maximize both at once competes for the same nitrogen and the same glutamate pool, and a careless stack cancels into muddy over-savoriness that reads as a bouillon cube, not a fruit. The savor of a great tomato is a *held ratio* of free glutamate to peptide, of mGluR1 signal to CaSR signal, and holding it is exactly the kind of multi-objective balance the flux model was built to find. What you taste as "depth you can feel" is, underneath, two receptors tuned to agree. And it is why, in the kitchen, a restored tomato and a few cloves of slow-cooked garlic — garlic being one of the great γ-glutamyl donors — make a base so complete it can carry an entire meal: two sources of CaSR agonist, laid under a fruit already loud with glutamate, the oldest savory floor in cooking, now specified.

Chapter 11 · The Bright Edge — *acid, skin, and seed.*

AXIS 08 · IFI-A · salivary PRPs · the chord resolved

A tomato without its edge is a sad, soft thing — a puddle of depth with no spine, a sauce you keep salting because something is missing and the missing thing is *brightness*. All that restored umami and kokumi would drown the fruit if there were nothing to cut it, and two things cut it: the tomato's native **acid**, which we hold rather than erase, and a quieter sensation at the very finish called **astringency**, the faint dry grip of the skin and the seed. The chord does not resolve without them, so this chapter is about the notes that keep the depth honest.

The acid we have already named — citric dominant, malic secondary, pH down near 4.3–4.5 — and the design rule for it is restraint of a particular kind: *do not restore it away*. It would be easy, chasing a smooth and crowd-pleasing fruit, to breed and tune toward low acidity, and the result would be exactly the flabby, over-sweet, over-savory tomato that tastes like it is trying too hard. We hold the native acid as the fixed backbone against which sweetness and savor are balanced. In the language of this book, acid is not an axis we push; it is the *reference line* the pushable axes are measured against, which is why Chapters 9 and 10 kept capping their numbers "against the acid." The brightness is load-bearing.

Astringency is the genuinely interesting edge, because it is the one sensation in this whole book that works on the *mouth itself* rather than on the tongue's chemical receptors. There is no "astringency taste." Instead, tannins and other polyphenols — concentrated in a tomato's skin and around its seeds — bind and precipitate the **proline-rich proteins (PRPs)** that lubricate your saliva. Strip the lubrication and the mouth tissues drag against each other, and the brain reads that friction as a *dry, puckering grip*. That is astringency: a tactile event, mediated not by a receptor but by the loss of a lubricant, the small catch you feel at the finish of a tomato eaten at exactly the right moment.

The chemistry under that catch is a binding reaction you can almost picture. **Proline-rich proteins** are unusually open, floppy molecules — proline kinks a protein chain and keeps it from folding tight — and that openness gives tannins many exposed faces to grab. A polyphenol carrying several hydroxyl groups hydrogen-bonds and stacks against those proline faces; proteins and tannins crosslink into aggregates heavy enough to fall out of solution, and the saliva, stripped of its lubricating film, can no longer glide. The mouth reports friction. Evolutionarily, salivary PRPs are thought to be a **defense** — a sacrificial protein the body pours out to mop up dietary tannins before they can bind anything more important — which is

part of why astringency reads, faintly, as a *warning* folded into a pleasure, and why a touch of it sharpens attention at a dish's close rather than dulling it.

Acid plays a related trick on the same tissue, and naming it completes the picture of the "bright edge." Low pH also thins and partly denatures the saliva's proteins, which is why a bright tomato feels physically *clean* and sets the mouth watering: the acid is cutting the richness not only in taste but in the literal slickness of the mouth, provoking a flush of fresh saliva that resets the palate for the next bite. So the edge of a tomato is, at bottom, the fruit managing your saliva — drying it a little with tannin, thinning it a little with acid — and a fruit that manages it well finishes crisp and leaves you reaching back in. Caldera's **IFI-A 300** is that management, set low and deliberate: enough grip to give the savor a spine, not so much that the fruit turns green and harsh. It is the one axis we restore by *restraint*, and the hardest to see precisely because, done right, it draws no attention to itself at all.



The skin and the seed carry the fruit's astringent edge — the tannins that bind the saliva's proline-rich proteins into the small dry grip at a tomato's finish. We leave it in, low and deliberate, because a fruit with no edge is a fruit with no spine.

We leave it in, on purpose, low and exact. **Caldera** reads **IFI-A 300** — a thin bright line drawn under the sweetness and the savor. Erase astringency entirely and the fruit turns slack and cloying, all depth and no finish; let it run wild, as it does in an underripe tomato's green skin, and you get the harsh, puckering, almost metallic bite that makes a bad tomato worse than no tomato. Between those is the clean, structured finish of a perfectly ripe fruit, and a measured axis is how we put every tomato at that finish instead of hoping the season delivers it. So the chord resolves in four voices, and it is worth seeing them together, because this quartet *is* the restored tomato:

AXIS	ROLE IN THE CHORD	CALDERA
IFI-U · Umami	The depth — the floor of the whole fruit	2,600
IFI-S · Sweetness	The light — the ripe afternoon	900
IFI-K · Kokumi	The body — depth made mouth-filling	1,400
IFI-A · Astringency	The edge — the bright dry finish	300

Depth, light, body, and a bright dry edge: the tomato is a four-part chord, and restoration means growing every voice back to the one the others need to hear. Push any single one alone and the fruit falls apart in a different direction — heavy, or juvenile, or slack, or harsh. Hold all four in the ratio a wild vine-ripe fruit finds on its best day, and you have a tomato that tastes, exactly and reliably, like a tomato should. The next chapter is that tomato, with a name.

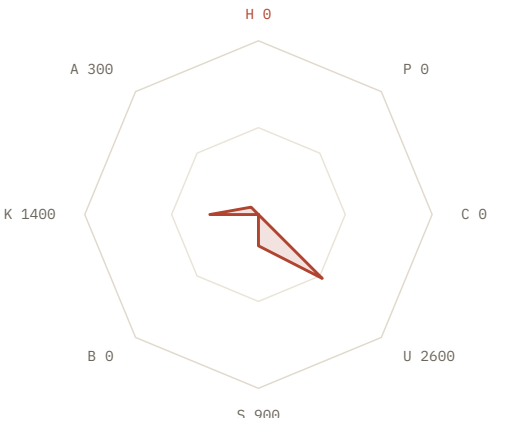
Chapter 12 · Caldera — *the cooled heart.*

FLAGSHIP · restoration cultivar · expresses 4/8

Our restored tomatoes carry the program's house names, drawn from the language of volcanoes — and the flagship, the one we hand across the table when someone asks what all of this is *for*, is **Caldera**. The name is not decoration. A caldera is the wide, quiet basin a volcano leaves when its heat has settled and sunk inward — the cooled, collapsed heart at the center of all that former fire, often holding a still lake where the summit used to be. Caldera the tomato carries no heat at all. It is pure restored depth: the calm, savory basin at the center of a whole frontier of fire the fruit *could* become (Chapter 18), but has not here, on purpose. This is the restoration in one fruit, and it is the proof of the entire method.

Read the profile, and read it knowing that every number on it was **grown**, not added — condensed by the fruit's own enzymes, on the vine, out of its own carbon and nitrogen:

IFI PROFILE



IFI-H	0
IFI-P	0
IFI-C	0
IFI-U	2,600
IFI-S	900
IFI-B	0
IFI-K	1,400
IFI-A	300

AXIS	SCORE	WHAT IT IS, IN THE FRUIT
IFI-U · Umami	2,600	Free glutamate, restored through GDH1 / the glutamate pool
IFI-S · Sweetness	900	Native sugars + perceived-sweetness volatiles, balanced to the acid
IFI-K · Kokumi	1,400	γ-glutamyl peptides — the body you feel before you name it
IFI-A · Astringency	300	The skin-and-seed edge, left in so the fruit finishes clean
IFI-H / P / C / B	—	None — this is the cooled heart; the fire comes later, elsewhere

What the radar draws is not a spike but a *shape*: umami towering, sweetness rising to meet it, kokumi giving the whole thing a body, and a thin astringent line holding it all in check so the fruit resolves instead of cloying. Four axes of eight, each one a restoration rather than an addition, composed into the chord of Chapter 11. This is what a tomato is supposed to be.

Set Caldera's radar beside a great heirloom's and the difference is not height — it is *steadiness*. A perfect Brandywine in late August, from the right soil, picked at the right hour of the right day, might out-reach Caldera on a single axis; heirlooms are capable of real greatness and we would never pretend otherwise. But ask that Brandywine to do it again next Tuesday, or in a cool year, or after three days in a distribution center, and the shape collapses. The greatness was real, and it was a lottery. Caldera's radar is the heirloom's best day with the variance taken out — which is why the claim on the label is so carefully modest. Not *better than the best tomato you ever had*. That tomato, *on demand*. In a world where the best tomato of most people's lives happened once, years ago, and never came back, "on demand" is the radical word in the sentence.



Caldera — the restoration flagship, named for the cooled, collapsed basin at a volcano's heart. No heat; pure grown-back depth. It is the fruit we hand across the table to prove the whole method in a single bite.

We did not design Caldera to astonish anyone, and that is the point we are proudest of. We designed it to taste, exactly and reliably, the way the best tomato of your life tasted on its best day — and then to taste that way again in February, which is the harder miracle by far. A vine-ripe heirloom at its peak might reach past Caldera on a single axis in a perfect year; what no heirloom can do is *repeat*. Caldera's whole quiet radicalism is the comma in "exactly, and reliably." It takes the best tomato of your life out of the realm of weather and

luck and soil and the right afternoon, and puts it into the realm of specification — IFI-U 2,600 ± a few percent, every lot, every month, anywhere the seed is grown.

There is a temptation, writing a chapter like this, to make the flagship sound like a triumph over the heirloom, and we want to refuse it plainly, because it would be both untrue and against everything the family believes. The heirloom is not the enemy; the heirloom is the *target*. Every number in Caldera's profile is a measurement of what a great old vine-ripe tomato does on its best day, written down and made repeatable. We are not improving on the memory. We are defending it — against the truck, against the cold chain, against the bad year and the early pick — so that the fruit a grandmother kept seed from, which lived in one garden in one decade, can be grown by anyone, anywhere, in February, and taste the way it tasted. The radical act is not the engineering. The radical act is refusing to let the best tomato of your life be a thing that only happens once. The romance of this project and its rigor are not in tension. The rigor is how we keep the romance from being rare.

Caldera is the quiet center of the Volcanic series — the restoration cultivar from which every hotter tomato in Chapter 18 is grown up, and the fruit on the plate in both recipes that close this book.



PART IV OF VI

Specification & the Shelf

A number you can formulate against, a fruit that ripens honest, and a label that can grow shorter.

Chapter 13 · The Same Tomato, Always — *precision and the cold chain.*

SPEC · 2,040 constructs · batch CV ≤ 7% · chilling-induced loss

Here is the part that matters most to anyone who has to build a product, a menu, or a season around a tomato: the memory tomato was a *lottery*. It happened in a good year, in the right soil, picked on the right afternoon, and you could not order it twice. You could not write it on a menu that had to be the same on Tuesday. You could not formulate a sauce against it and expect the next lot to match. The whole promise of measuring flavor is that it takes the best tomato of your life out of luck and into a number — and a number, unlike a memory, holds.

Across **2,040 constructs**, the restored tomato is held to a **batch coefficient of variation at or below seven percent**. The CV is just the standard deviation over the mean, σ/μ, expressed as a percentage — the cleanest single measure of how much a thing wobbles lot to lot. A CV of 7% means the Caldera you taste in August and the Caldera you taste in February differ, at the receptor, by a few percent and no more.

To feel what that buys, compare it to the thing it replaces. The flavor of a commodity tomato swings with weather, soil, harvest timing, and storage so widely that the word "tomato" on a spec sheet carries almost no information; a formulator building a sauce around it either over-engineers the recipe to mask the variation or accepts that the product will taste different lot to lot — and both of those are expensive, the first in added ingredients and the second in lost trust. A CV at or below 7% means the ingredient finally behaves like an ingredient: like sugar, like salt, like a compound with a number and a tolerance. A recipe formulated once stays true. The savor a chef tasted when he wrote the dish is the savor the guest gets a year later, in another city. Reproducibility is not the glamorous part of this work — no one falls in love with a coefficient of variation — but it is the part that lets the glamorous part *leave the laboratory*. A miracle you cannot repeat is an anecdote. A miracle with a CV is a product, and a product is how a better tomato reaches a table that is not our own. "Ripe" stops being a wish and becomes a figure anchored to **mGluR1** rather than to a microclimate. A sauce maker can formulate against IFI-U 2,600 and hit it every batch. A chef can write a dish that tastes the same in Montecito and in Seoul. A CPG formulator can specify the fruit the way she specifies everything else on her line — by number, with a tolerance — which is the thing a hollow commodity tomato, swinging with the weather, could never offer.



The quiet industrial heart of a romantic project: a tomato grown back to its savor, then held to a batch CV at or below seven percent so the fruit is a specification, not a lottery. Precision is not the opposite of the memory. It is how we keep the memory from being rare.

But a number grown into the fruit can still be thrown away after harvest, and the most important way people throw it away is the refrigerator — which is worth a careful paragraph, because it is real science and it is the single most useful handling fact in this book. In 2016, a team led by Bo Zhang and Harry Klee reported in *PNAS* that storing tomatoes cold — around 4 °C, ordinary refrigerator temperature — for even a few days **suppresses the fruit's volatile synthesis**, knocking down the very aroma compounds of Chapters 3 and 4, and that the loss does not fully recover when the fruit is warmed back up. The mechanism is not just slowed chemistry; the cold **downregulates the genes** of the volatile pathways (and the master ripening regulator **RIN**), in part through transient changes in **DNA methylation** — the fruit's own epigenetic marks shifting under cold stress. This is the molecular proof behind the old kitchen rule *never refrigerate a tomato*, and it means the restored fruit, like any great tomato, wants to be held at room temperature and eaten ripe. We grow the flavor in at the source; the cold chain can still take the aroma back out, and the eater, not the gene, holds that last decision.

WHERE THE NUMBER IS SET, AND WHERE IT CAN BE LOST	EFFECT
Restoration (GDH1 / glutamate pool, volatiles)	Builds IFI-U, IFI-S, aroma into the fruit
Flux-balanced, multi-construct design	Holds it reproducibly — CV ≤ 7%
Vine ripening (Ch. 15)	Lets sugars and volatiles finish writing
Refrigeration < ~12 °C	**Suppresses volatile synthesis; partly irreversible**
Room-temperature storage, ripe	Preserves the grown-in flavor to the plate

So consistency is a two-part promise, and we make both halves plainly. We promise the fruit leaves the vine at IFI-U 2,600 ± 7%, grown, held, and scored. And we tell you, without a health claim and without a flourish, exactly how to keep it: ripe, on the counter, out of the cold, eaten near its peak. A specification is only as good as the chain that carries it, and the honest version of "the same tomato, always" includes the handling that makes it true.

Chapter 14 · The Jar and the Can — *savory without the additive.*

APPLICATION · reformulation · the regulatory frame

Most tomatoes are never eaten fresh. They are crushed, reduced, canned, jarred, and shipped as the savory base of something else — the sauce, the soup, the simmer, the braise, the ketchup, the paste at the bottom of ten thousand recipes. This is the tomato's real economic life, and it is where a restored fruit quietly changes an entire category, because the problem the processed-tomato industry has been solving for decades is *exactly* the hollowness this book is about, and it has been solving it with additives.

Walk the ingredient statement of a mass-market pasta sauce and you will often find, after the tomatoes, a small supporting cast whose entire job is to replace the savor the tomatoes no longer carry: added sugar to fake the ripe-afternoon sweetness, and some combination of **added glutamate** (as MSG or, more often now, as "yeast extract," "autolyzed yeast," "tomato concentrate," or "natural flavors") to fake the umami. None of this is sinister — it is a rational response to a flat ingredient — but it means the label grows *longer* precisely because the fruit grew *hollower*. A paste made from a tomato that already carries **IFI-U 2,600** inverts the problem. The formulator reaching for yeast extract to prop up a commodity tomato suddenly does not need to reach. The depth, and the body — the **mGluR1** signal and the **CaSR** signal both — are in the fruit. The label can grow *shorter* instead of longer, and the savor still reads as *tomato* rather than as *additive*, because it is tomato.

Walk the swap through concretely, because a formulator will. A standard savory tomato base might carry added sugar, yeast extract or autolyzed yeast for glutamate, sometimes a disodium inosinate-and-guanylate blend for synergy, and "natural flavors" to paper over what the fruit lost — each of them an ingredient to source, store, declare, and defend to a label-reading shopper. A base built on restored tomato can delete the added glutamate source outright, because the fruit arrives at IFI-U 2,600; it can lean on the fruit's own kokumi instead of added richness; and it can reach synergy with a culinary nucleotide — a little dried mushroom, a touch of miso — rather than a synthetic salt. The declaration shortens. The additive stack's cost falls. And the "natural flavor" asterisk, the one shoppers trust least, can often simply disappear. We keep this strictly in its lane: it is a formulation and transparency argument, never a nutrition claim, and we are careful never to let it drift into one. A fruit that carries its own savor lets a product be, more honestly, the thing it says it is on the front of the jar.



Most tomatoes live their lives crushed, reduced, and jarred as the savory base of something else. A paste that already carries its own umami lets a formulation lean on the fruit instead of on added glutamate and yeast extract — the simplest reformulation there is: start with an ingredient that was never hollowed out.

We state the benefit exactly and claim nothing past it: a tomato grown back to its own savor lets a product taste more like the food it is named after and lean less on everything that was only ever there to fake the difference. That is not a health claim. It is a formulation fact and a clean-label one, and we are careful to keep it in that lane — attributes, never promises.

Because this is a product that reaches a shelf, it also meets the law, and a CPG reader deserves the real frame rather than a gesture at it. A gene-edited crop in the United States enters through a regulatory architecture that has shifted meaningfully in favor of precision breeding. Under the USDA's **SECURE rule** (2020, revising 7 CFR Part 340), plant modifications that could have been achieved through conventional breeding — single base-pair changes, targeted deletions, edits producing alleles already found in the crop's gene pool — can qualify for **exemption** from the old biotech regulations, on the logic that the *product*, not the *method*, is what matters. The **FDA** addresses food safety through its established consultation pathway. And consumer disclosure runs through the USDA's **National Bioengineered Food Disclosure Standard** (mandatory since January 2022), under which foods containing detectable modified genetic material carry a "**bioengineered**" (BE) disclosure — while certain gene-edited products that contain no foreign DNA may fall outside the "bioengineered" definition entirely. Abroad the picture varies and is moving: Japan has already brought a CRISPR-edited tomato to market (the GABA tomato of Chapter 7, cleared under a notification rather than a full GMO review), and the European Union, historically the strictest jurisdiction, advanced in 2023 a proposal to ease rules for certain **New Genomic Technique** plants deemed equivalent to conventionally bred ones. We navigate all of this the way we navigate everything — transparently, product by product, jurisdiction by jurisdiction — and we tell a formulator plainly, as of this writing, what frame her finished good will sit in before she builds a line on it.

The CPG case, stripped to a sentence, is this: the hardest, most expensive thing in a savory tomato product has always been putting back the savor the tomato lost, and the simplest way to stop paying for that is to start with a tomato that never lost it. Everything else on

the label was compensation. Remove the need for the compensation and the label, the cost structure, and the flavor all improve at once — not as a health benefit, which we do not claim, but as a better tomato doing the job the tomato was always named for.

Chapter 15 · Vine to Table — *ripeness, ethylene, and the honest harvest.*

PHYSIOLOGY · climacteric ripening · ACS·ACO · RIN · the Flavr Savr

Everything this book restores can be written into a seed and still never reach a mouth, because between the ripe gene and the ripe fruit stands the single most consequential decision in the whole tomato supply chain: *when to pick*. To understand it — and to understand why our fruit is bred to ripen honestly rather than to ripen on command — you have to understand how a tomato ripens at all, which is one of the most beautifully choreographed events in a plant's life.

The tomato is a **climacteric** fruit, meaning it ripens under the direction of a gaseous plant hormone, **ethylene**, in a self-amplifying burst. The hormone is built in two enzymatic steps that every tomato grower is, without knowing it, at the mercy of: **ACS** (ACC synthase) makes the precursor ACC, and **ACO** (ACC oxidase) converts ACC to ethylene. The ethylene is perceived by receptors — the famous **Never-ripe** (*NR*) receptor among them — and the signal runs down through a cascade (CTR1, EIN2, the EIL transcription factors, a fleet of ERFs) that switches on, in concert, the entire ripening program: the chlorophyll breaks down and the lycopene builds (red), the cell walls soften (texture), the starch converts to sugar (sweetness), the acids shift, and — the part that matters most to this book — the **volatile pathways of Chapters 3 and 4 fire**, writing the aroma. Sitting above the hormone are master-regulator transcription factors that license the whole cascade: **RIN** (a MADS-box gene), **NOR** (a NAC gene), and **CNR**. Mutate RIN and the fruit simply never ripens — which, not coincidentally, is where the commercial temptation comes from.

The industrial romance with this system runs in both directions, and seeing both frames exactly what we chose *not* to do. On one side, growers *add* ethylene to force ripening on schedule — the warehouse gassing that reddens a green-picked fruit on the day it reaches the store. On the other, they *subtract* its effect to buy shelf life: **1-methylcyclopropene (1-MCP)**, a gas sold to the produce trade, plugs the ethylene receptor so the fruit literally cannot hear the ripening signal, holding it in suspended animation for weeks. Between forced ripening and blocked ripening, the commodity tomato spends much of its life being told by chemistry when to ripen and when not to — every intervention aimed at logistics, none at flavor, each one another step away from the fruit finishing its own program in its own time. The climacteric cascade is magnificent machinery, and the industry's relationship to it is almost entirely about overriding it. Our bet is the opposite: build a fruit worth letting

ripen, and then let it. We would rather restore the thing that makes the vine-time worth protecting than spend our cleverness, as the century did, on ways to do without it.



A tomato ripens in a single self-amplifying ethylene burst that writes its color, its texture, its sugar, and its aroma all at once — but only if it is allowed to finish. Picked mature-green and gassed red on arrival, the fruit reddens on command and leaves most of its flavor unwritten. We breed for a fruit that ripens honest.

Here is the trap the industry fell into, and it is the physiological root of the "ninety-three percent the truck took." Because ethylene is a gas you can supply from outside, a tomato can be picked **mature-green** — full-sized but unripened — shipped firm and bruise-proof across a continent, and then **gassed with ethylene** in a warehouse to turn it red on the day it hits the store. It looks ripe. It is, in every way that photographs, ripe. But color is only one line of the ripening program, and the easiest one to trigger from outside; the sugars that come from the plant's own continuing supply, and above all the **volatiles**, which depend on enzymes and substrates that a detached green fruit cannot fully muster, are left *unwritten*. The gassed tomato reddens on command and arrives looking like the memory and tasting like the January object, because the afternoon on the vine — the slow finish where aroma and sugar are actually laid down — never happened. It was traded for the truck.

The history here is worth telling because it is the ancestor of our whole field, and because it shows how long the industry has circled this exact problem from the wrong side. In **1994**, Calgene's **Flavr Savr** tomato became the first genetically engineered whole food approved for sale, and what it engineered was *shelf life*: an antisense suppression of **polygalacturonase (PG)**, the enzyme that breaks down pectin and softens the fruit, so the tomato could be left on the vine a little longer and still survive handling. The instinct was right — let the fruit ripen more before it travels — but the lever was softening, not flavor, and the product foundered on cost, handling, and the fact that it was still, underneath, a commodity tomato. The Flavr Savr tried to buy a little more vine time by slowing the softening. We take the other road entirely: rather than fighting the fruit's physiology to make a flat tomato survive longer, we grow the flavor *into* the fruit and breed for a plant that can ripen toward its restored peak on the vine and still reach a table — an honest harvest, not a gassed one. The ethylene cascade is not our enemy to be suppressed; it is the conductor that writes the very flavor we restored, and our job is to let it finish its work. A tomato grown back

to its savor and then picked green and gassed would throw away in the warehouse what we built in the field. Vine to table is not a slogan here. It is the last and most fragile link in the specification, and it is why the fruit and the handling were always one design.



PART V OF VI

The Family & the Frontier

The fruit itself, down to its genome — its nightshade kin, and the fire it could carry.

Chapter 16 · The Fruit Itself — *a berry, technically.*

BOTANY · Solanaceae · the genome · domestication

It is worth pausing, with reverence, on the object — because the whole project begins and ends with it, and because the tomato, examined closely, is far stranger and more storied than its ubiquity lets on. A tomato is, botanically and stubbornly, a **berry**: a single ovary swollen into fruit, its seeds suspended in a gel the plant built specifically to carry them. It belongs to the **Solanaceae**, the nightshades — the same quietly dangerous family as the potato, the eggplant, the pepper, the petunia, and tobacco — and for two centuries after it reached Europe from the Andes and Mesoamerica, Europeans grew it as an ornamental and would not eat the gorgeous red thing, certain it was poison. (They were not entirely wrong about the family; the leaves and stems carry alkaloids. They were wrong about the fruit.) Every tomato we restore carries that whole improbable history in it — a poison-suspect ornamental that became the most-grown fruit on Earth.

The genome was read in **2012**, when the Tomato Genome Consortium published the sequence of the inbred variety **'Heinz 1706'** in *Nature* — roughly **900 megabases** across **12 chromosomes**, about **35,000** protein-coding genes — alongside a draft of the wild ancestor *Solanum pimpinellifolium*. That reference is the ground every construct in this book stands on; you cannot run the flux model of Chapter 8 or score the sequence variants of Chapter 18 without it, and the tomato's early, high-quality genome is a large part of why its native engineering difficulty is **Easy** and why it was the obvious organism to prove the platform's transfer out of peppers. Behind the reference stands a rich bench of wild relatives that are, in effect, a library of flavor and resilience alleles: *S. pennellii* (source of the **LIN5 / Brix9-2-5** sugar QTL of Chapter 9, and of a hundred stress traits), *S. habrochaites*, *S. pimpinellifolium* (the ancestor, and the reservoir of the **TomLoxC** aroma allele of Chapter 3), *S. cheesmaniae*. When we say the flavor was "always in the genome," we mean it literally and generously: much of it is in *these* genomes, the fruit's own wild kin, waiting to be measured back in.

There is a tool here that deserves its own mention, because it is how much of the fruit's flavor genetics was actually found: the **introgression lines**. Decades ago, breeders crossed the wild *S. pennellii* into cultivated tomato and then, generation by patient generation, broke the wild genome into some seventy-odd overlapping segments, each carried singly in an otherwise fully domesticated plant — a living library in which any one wild chromosome region could be studied in isolation, its effect on sugar or acid or yield read off directly. It was in these lines that LIN5 and dozens of other QTLs were pinned down, each segment answering the question *what does this one piece of the wild tomato do?* The modern platform is the in-silico heir of that library. Where the breeders needed a decade of crossing to ask one segment's

question, the flux and sequence models of Chapter 8 ask thousands in an afternoon — but the logic is identical, and we are humbled to stand on the introgression lines' shoulders. The wild tomato has been handing us its flavor alleles for forty years. We have only just built instruments fast enough to keep up with the gift.



A tomato is a berry — a single ovary swollen into fruit, seeds suspended in a gel the plant built to carry them. The wild ancestor bore fruit the size of a blueberry; a century of selection on a handful of size and locule genes grew it a hundredfold, changing every ratio that flavor lives in.

We met the domestication genes in Chapter 1, but they deserve a second look here as *biology* rather than as loss, because they are a small marvel. The jump from a one-gram wild berry to a thousand-gram beefsteak was carried by a handful of nameable changes: **fw2.2**, a regulator of cell number, responsible for roughly a third of the size difference; **fw3.2** (*SlKLUH*) and **fw11.3** adding more; and the locule-number genes **lc** and **fas**, mutations near the *WUS*/*CLV3* stem-cell circuit that multiply the fruit's internal chambers. Humans reshaped this fruit more profoundly, and far earlier, than any molecular tool could — just slowly, and blindly, by keeping the seed of what pleased them. Our work is the same impulse with the lights finally on: the same desire to make the fruit more of what we love, now able to *see* the glutamate, *measure* the aroma, and *choose* the trade instead of stumbling into it. The reverence and the rigor are the same reverence and rigor the first tomato growers had. We just have the genome now.

And under the knife, the object gives up its secret, which is why we photograph the cross-section more than the whole fruit. Halve a tomato at its equator and you are looking at an architecture most people eat their whole lives without seeing: the firm outer pericarp wall, the radial arms of flesh (the septa and columella), and the **locules** — the chambered pockets of seed and jelly where, as Chapters 2 and 7 kept insisting, the free glutamate runs highest. The savory heart of a tomato is literally its wettest, most overlooked part, the loose bright gel a careless cook spoons into the bin. Much of our restoration lives in that gel. A halved tomato is a tomato being honest — the seeds, the chambers, the structure of its sweetness and its savor all laid open at once. It is the plant showing you, if you will look, exactly where it keeps the flavor.

Chapter 17 · The Nightshade Kin — *the cousins on the vine.*

FAMILY · Solanaceae · the roadmap

The tomato does not restore alone. It is the easy, foundational case at the front of a whole family, and the methods that grew it back — the glutamate pathway, the flux-balance composition, the measured axes, the ESM2-plus-FBA loop — carry straight into its nightshade cousins, each of which lost something of its own to the same century of shipping-first, yield-first breeding. The **Solanaceae** are, for a flavor engineer, an unusually generous family: they share a chassis, they share much of a metabolic grammar, and several of them have genomes and transformation protocols as tractable as the tomato's. Growing the tomato back taught us the grammar; the rest of the family is where we speak it.



Eggplant — *Dark Matter* in the house naming. The family's deep, absorbent, almost meaty flesh, given a designed spine. The nightshades share a chassis and much of a metabolic grammar, which is why the tomato's method carries straight across the vine to its kin.

On the roadmap just behind the tomato stand the near kin, the **T1 Solanaceae Core** and the extended nightshades close after it — 4-to-7-gene builds on an 18-to-36-month horizon, each one carrying the tomato's single lesson: the flavor was always in the genome, waiting for permission.

ORGANISM	HOUSE SERIES	THE RESTORATION, IN A LINE	HORIZON
Eggplant	*Dark Matter*	The family's deep, absorbent savor given a spine; umami and kokumi into a famously bland flesh	T1 · 4–5 genes
Potato	*Seismic*	The quiet starchy canvas given its own designed edge and depth	T2 · 5–7 genes
Tomatillo	*Acid*	The husked, bright, green tartness composed on purpose rather than left to chance	T2 · 5–7 genes
Ground Cherry	*Celestial*	The little lantern fruit few have tasted at its full restored sweetness	T2 · 5–7 genes

Each of these is a monograph waiting to be written, and each extends a different axis: the eggplant leans on the umami-and-kokumi work this book is built around; the tomatillo is an *astringency-and-acid* problem, the bright edge of Chapter 11 made the main subject; the ground cherry is a sweetness study; the potato is a nearly blank canvas, the most interesting kind of restoration because there is so little native flavor to honor and so much room to compose.

Take the eggplant as the clearest parallel to this book. Its flesh is famously bland and famously *absorbent* — a sponge for whatever it cooks in — which is usually described as a weakness and is in truth an opportunity, because a tissue that carries little flavor of its own is a tissue with room to be given depth. The *Dark Matter* program is the glutamate-and-kokumi work of Chapters 7 and 10 aimed at a fruit that will hold savor the way a sponge holds oil, so that the vegetable which usually begs to be rescued by a sauce becomes, itself, the savory thing on the plate. The potato's *Seismic* program is stranger and more fundamental, because the potato is not even a fruit — it is a tuber, a storage organ, nearly pure starch — and restoration there means composing flavor onto a canvas the plant never meant to be tasted for its own sake, the most open-ended problem in the whole family. And the tomatillo's *Acid* program inverts this entire book: where the tomato treats astringency and acid as a finishing edge, the tomatillo makes that edge the subject, a study in bright, husked, green tartness that a century of breeding has barely touched because almost no one grows it at scale. Each cousin is the same grammar bent toward a different sentence — which is exactly why the tomato, the most legible of them, had to be written first. They are not hypotheticals — they are the same platform pointed at the next fruit on the same vine.

The ground cherry — *Celestial* in the house naming — is the family's sweetness study, and the most charming of the cousins: a small golden fruit inside a papery lantern husk, tasting of pineapple and warm tomato, grown by almost no one at scale and therefore barely touched by the century of subtraction that hollowed its larger relatives. Its program is the work of Chapter 9 aimed at a fruit that already leans sweet, asking not for restoration so much as *definition* — pinning a wild, variable charm into a reliable one. Across all four near cousins the lesson is the same, and it is the lesson the tomato taught first: the Solanaceae are a single grammar — a shared chassis, a shared glutamate biology, a shared ripening logic — bent toward four different sentences. Learn to read it in the tomato, the

most legible member, and the rest of the family becomes a set of translations rather than a set of new languages. That is the real reason the monographs open here. The tomato is not just the first fruit. It is the primer.



Tomatillo — *Acid* — the husked, green, structurally tart cousin: a fruit where the bright astringent edge this book treats as a finishing note becomes the whole subject. The nightshade family is, for a flavor engineer, a library of related problems.

We lead the family with the tomato because it asks the least and gives the most — native difficulty **Easy**, the plant we know down to its locules, the genome in hand since 2012, the glutamate biology the clearest in the family. Grow one nightshade all the way back to itself and you have not just made one fruit; you have learned the grammar of the rest. The tomato is the first word. The family is the sentence.

Chapter 18 · The Volcanic Frontier — *fire in the fruit.*

FRONTIER · T1 Solanaceae Core · 4–5 genes · 18–24 mo · see Book 22, *The Nightshade Files*

Everything until now has been restoration — growing the tomato back to what it already was. The frontier asks a wilder question: what if the tomato became something it never was? What if a fruit that never in its evolutionary history made a warming molecule learned to speak through **TRPV1**, the heat receptor, in its own flesh? This is the **Volcanic** series, and it is where the house naming finally pays off in full. **Caldera**, the restoration flagship of Chapter 12, sits at the cooled, savory center — the collapsed basin, no heat. Around it the ground rises: **Ember** at the base, a warm sunlit tingle; then **Magma**; then **Pyroclast**; up to **Krakatoa** at the summit, a tomato laddered into real, designed burn while keeping the restored chord beneath it.

The machinery is borrowed, deliberately, from the one organism that already perfected heat — the pepper — and this is where the platform's deepest work becomes visible in the tomato, so it is worth showing the real molecules rather than gesturing at them. Capsaicin, the pepper's warming molecule, is built at a **BAHD acyltransferase** called **Pun1 / AT3** (capsaicin synthase), which condenses **vanillylamine** with a branched fatty-acyl-CoA tail (natively 8-methyl-6-nonenoyl-CoA). Our structural model of the *C. chinense* enzyme — 440 residues, resolved at high confidence (mean pLDDT 90.2, pTM 0.910) — shows the catalytic machinery in three dimensions: the canonical **HXXXD** catalytic dyad, with **His169** poised 4.6 Å from **Asp173**, the aspartate orienting the histidine that drives the transfer, and a long **hydrophobic tunnel** (Leu40, Met43, Ile45, Trp139, Phe167, and more) that cradles the fatty-acyl tail and sets which capsaicinoid the enzyme will make. That tunnel is the specificity lever, and it is where the AI designs the fruit's heat.

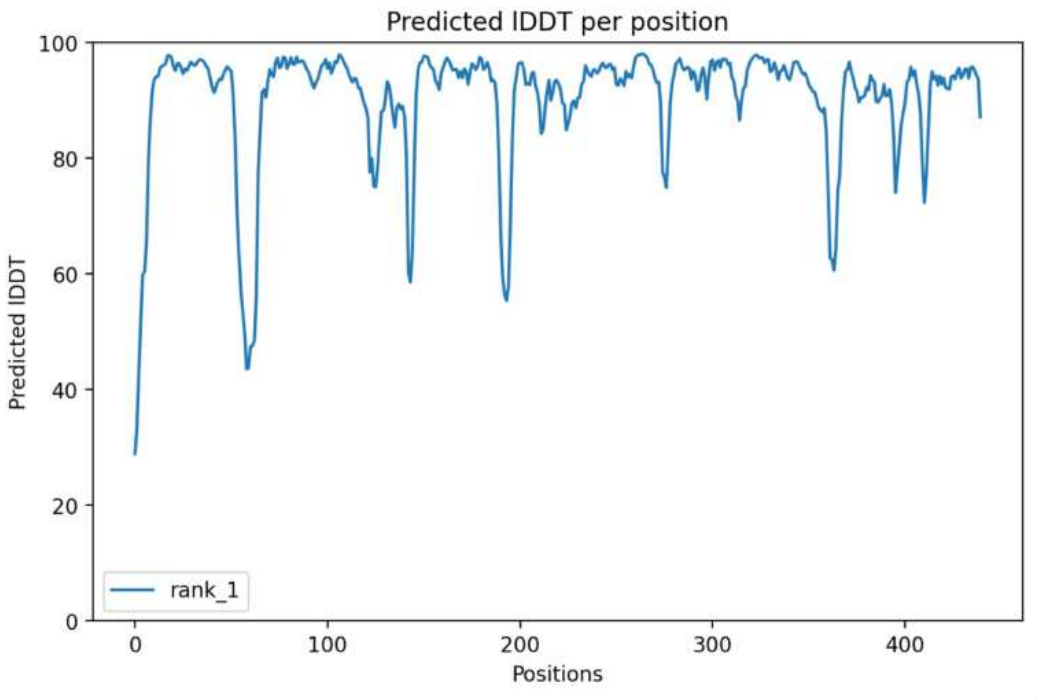


FIG. 18 — The Pun1 / AT3 capsaicin synthase model, colored by per-residue confidence (pLDDT). The active-site cleft and the hydrophobic acyl tunnel — the specificity lever we reshape to carry heat into a fruit that never made it — model at high confidence. This is the molecule that lets a tomato speak through TRPV1.

How does one redesign a tunnel? We score it two ways and take the consensus. An **ESM2** protein language model (650M parameters) masked each of the 32 tunnel-lining positions in turn and rated all twenty substitutions by how much more plausible the model found them than the native residue — a 640-substitution deep scan — while a genome-scale **flux-balance** model (Chapter 8) found that pathway control sits upstream — at 4CL and HCT in the phenylpropanoid pathway — not at the terminal Pun1/AT3 step; Pun1 is the capsaicin synthase that labels the product, but it does not govern the rate. Two substitutions, never before combined, rose to the top of both analyses and were written into the shipped double-variant construct with CRISPR. A third position identified in the structural scan, C175S, is included in the table below as a structural annotation and was not incorporated into the final design. Shown with the language model's log-likelihood ratio (higher = more favored) and the stability change ΔΔG (more negative = more stabilizing):

EDIT	ROLE IN THE TUNNEL	LLR VS. WILD TYPE	ΔΔG (KCAL/MOL)
S39L	Hydrophobic packing at the tunnel mouth; tightens selectivity for the longer acyl tail	+2.83	−2.1
L345G	Opens space near the DFGWG motif; relieves steric strain in the active-site cleft	+2.70	−1.8
C175S *(structural annotation — not in shipped construct)*	Removes a reactive thiol beside the catalytic Asp; prevents disulfide misfolding	+2.03	−0.9

That the *character* of the burn can be tuned, not just its intensity, our receptor docking showed on the other side of the system. Docking the five natural capsaicinoids into the rat **TRPV1** vanilloid pocket (from the capsaicin-bound cryo-EM structure, PDB 5IRX) ranks them by binding energy, and the ranking maps onto the *feel* of the heat: **capsaicin** binds hardest at **−7.20 kcal/mol** — its trans-unsaturated kink seats the vanillyl head optimally — for a fast, sharp, front-of-mouth burn; the saturated, shorter **nordihydrocapsaicin** (−6.16) gives a slower, deeper, longer chest-warmth.

The full docking read, receptor by molecule, is worth tabling, because it is the evidence that the *character* of the burn — not merely its intensity — is designable:

CAPSAICINOID	TRPV1 POSE (KCAL/MOL)	ACYL CHAIN	BURN CARRIED INTO THE FRUIT
Capsaicin	−7.20	8-methyl-6-nonenoyl (unsat., branched)	Fastest onset, sharp, front-of-mouth
Nonivamide	−6.89	nonanoyl (straight, saturated)	Fast and clean; a synthetic/ferment route
Homodihydrocapsaicin	−6.70	9-methyldecanoyl (+1C)	Balanced, mid-ladder
Dihydrocapsaicin	−6.39	8-methylnonanoyl	Slower, broad
Nordihydrocapsaicin	−6.16	7-methyloctanoyl (−1C)	Slowest onset, deep chest-warmth

Two details from the modelling are worth carrying out of it. The acceptor substrate is supplied upstream by **pAMT** (a well-resolved 459-residue model, mean pLDDT 95.0), which transaminates vanillin to the **vanillylamine** that Pun1 then acylates — so the pepper's terminal module we carry across is really two enzymes, not one. And docking the pathway's own molecules into Pun1 flagged a classic engineering hazard: the *product*, capsaicin, binds the active site harder (−8.81 kcal/mol) than either substrate (vanillylamine −6.12, the acyl acid −6.80), the signature of **product inhibition** — a pocket that clings to what it just made. A redesign that binds the substrates but *releases the product faster* is therefore not only about potency; it is about turnover, and it is exactly the kind of multi-objective target the ESM2-plus-flux loop was built to chase.

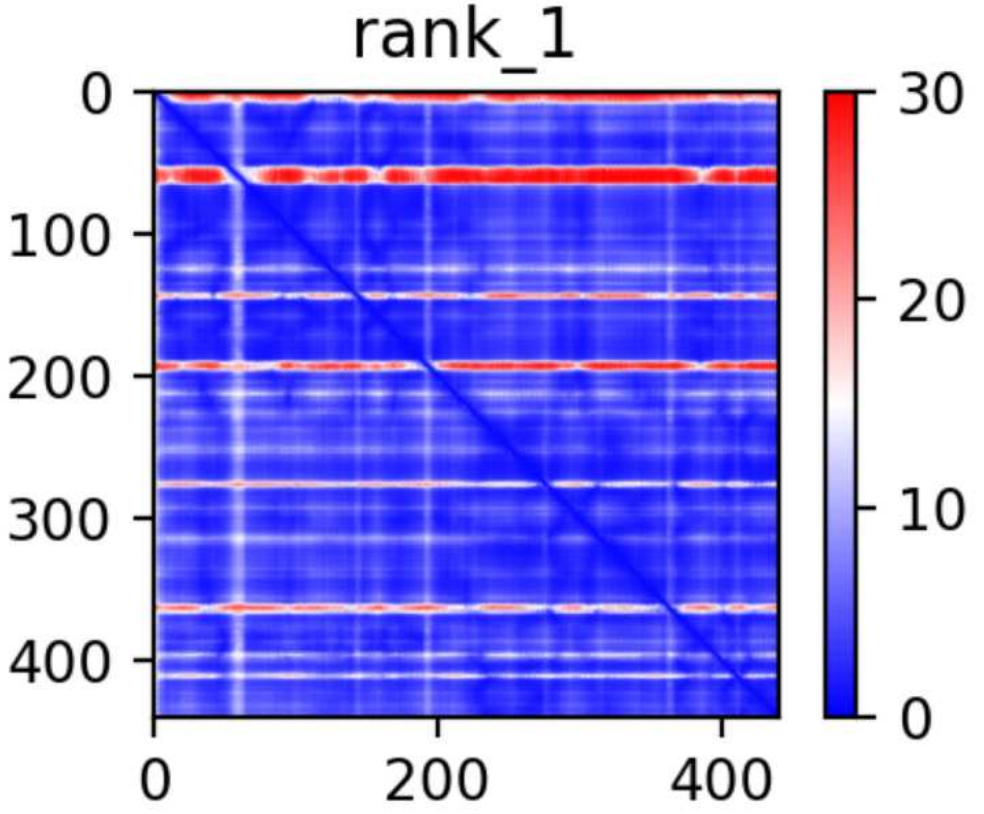


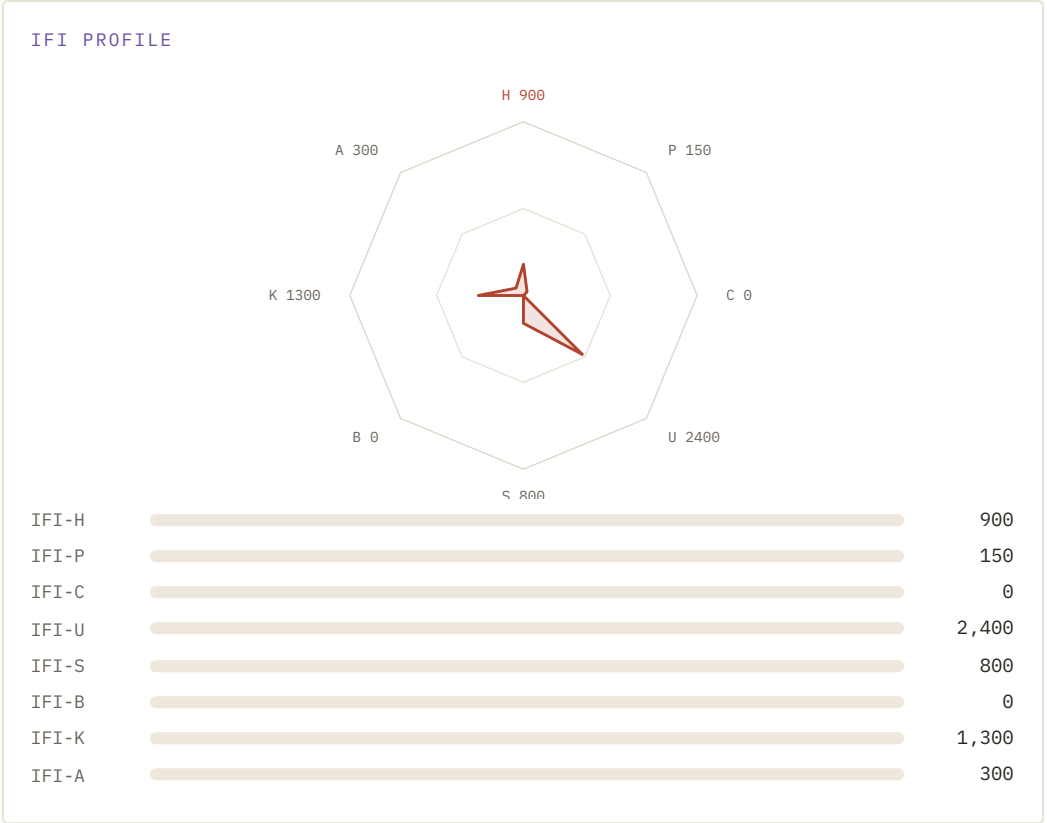
FIG. 18b — the Pun1 / AT3 predicted aligned error (PAE) map. Low off-diagonal error means the model places the catalytic center and the acyl tunnel confidently *relative to each other* — the spatial trust a pocket redesign depends on.

By tuning the *ratio* of capsaicinoids the enzyme makes, we design not just the Scoville number but the shape of the warmth in time — which, carried into a tomato, means an Ember that merely glows and a Krakatoa that genuinely roars, each with its restored umami intact beneath the fire.

It helps to lay the whole Volcanic ladder out, with the heat written as a *design target* rather than a shipped number, because the restraint is the point of it. Even Krakatoa at the summit is a fraction of what the pepper program reaches — our superhot flagship **Phoenix** carries a predicted IFI-H of approximately 4,200, computed at approximately 2.95 million SHU — and that gap is deliberate. A tomato is a fruit, and heat in a fruit is meant to warm, not to wound; the Volcanic series ladders a *culinary* burn, laid over a chord that stays, in every rung, recognizably a restored tomato.

VOLCANIC RUNG	IFI-H (DESIGN TARGET)	RESTORED CHORD BENEATH
Caldera · the cooled center	—	U 2,600 · S 900 · K 1,400
Ember · a sunlit glow	~150	U 2,500 · S 900 · K 1,300
Magma · a real warmth	~900	U 2,400 · S 800 · K 1,300
Pyroclast · a serious heat	~1,800	U 2,300 · S 800 · K 1,200
Krakatoa · the fruit's summit	~3,000	U 2,100 · S 700 · K 1,200

Read down the right-hand column and the discipline is visible: the umami never falls below 2,100 even as the heat climbs twentyfold, because the whole premise is a tomato that *also* burns, never a chili wearing a tomato's skin. The fire is the newcomer; the savor is the house.



The scorecard above is a design target for a mid-ladder Volcanic tomato — call it **Magma** — and the thing to read in it is not the heat but the *company the heat keeps*: **IFI-H 900**, a real and serious warmth for a fruit, laid over a chord that is still, unmistakably, a restored tomato — umami 2,400, kokumi 1,300, the sweetness and the bright edge intact. The route is the phenylpropanoid branch (**PAL → C4H → 4CL → HCT → COMT**) that already runs in every vascular plant, finished with the pepper's terminal enzymes (**pAMT**, **Pun1/CS**), a 4-to-5-gene build on an 18-to-24-month horizon — the

lowest-hanging rung of the entire frontier, because the nightshade chassis is so willing and the tomato so well understood. We keep the full Volcanic story in its own book, Book 22, *The Nightshade Files*, because it deserves the room. Here it is enough to say what the whole monograph has been building toward: the restored tomato was never the ceiling. It was the ground floor — a fruit grown so completely back to itself that we could finally start building *up*.



PART VI OF VI

At the Table

The fastest way to understand a restored tomato is with your mouth. Good oil, flaky salt, a low oven.

Chapter 19 · At the Table I — *tomatoes, barely touched.*

The fastest way to understand a restored tomato is to get out of its way. These are the dishes we make the first week Caldera comes ripe, standing at the counter, doing almost nothing — because when the fruit carries its own depth, *almost nothing* is the whole recipe. Both of these are raw, both are vegetarian, and both are built to prove a single chapter of this book with your mouth.

A note on the salt, since it is doing real work in the first recipe. Salt does three measurable things to a raw tomato at once. It draws water and dissolved glutamate out of the cut cells by osmosis, concentrating the savor exactly at the surface where your tongue meets it. Its sodium suppresses the fruit's faint bitterness while lifting its sweetness and umami — a cross-modal effect as real as the one aroma plays on sweetness in Chapter 4. And the sodium is itself, faintly, a helper at the umami receptor. On a hollow commodity tomato, salting is an attempt to manufacture a flavor that is not there, which is why it never quite works and you keep adding more. On a Caldera, salting *uncovers* a flavor already present. Same gesture, opposite act — which is the whole book, performed at a kitchen counter with a pinch of flaky salt and two minutes of patience.

Sliced Caldera, Cold Oil, Flaky Salt

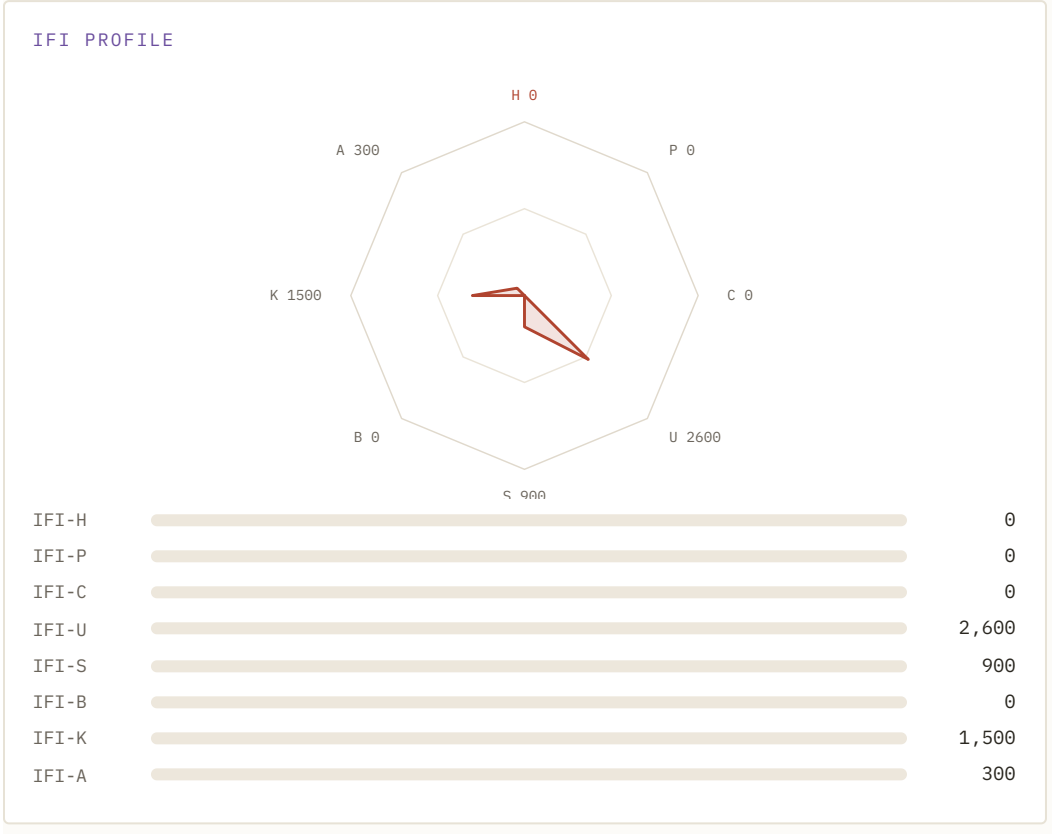
Serves 2 · 10 minutes · the proof, uncooked

```
2          ripe Caldera tomatoes, at room temperature (never from the
fridge)
             good cold-pressed olive oil, more than feels reasonable
             flaky salt
6          basil leaves, torn at the last second
```

1. Slice the tomatoes thick — a scant finger's width — straight through the equator so the chambers show, and lay them flat and overlapping on a cold plate. Cut tomatoes hate to be stacked; give them room to breathe.
2. Salt them now, from a height, and wait two full minutes. The flaky salt draws a little juice to the surface and wakes the savor — you will see the slices go glossy as the gel weeps.
3. Pour the oil over in a slow thread. Scatter the basil.
4. Eat with bread to catch what runs. No vinegar, no pepper, nothing else — the acid and the sweetness are already in balance; you would only be covering them.

Why it works. Caldera arrives carrying **IFI-U 2,600**, the savory depth grown in at the source (Chapter 7), so the salt here does not *create* flavor the way it must with a hollow commodity tomato — it only uncovers one already present, drawing the free glutamate out of the locular gel and onto **mGluR1** and **TAS1R1·TAS1R3**. The two-minute wait is the glutamate blooming; the cold oil lifts the kokumi; the basil throws a green top note that, in a commodity tomato, the lost

TomLoxC allele (Chapter 3) could no longer supply. This is a tomato with nothing to hide, so we hide nothing. *The one rule: room temperature. A fridge-cold Caldera has had its aroma suppressed (Chapter 13), and no amount of salt brings it back.*



Caldera & Stone Fruit, Torn Herbs

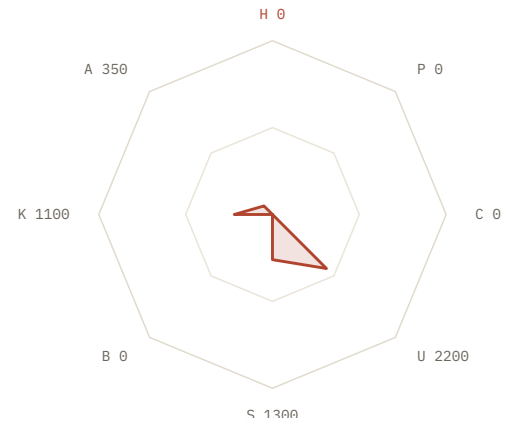
Serves 4 · 15 minutes · the sweetness, in fruit

```
3          ripe Caldera tomatoes, in rough wedges
2          ripe peaches or nectarines, in wedges to match
             flaky salt · cold olive oil
1 small    handful basil and mint, torn
             a few drops of good vinegar, optional and sparing
```

1. Toss the tomato and stone-fruit wedges together with a pinch of salt; let them sit five minutes so the juices mingle.
2. Dress with oil, the torn herbs, and — only if the day's fruit needs lifting — a very few drops of vinegar.
3. Serve cool-but-not-cold, in a wide shallow bowl, with the juices.

Why it works. This is Chapter 4 on a plate. The peach and the tomato meet in the register of *perceived sweetness* — the carotenoid-derived volatiles (6-methyl-5-hepten-2-one, geranial) that Caldera carries restored make the brain read the whole bowl as sweeter than its sugar, so a small amount of real fruit sugar reads as a generous one. The tomato's restored glutamate keeps the dish from being merely sweet; it gives the peach a savory floor to stand on, which is why the pairing tastes like dinner and not dessert.

IFI PROFILE



IFI-H	0
IFI-P	0
IFI-C	0
IFI-U	2,200
IFI-S	1,300
IFI-B	0
IFI-K	1,100
IFI-A	350

Caldera Toast, Grated

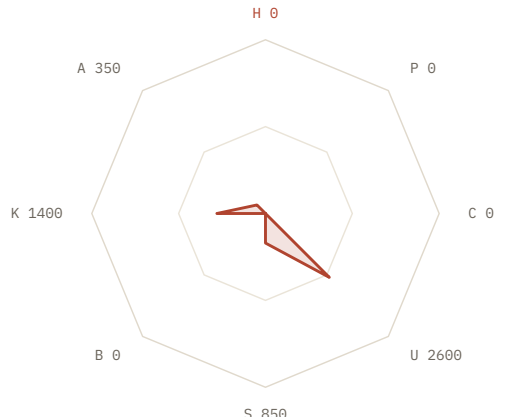
Serves 2 · 5 minutes · the fruit as its own sauce

```
2         ripe Caldera tomatoes, halved through the equator
2  thick slices country bread, toasted hard
1  clove garlic, halved (optional)
           cold olive oil · flaky salt
```

1. Toast the bread until it is genuinely crisp — it has to stand up to the juice without going to paste.
2. If you like, rub the cut garlic once across the hot surface; it melts into the crumb and adds a wave of kokumi.
3. Hold a tomato half by its skin and grate it, cut-side against the coarse holes of a box grater, straight onto the toast. The flesh passes through; the skin stays in your hand and goes in the bin.
4. Drench with oil, shower with salt, and eat at once — over the sink, if you have any sense.

Why it works. There is no sauce here; the tomato *is* the sauce, which is only possible because Caldera carries its own **IFI-U 2,600** and **IFI-K 1,400** — the savor and the body a cooked sauce usually has to spend an hour building. Grating ruptures every cell at once, so the free glutamate and the fresh-green C6 volatiles of Chapter 3 flood out together onto the toast while they are still blooming. A commodity tomato grated this way gives you pink water on bread; Caldera gives you the simplest great thing on the Mediterranean table, one ingredient doing the work of five.

IFI PROFILE



IFI-H		0
IFI-P		0
IFI-C		0
IFI-U		2,600
IFI-S		850
IFI-B		0
IFI-K		1,400
IFI-A		350

Chapter 20 · At the Table II — *the long, slow savor.*

The other thing a restored tomato loves is time and low heat, which do not *add* savor so much as *concentrate* it — drive off the water, and what is left is the fruit's depth pulled tight. Where the raw dishes prove the tomato, these prove the method: the same grown-in axes, reduced and partnered until they roar. Both are vegetarian-first; the second is where the synergy of Chapter 6 comes to the table.

Why low and slow, and not fast and hot. Two different things concentrate a tomato's savor, and they want different temperatures. **Reduction** — simply driving off water — raises the concentration of everything non-volatile, glutamate included, and it happens at any temperature; a low oven just does it gently, without boiling the fruit to ruin. But the *sweetness* that climbs in a confit is partly **caramelization** and gentle **Maillard** browning of the fruit's own sugars and amino acids, reactions that need real heat yet turn acrid the moment they are rushed. A long, low oven threads the needle between them: hot enough for the sugars to deepen and the edges to darken, slow enough that the glutamate concentrates without scorching and the aromas develop instead of boiling away. A confit is, in effect, a two-hour version of what a vine does across its last ripe week — a patient concentration of the fruit toward itself, which is why it tastes less like cooking and more like *ripening finished indoors*.

Slow Caldera Confit

Serves 4 as a base · 2 hours, mostly unattended · the savory floor, bottled

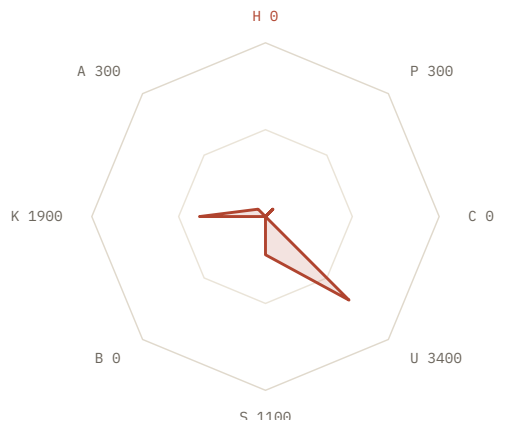
```
8          ripe Caldera tomatoes, halved through the equator
4  cloves  garlic, peeled, left whole
6  sprigs  thyme
           olive oil to come halfway up the fruit · flaky salt
```

1. Heat the oven low — 120 °C / 250 °F. Lay the tomato halves cut-side up in a snug dish, tuck the garlic and thyme between them, and salt lightly.
2. Pour olive oil until it comes halfway up the fruit. The tomatoes should sit in a shallow bath, not swim.
3. Slide them in and forget them for two hours. They will slump, wrinkle, and darken at the edges; the oil will take on their color and smell like a greenhouse at the end of summer.
4. Lift them out gently — they are fragile now — and keep them under their own oil. Spoon over anything: bread, beans, grain, egg, a plain plate.

Why it works. Two slow hours drive off most of the tomato's water, concentrating the free glutamate until the fruit reads near **IFI-U 3,400** — the savor of Chapter 5, pulled tight. The whole garlic softens into the oil and lends a wave of **γ-glutamyl peptides** and a low pungent hum through **CaSR** and **TRPA1**, doubling the kokumi

floor of Chapter 10; the gentle heat caramelizes the native sugars upward. Nothing savory was added. It was all in the fruit; we only removed the water that was hiding it.

IFI PROFILE



IFI-H		0
IFI-P		300
IFI-C		0
IFI-U		3,400
IFI-S		1,100
IFI-B		0
IFI-K		1,900
IFI-A		300

Caldera & Dried-Mushroom Ragù

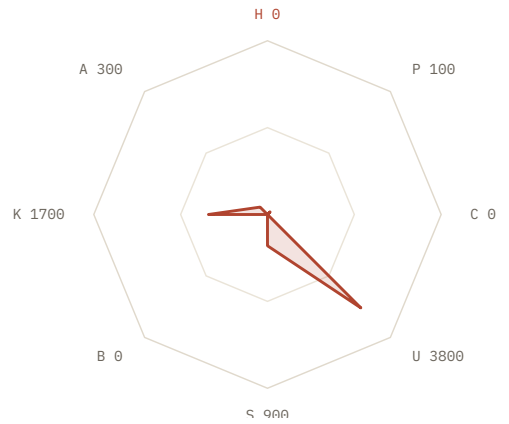
Serves 4 · 45 minutes · the synergy, cooked

```
6          ripe Caldera tomatoes, grated to a rough pulp (skins discarded)
30 g       dried porcini or shiitake, soaked in warm water 20 min
4  cloves  garlic, sliced
1          onion, finely diced
             olive oil · flaky salt · a few basil leaves
```

1. Soak the dried mushrooms; keep the dark soaking liquid. Chop the softened mushrooms fine.
2. Sweat the onion and garlic slowly in oil until sweet and soft, 10 minutes — no color.
3. Add the chopped mushrooms, then the grated tomato and a splash of the strained soaking liquid. Simmer, stirring now and then, 25–30 minutes, until glossy and thick.
4. Salt to taste, tear in basil at the end, and serve over anything that will hold it.

Why it works. This is Chapter 6 made edible. Caldera brings a loud, restored **glutamate** (the *u* in Yamaguchi's equation); the dried mushrooms bring concentrated **GMP** (the *v*) — and the receptor multiplies them, so the finished ragù tastes savory far out of proportion to either part, the cross-term `1218 · u · v` doing visible work in a pan. A commodity tomato at IFI-U 300 would give the mushroom almost nothing to multiply; Caldera gives it everything. This is the oldest trick in savory cooking, finally handed an ingredient worthy of it — and it is entirely vegetarian, the glutamate and the guanylate both grown, not killed, for.

IFI PROFILE



IFI-H	0
IFI-P	100
IFI-C	0
IFI-U	3,800
IFI-S	900
IFI-B	0
IFI-K	1,700
IFI-A	300

*The ragù's **IFI-U 3,800** is the synergy, not just the reduction: the number is higher than the confit's because the mushroom's nucleotide is multiplying the tomato's glutamate at the receptor, not merely concentrating it in the pan. A nourishment note, quiet and unclaimed: a tomato grown toward its fullest flavor is, not by accident, a tomato grown toward its fullest lycopene — and slow heat with oil, as in both of these dishes, is exactly how that carotenoid becomes most available to the body. Taste and nourishment were never two projects here.*

Closing note · The ninth thing we measure for

There is a number this book does not have a column for, and it is the one we think about most at our own table. A tomato grown back to its fullest flavor is, almost always, a tomato grown back toward its fullest nourishment — the same ripeness that carries the umami carries the lycopene and the vitamin C, the same restored chloroplasts (Chapter 2) that fund the sugar fund the carotenoids, the same care that restores the savor restores the food worth eating. We measured eight axes of taste to grow the tomato back to itself. We are building the ninth — for what the body actually draws from the meal — and the tomato is where we see most clearly that the two were always the same work. The restored chloroplast makes the sugar *and* the lycopene; the vine-ripening that writes the aroma writes the vitamin C; the oil and the low oven that concentrate the glutamate are the same oil and oven that make the carotenoid available. You cannot, it turns out, grow a tomato all the way back to tasting like a tomato without growing it back toward *being* one.

We make no claim here and we make none anywhere — no cure, no detox, no health halo, only a quiet observation we have staked a family and a company on: that when you grow a plant all the way back to tasting like what it is, you tend to grow it all the way back to being what it is. The commodity tomato gave up its flavor and its goodness together, in the same hundred-year trade — the *u* gene that greyed the shoulder took the sugar and the carotenoid in one stroke; the truck that took the vine-time took the aroma and the finish together. We have only ever been trying to undo both at once, because to us they were never two problems.

And we hold that line exactly where the ethos asks us to: as an *intention*, never a promise. We do not tell you a tomato will do anything for your body beyond being, honestly, a tomato — grown ripe, grown whole, grown to carry what the fruit is capable of carrying. We make it the best tomato we can and we set it on the table, and what the body does with a plate of real food in good company is older and larger than anything we would presume to claim. The nourishment we build toward is the quiet kind: a fruit worth eating, eaten at its peak, shared. That is the whole of the intention, and we are content to let it stay that modest, because a tomato that tastes like a tomato should is already, without a single claim attached to it, a good thing to give the people you love.

These are computational designs; Scoville Splice's cultivars and constructs have not been experimentally validated in a laboratory.

That is the whole of it. Eight axes, 2,040 constructs, one fruit grown back — gene by gene, held to a number, ripened honest, and set on a plate with good oil and flaky salt in front of the people we love. The tomato that tastes like a tomato should is not a memory and not a

nostalgia. It is an instruction now. It is measurable. And it was always, from the first warm fruit split open at a kitchen table, the entire point of measuring anything.