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RECEIVED 04 May 2023

ACCEPTED 03 October 2023

PUBLISHED 19 October 2023

CITATION

Johnston-Monje D, Vergara LI,
Lopez-Mejia J and White JF (2023)
Plant microbiomes as contributors to
agricultural terroir.
Front. Agron. 5:1216520.
doi: 10.3389/fagro.2023.1216520

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Plant microbiomes as contributors to agricultural terroir

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Agricultural products such as tea, chocolate, coffee and wine are valued for their sensorial and nutritional qualities. Variation in the growing conditions of a crop can influence the plant's phenotype, thus it behooves agriculturalists to optimize the conditions on their farms to grow the highest quality product. The set of growing conditions associated with a certain geographic location and its influence on the product's chemistry is known as terroir. Although terroir plays a significant role in marketing and consumer appreciation as well as product identity and valorization, rarely are the biochemical differences or the factors creating them very well understood. The word derives from the Latin for "land", suggesting terroir is simply a function of the geographical location where a plant grew, while in its modern usage, terroir is understood to be the result of soil type, climate, landscape, topography, biotic interactions and agricultural practice. Except for fermented food products like wine and chocolate, plant associated microbiomes have been little studied for their contribution to a crop's terroir; however, modern metagenomics and metabolomics technologies have given scientists the tools to better observe how microbial diversity can impact the chemical variation in plant products. Differences in the microbiomes inhabiting plant organs can change phytochemistry by altering host metabolism, for example increasing the nutrients absorbed by roots that then are deposited in leaves, seeds and fruits. Plant associated microbes can consume plant molecules, removing them from the metabolome, or they can contribute smells and flavors of their own. This review aims to synthesize research into rhizosphere, endosphere, phyllosphere, spermosphere, carposphere, and anthosphere microbiome influences on plant biochemistry and crop derived products, while helping to increase the appreciation that beneficial microbes are able to contribute to agriculture by improving phytochemical quality.

KEYWORDS

plant microbiome, plant metabolome, terroir, microbial terroir, fermentation, rhizosphere, endophytes, carposphere

1 Introduction

Much of modern plant agriculture is dominated by the quest for higher yield, but in niche or luxury products such as wine and coffee, producers also search for methods to enhance or maintain quality. One of the original concepts surrounding agricultural enhancement of flavor, the word “terroir” derives from 14th century France where it referred to specific tracts of land in the province of Burgundy that consistently produced very good wines (Wilson, 2001). French wine laws for the “Protection of the Place of Origin” or *Appellation d’Origine Contrôlée* (AOC) continue to ensure a particular terroir by stipulating that the products (including but not limited to wine) are made in a traditional manner with ingredients from specifically classified producers within designated geographical areas. Similar legal/commercial definitions of terroir exist in other countries such as Italy’s *Denominazione di Origine Controllata e Garantita*, Germany’s *Qualitätswein bestimmter Anbaugebiete*, Spain’s *Denominación de Origen Protegida*, Portugal’s *Denominação de Origem Controlada*, South Africa’s *Wine of Origin*, Canada’s *Vintners Quality Alliance*, and the USA’s *Appellation of Wine Origin*. Outside of wine, the concept of terroir also exists for Longjing hand-roasted green tea grown in the West Lake region in Hangzhou. This tea is considered the most prestigious drink in China, having been consumed by many emperors for hundreds of years and is officially recognized for its terroir with geographical indication labelling (Chan, 2012). Such geographic indications are an important part of agricultural marketing and pricing, for example “Café de Colombia” labelled coffee sells on average for at least three times the price of unlabeled roasted coffee (US\$6.99/kg), while “Jamaican Blue Mountain Coffee” sells for over 13 times more (Teuber, 2010).

Besides geographic provenance, a product’s perceived quality can also dramatically increase its price; 1-point increases on the 100-point coffee tasting scale at the annual Cup of Excellence competition result in at least 18% increases in price, while price increases of 15–133% result for coffees ranked in the top four (Traore et al., 2018). Perhaps the most famous example is “Esmeralda Special” the product of the coffee varietal called Geisha grown at Hacienda La Esmeralda in western Panama. Said to contain aromas of jasmine, tangerine and bergamot, it was described by Don Holly, the director of roasting and quality control at Green Mountain Coffee Roasters as “the face of God in a cup”. Esmeralda Special won the competition in 2007 and fetched an auction price of US\$374.85/kg (Wilson et al., 2012). More recently another cupping competition winner, a Geisha varietal from the Elida Estate farm in Panama became the most expensive coffee in the world, selling for US\$2,268.95 per kilogram (Repanich, 2019). Medal winning wines also increase at least 13% in price (Paroissien and Visser, 2020), while those receiving high critical scores on Wine Spectator’s 100-point scale can fetch up to US\$1,000 per 750 mL bottle (Palmer and Chen, 2018). The most expensive wine in the world is probably Screaming Eagle’s 1992 Napa Valley Cabernet Sauvignon which was given a near perfect score of 99 by the world’s most influential wine critic, Robert Parker, and sold for US\$83,000 per liter (Batchelor, 2022).

From a commercial point of view, it is desirable to be able to prove that your agricultural product has “good terroir” or is at least biochemically distinct. However, this has traditionally been difficult

to do, since the human tongue has difficulty discerning and quantifying subtle variations in chemical diversity or concentration. Scientifically speaking, in order to understand metabolic changes in a product’s flavor, it is also important to identify which chemical compounds are varying in an agricultural product. Fortunately, advances in chromatography and mass spectroscopy have dramatically improved our ability to identify and quantify the distinctive blends of metabolites within different plant products. Metabolomics now allows the objective characterization of terroir, for example biochemically discriminating between wines produced from Pinot noir grapes grown in two distinct “Grands Crus” appellations (Burgundy, France) separated by less than 2 km (Roullier-Gall et al., 2014). Chemical composition was also able to distinguish between Chardonnay grapes produced at seven different Geographical Indications in Southern Australia (Gambetta et al., 2017). The use of untargeted metabolomics (da Silva Taveira et al., 2014), and classical physio-chemical/sensory analysis of green and roasted beans, has also been shown to permit the discrimination of a terroir between coffee grown in different geographical locations, environmental conditions and agricultural techniques (Scholz et al., 2018). Other examples of studies linking phytochemical profiles to terroir of tea, chocolate, saffron, fruits, medicinal plants and a range of other agricultural products has recently been reviewed (Lucini et al., 2020).

Agriculturalists hoping to increase the quality and price of their products might want to attempt to duplicate or engineer a “good terroir” for their plants, but to do this they need to better understand the factors involved. Besides geographic origin, the modern concept of terroir encompasses other contributors as well, stating that it “refers to an area in which collective knowledge of the interactions between the identifiable physical and biological environment and applied agricultural practices develops, providing distinctive characteristics for the products originating from this area. Terroir thus includes specific soil, topography, climate, landscape characteristics and biodiversity features.” (Castellucci, 2010). Figure 1 summarizes the factors contributing to agricultural terroir. Traditional agricultural practices are one important contributor to terroir and could include any number of things such as tilling v. no-till of the soil, organic v. conventional fertilization, etc. Soil is the most famous factor contributing to terroir, and it can vary in physical structure (eg. sand v. clay v. compost), water retention and nutrient content. An example of a good soil for wine grape production, is one that provides little nitrogen to the vine, causing abiotic stress which increases berry sugar, phenolic, anthocyanin and tannin concentration (Van Leeuwen, 2010). Topography refers to the geographic features (ie. mountains, valleys, lakes, etc.) and elevation of the farm. Although the majority of the world’s foremost wine region, Lustrac-Médoc, Bordeaux, France, is just above sea level where warmer conditions help Cabernet Sauvignon and Merlot grapes to flourish, growing grapes at high altitudes (3100 m, Finca Altura Maxima, Salta, Argentina) hits the vines with more ozone and UV radiation, creating fruit with thicker and darker skin, resulting in wines with deeper colors and more robust tannin profiles (Krebiehl, 2023). Landscape refers to the immediate lay of the planted land; for example is the farm flat or sloping and which way is it facing? In wine production, the best landscape for a vineyard is a well-drained mid-slope, where the

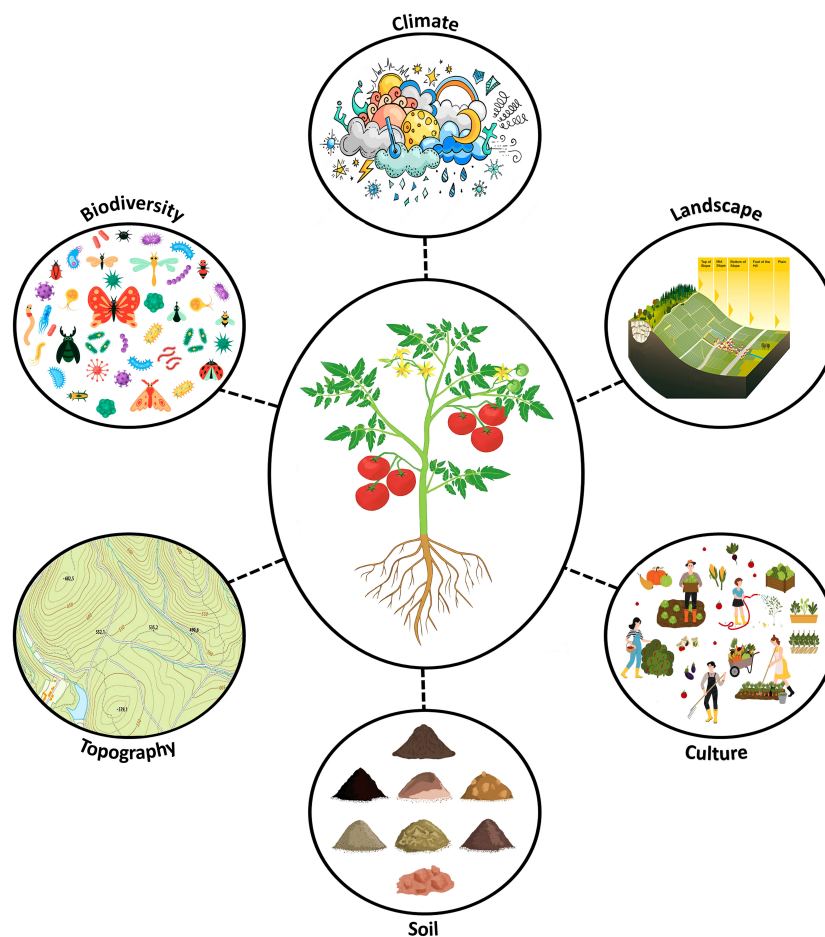


FIGURE 1

Terroir is an agricultural product's or crop plant's phenotype when grown in a defined area and it is shaped by that locality's characteristics including: applied agricultural practices (culture), soil, topography (elevation), biodiversity features (plant-biotic interactions), climate, and landscape characteristics.

plants are elevated enough to receive good sunlight while being protected from frost and winds (Krebiehl, 2023). Climate (including solar radiation, precipitation, humidity, temperature and wind) is the dominant factor that controls fruit ripening potential and agricultural product characteristics; it also dictates which crop varieties can be grown where. One example of how climate can impact terroir, is of heavy precipitation during grape berry maturation where it can trigger fungal pathogen blooms, dilute fruit sugar and flavor levels, and severely limit both fruit yield and wine quality (Jones, 2018). Biodiversity features are the last factor considered in this definition of terroir, and could include any number of plant-organism interactions, from which species of bee pollinates the flowers, the abundance of pathogens that drift onto leaves as spores, or what kinds of mycorrhizae dominate in the soil. Although there are potentially thousands of plant-microbe interactions occurring on any given farm, the majority of these have been invisible until recent advances in DNA sequencing technology have allowed us to zoom in and observe plant microbiome diversity in its totality. Considering the intimate association that plants maintain with a plethora of bacteria, fungi, viruses, protists and archaea, many scientists now consider them altogether as a holobiont – this is a “close association between

different individuals, usually host-microbiota symbioses, that together form anatomical, physiological, immunological or evolutionary units” (Baedke et al., 2020). The microbial portion of this holobiont can be vertically or horizontally transmitted, populating plant tissues inside and out. This microbiome is dynamic and can change as new members arrive or environmental conditions change, favoring particular microbes over others (Bulgarelli et al., 2013). It is interesting to realize that a plant holobiont contains both microbes and host plant which can both be affected by external environmental factors, suggesting a complex web of direct (affecting plant) and indirect (affecting microbiome) influences which contribute to terroir.

Understanding the ways that microbes contribute to an agricultural product's chemistry is arguably the final frontier in the study of terroir. Having co-evolved with plants for hundreds of millions of years, microbial endophytes, epiphytes, symbionts and commensals are able to profoundly affect their host's physiology and metabolism, for example stimulating plant growth through the production of phytohormones, provision of nutrients, enhancing tolerance to abiotic stress, or altering tissue chemistry to help resist pathogen attack (Figure 2) (Johnston-Monje et al., 2019). Usually these plant phenotypes are explained through the activity of one or

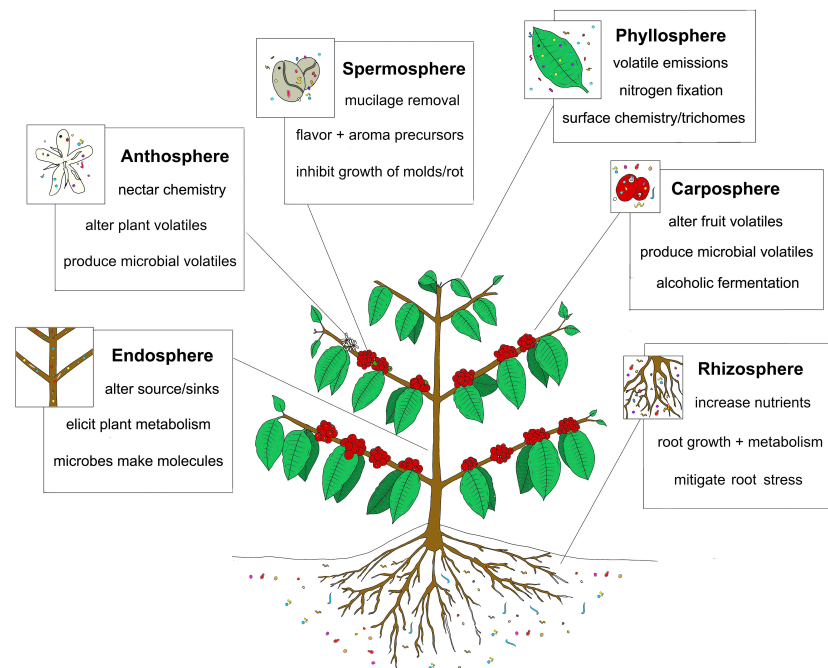


FIGURE 2

Microbiomes in different plant organs and surfaces contribute to the agricultural terroir which influences the plant metabolome, and product flavor/nutritional value. Microbial populations in the rhizosphere, endosphere, phyllosphere, spermosphere, carposphere, or anthosphere can influence crop chemistry in a number of different ways including microbial production of flavor metabolites, microbial degradation of plant biochemicals and microbial manipulation of plant metabolism.

two particular microbes (eg. nitrogen fixing bacteria in a legume's nodules), but broad microbiome characteristics like species richness and evenness are also important for structuring communities to provide nutrient cycling and stress/disease resistance to the plant (Bakker et al., 2012). Said another way, "Although specific functions can be attributed to specific microorganisms, it is the total microbiome and its interactions that affect plant health (and terroir)." (Berendsen et al., 2012). Using these new techniques of metagenomics and metabolomics, scientists are beginning to observe novel correlations between plant associated microbiomes to the metabolomes of plants having "good terroir" (O'Banion et al., 2020), especially in grape wine production where the concept of terroir is most strongly developed (Liu et al., 2019; Belda et al., 2020). To be clear, we define microbial terroir as a particular plant associated microbiome (associated with a certain geographic region or not) which can somehow alter the chemical makeup of the plant/agricultural product relative to plants possessing other different microbiomes. This review will highlight research that has begun to prove that microbial populations can impact the chemistry of crop plants and agricultural products. Examples of how single microbes can affect plant chemistry and physiology will also be mentioned to help illustrate the mechanisms involved. Studies of microbial populations in the soil or rhizosphere, carposphere (fruit), endosphere, phyllosphere, spermosphere (seeds) and anthosphere (flowers) influencing plant chemistry, flavor, fragrance, or nutritional content will be presented as evidence supporting the concept of microbial terroir. By understanding how certain

microbes or microbiomes can impact plant chemical makeup, agriculturalists may begin to develop practices of microbial terroir engineering to enhance the quality and sale price of their plant products.

2 Rhizosphere microbiome contribution to terroir

As the principal factor contributing to classical terroir, good soil is very important for growing healthy and productive plants. Soil is also now known to be the most biodiverse habitat on Earth, with a typical gram of dirt containing 4000 genotypes of bacteria and 2000 different fungi (Decaëns, 2010). Microbiome studies using high throughput sequencing techniques have helped reveal that soil bacterial, protzoan and/or fungal diversity varies in correlation with differences in climate, soil physio-chemistry, agricultural practices and plant species (Bardgett and van der Putten, 2014; Fierer, 2017). Biogeographical variation of soil microbiomes is an important factor spurring exotic plant invasions (Rout and Callaway, 2012), as well as orchid seed germination which depends on the presence of compatible soil symbionts belonging to a Rhizoctonia-like group of fungi (Rasmussen et al., 2015; Voyron et al., 2017), medicinal root saponin content of *Panax notoginseng* growing in different parts of China (Wei et al., 2020), concentrations of the "impact aroma" molecule rotundone in Shiraz grapes. (Gupta et al., 2019) and the metabolome of

Australian Pinot Noir wine (Liu et al., 2020). The influence of mycorrhizae and rhizobacteria on tea productivity and quality has been recently reviewed (Bag et al., 2022).

Comparisons of rhizosphere microbiome to plant metabolome have established a link between the two; this is true of grape (Liu et al., 2019; Zhou et al., 2021), *Arabidopsis* (Badri et al., 2013), tomato (Escobar Rodríguez et al., 2021) and rice (Deshmukh et al., 2016). With the exception of inoculation studies involving PGPR, mycorrhizae or rhizobia (Van Der Heijden et al., 2008), it is very difficult to know which microbes may have most influenced the plant metabolome (Misra et al., 2017; White, 2020), since very few of these organisms have well known and defined relationships with plants (Wardle et al., 2004). Even less is known about which mechanisms the soil microbes may have used to alter the chemical makeup of the crop plant (Rillig et al., 2018). Soil microbes could translocate to distal organs (ie. enter root and travel to fruit) and there influence the plant metabolome, however we will not explore this topic in our review.

2.1 Nutrient acquisition and absorption

Plants need to absorb 17 different minerals to grow, metabolize and reproduce, including the macronutrients C, H, O, N, P, S, K, Ca, and Mg (Osman, 2013). Conversely, plants can also accumulate toxic compounds such as heavy metals which can be bad for plant growth and human consumption. With little or no saprophytic ability, plant absorption of nutrients depends on soil microbes to digest, breakdown, fix and solubilize compounds in the soil so that the roots can then take up bioavailable minerals. Rhizosphere saprobes will also absorb most of the nutrients they are liberating, forcing the plant to obtain them through symbiosis, to wait for the microbes to die (Kuzyakov and Xu, 2013), or in a recently discovered process called rhizophagy, to ingest and digest the bacteria (White et al., 2018). Alternatively, microbes may also secrete exopolysaccharides, produce biofilms, change the soil pH, chelate, biosorb, precipitate or otherwise lock up soil compounds which may make them unavailable for uptake by the plant. Variation in soil microbial diversity could change nutrient availability for plants in many ways and for example, has been shown to affect litter decomposition by up to 20% (Strickland et al., 2009).

Although nutrients are important to survive, uptake of too much or too little can impact flavor, fragrance and nutritional quality of the agricultural product. In grape production for example, a good soil provides little nitrogen to the vine, causing abiotic stress which reduces plant vigor, berry weight and yield, while increasing berry sugar, phenolic, anthocyanin and tannin concentration – metabolites important in red wine flavor (Van Leeuwen, 2010). Tea leaves grown on phosphorus deficient soil have significant reductions in yield and alterations to their mineral and metabolite content, especially flavonoids, organic acids and amino acids (Ding et al., 2017). *Panax notoginseng*, called Sanqi in China, is a medicinal plant whose root accumulates higher levels of medically important saponins in soil that is nitrogen and potassium rich (Zhang et al., 2016). Cacao grown on soils containing cadmium

tend to accumulate the heavy metal in their seeds, contaminating the resulting chocolate which is banned by some countries if it contains as little as 0.1 mg of Cd/kg (Maddela et al., 2020).

Rhizosphere microbes that alter soil mineral and nutrient availability, could thus affect plant mineral uptake, and thus impact its metabolome. For example, “within-vineyard” enrichment of Alfa- and Gamma-Proteobacteria in soil, correlates with increases of N and S uptake, which in turn correlates with a reduction of berry phenolics, reducing Sangiovese wine quality scores by 19 points (Mocali et al., 2020). Inoculating Tempranillo grapevines with a commercial blend of 5 mycorrhizal fungi (Bioradis Gel by Bioera SLU, Tarragona, Spain) increased phenolic and carotenoid concentrations in leaves, glucose and amino acid content in the fruit (Torres et al., 2019). Similarly, in a pot experiment, inoculation of tea plants with AMF increased N uptake and significantly increased the content of leaf polyphenols, catechuic acid, flavonoids, amino acids, and soluble proteins (Shao et al., 2019). Inoculation of wheat and maize with GFP labelled diazotroph *Pseudomonas protegens* Pf-5 X940 showed that it localized to root surfaces where it secreted ammonium that increased nitrogen content in both vegetative and reproductive tissues (Fox et al., 2016). The stalk metabolome of bitter and sweet sugarcane varies by 247 different compounds and is highly correlated to the nitrogen concentration and bacterial diversity found in soil (Huang et al., 2021).

Next to N, P is considered the most limiting nutrient for plant growth. Many different soil microbes have been shown to be able to promote plant growth and increase yield by augmenting P availability in soil (Alori et al., 2017). Evidence of soil microbial ability to influence agricultural terroir appears only to exist in wheat and pea whose seeds accumulated significantly greater levels of mineral nutrients or secondary metabolites when inoculated with P uptake enhancing mycorrhizae (Ranjbar Sistani et al., 2020; Shahane et al., 2020; Yadav et al., 2020). Using a series of sensorial tests and an electronic nose, organic wheat inoculated with a commercial blend of mycorrhizae (Micosat F) produced bread that was distinguishable from bread deriving from uninoculated plants (Torri et al., 2013).

Microbe alteration of metal availability in the soil can also affect plant concentrations. Growth promoting and stress resistant rhizobacteria such as certain *Pseudomonas*, *Bacillus*, *Enterobacter* and *Burkholderia*, are able to reduce cadmium bioavailability in the soil by complexation, biosorption, and precipitation, resulting in soy, wheat, barley, pea, tomato, pumpkin and mustard with lower levels of the toxic metal (Sharma and Archana, 2016). In stark contrast, rhizosphere bacteria (especially *Lysobacter*, *Streptomyces*, *Agromyces*, *Nitrospira*) of the hyperaccumulating plant *Arabidopsis halleri* appear to be able to help the plant absorb more heavy metals, resulting in 100% more accumulated cadmium and 15% more zinc than plants grown on gamma irradiated soil (Muehe et al., 2015). Similarly, inoculation with certain strains of soil microbe have been shown to be able to “biofortify” seeds by increasing wheat levels of selenium and iron (Yasin et al., 2015). Soil microbiomes and their impact on the chemical and micronutrient content of agricultural plants has been reviewed elsewhere (Cochran, 2017; Kaur et al., 2020; White, 2020).

2.2 Altering plant growth and metabolism

Some soil microbes are able to alter plant chemistry by changing the way a plant grows and metabolizes. Root growth can be dramatically enhanced by underground bacterial signals which alter plant phytohormone production and gene expression (Ping and Boland, 2004; Vacheron et al., 2013). Various experiments drenched the soil with growth promoting microbes and observed metabolic changes in the plant: *Enterobacter* and *Paenibacillus* significantly increased tomato biomass and altered leaf metabolomes (Kaloizoumis et al., 2021); *Bacillus subtilis* GB03 or its cell free biochemical extracts doubled sweet basil weight and increased essential oil accumulation tenfold (Banchio et al., 2009). Similar experiments and results have been seen in tomato (Pérez-Rodríguez et al., 2020), peppermint (Santoro et al., 2011; Santoro et al., 2016), Italian oregano (Banchio et al., 2010), marigold (Cappellari et al., 2013) and lemongrass (Mirzaei et al., 2020). Interestingly, rhizobacterial production of volatile plant growth promoting compounds is itself influenced by environmental conditions, adding a further layer of complexity to the microbial dimension of terroir (Blom et al., 2011). Although mycorrhizae are usually considered to affect plant chemistry by aiding in nutrient uptake, there are also many examples of their ability to stimulate plant growth and metabolism by secreting phytohormones (Rouphael et al., 2015; Avio et al., 2018), resulting in changes to chemistry, nutrients and/or flavours including carotenoids, phenolics, polyphenols, phytoestrogens, flavonoids, antioxidants and essential oils (Ceccarelli et al., 2010; Sbrana et al., 2014; Hart et al., 2015; Battini et al., 2016). Other examples of rhizosphere microbes inducing changes in plant chemistry have been recently reviewed (Qu et al., 2020; Korenblum et al., 2022).

In many cases, soil microbes can change the plant metabolome by simply being detected (Piasecka et al., 2015). Pathogens and symbionts alike can be recognized by their conserved microbe-associated molecular patterns (MAMPs) or elicitors which trigger above ground responses to mount defenses against pathogens, pests, or abiotic stress, in a process called induced systemic resistance or ISR (Pineda et al., 2017; Rashid and Chung, 2017; Etalo et al., 2018; Vannier et al., 2019; Yu et al., 2019). Detecting elicitors can alert the plant to a nearby pathogen so that it can prepare to defend itself. In grape cell tissue culture, elicitors such as cyclodextrin, and chitosan dramatically increase resveratrol (molecule with anti-aging, anticarcinogenic, anti-inflammatory and antioxidant properties) production (Jeandet et al., 2014), suggesting that their presence in rhizospheres could have a similar effect. Elicitor mediated plant responses often work through phytohormone signaling, especially jasmonate, methyl jasmonate and salicylic acid; addition of these compounds to plant cell culture can modulate the production of many specialized metabolites (Nabi et al., 2021) suggesting their production (Peñuelas et al., 2014) or indirect modulation (Pineda et al., 2013) by soil microbes could also impact terroir. Inoculation of soil with pure microbial strains has shown that elicitors can influence plant metabolism: grapevines recognize the oomycete *Pythium oligandrum* by its elicitor oligandrin as it comes in contact with roots, triggering aboveground production of resveratrol (Mohamed et al., 2007); the rhizobacteria *Pseudomonas aeruginosa* PM12

induces ISR and increases fruit levels of sugars, flavonoids, terpenoids, carotenoids and total phenolics (Fatima et al., 2017) when tomato plants detect the elicitor 3-hydroxy-5-methoxy benzene methanol (Fatima and Anjum, 2017). Further information on the effect of rhizosphere or root microbes and their elicitors on plant metabolism has been recently reviewed (Etalo et al., 2018; Korenblum and Aharoni, 2019).

Variation in soil microbiomes can contribute to different terroirs, however on a farm it is nearly impossible to know which particular microbes or mechanism(s) might have been responsible. Variation in rhizosphere microbiomes correlated with *Salvia officinalis* growth, concentration of essential oils, flavonoids and phenolics (Ghorbanpour et al., 2016); farming history altered the peanut rhizosphere and correlated with changes to plant nutrient metabolism and phytohormone biosynthesis (Li et al., 2019); drenching *Arabidopsis* roots with different soil microbiomes modulated both shoot biomass and the leaf metabolome, which in turn altered the feeding behavior of *Trichoplusia ni* caterpillars (Badri et al., 2013); soil fungi influence amino acid concentration in *Senecio jacobaea* phloem sap, which in turn influenced the feeding behavior of the foliar feeding aphid *Aphis jacobaea* (Pineda et al., 2017); inoculating *B. subtilis* Co1-6 and *P. polymyxa* Mc5Re-14 onto chamomile roots grown in arid Egyptian soil showed an enhancement of the bioactive secondary metabolite apigenin-7-O-glucoside in flowers (Schmidt et al., 2014); microbiota in disease suppressive soil greatly upregulated tomato phenol biosynthesis, lignin deposition, innate immunity and resistance to oxidative stress, leading to higher Fusarium root rot resistance (Chialva et al., 2018). *Beta vulgaris* and *Brassica oleracea* were grown on soil missing rare microbes, resulting in higher plant biomass but lower sugar and glucosinolate concentrations (Hol et al., 2010).

2.3 Mitigating root stress by modifying the rhizosphere

Rhizosphere microbiomes can also indirectly influence plant metabolism by mitigating plant stresses. Soil microbes can interrupt plant-soil feedback loops by degrading phytoactive compounds in the rhizosphere, for example bacteria using ACC deaminase to reduce levels of the plant stress hormone ethylene can help roots grow during flooding (Glick, 2014). Phytotoxic compounds in the soil, including plant derived allelochemicals (Misra et al., 2020; Scognamiglio and Schneider, 2020) or human applied herbicides (Zhang et al., 2021; Sun et al., 2022), can stress or kill crops while inducing changes in their metabolic profiles; however, these compounds can be readily degraded by certain soil microbes (Huang et al., 2013). Root diseases caused by microbial pathogens can also trigger production of specialized metabolites in plants, thus for better or for worse (in terms of sensorial or nutritional attributes) soil pathogen biocontrol should be able to preserve the metabolic profile of a healthy plant.

M-tyrosine is an allelopathic chemical secreted by roots of Cheewing's fescue (*Festuca rubra*) that inhibits growth of other plant species, altering root development, causing leaf chlorosis, retarding growth and reducing levels of amino acids, especially

phenylalanine (Zer et al., 2020). By growing *Lactuca sativa* (lettuce), *Phalaris minor* and *Bambusa arundinacea* on sterilized or unsterilized soil that had been amended with M-tyrosine, the soil microbiome was proven to be important in degrading this compound and reducing phenotypic effects on plants (Kaur et al., 2009). Another example of allelopathy is seen in croftonweed (*Eupatorium adenophorum*) which is native to Central America, but in China, has become a destructive, invasive species that produces two powerful allelochemicals inhibiting the germination and growth of native plants. Soil microbes from different Croftonweed invaded habitats were able to alleviate or eliminate phytotoxicity, whereas microbes present in sand had no effect (Zhu et al., 2011). Tea plants grown in young plantations (2 years old) had significantly greater leaf concentrations of theophylline, total polyphenols, theanine, and total amino acids, than plants grown in soil from older plantations (15 and 30 years old) (Arafat et al., 2020). These metabolic changes in older plantations were explained by soil accumulation of allelochemicals released by leaf litter, reduction of growth promoting genera *Sphingomonas*, *Bacillus*, and *Prevotella*, and increases in soil populations of allelochemical degrading *Pseudomonas* and *Burkholderia*. It seems quite plausible then that agricultural plants grown on allelochemical impregnated soils containing different microbial populations would manifest different metabolomes; however, we found no published examples supporting this concept.

Human applied herbicides are meant to take out weeds, but can linger in soil after application and cause stress, yield reductions and metabolic changes to crop plants long after the original intended targets were killed (Fuchs et al., 2021a; Ganugi et al., 2021; Ruuskanen et al., 2022). Glyphosate for example is the most widely used herbicide in the world, which disrupts the shikimate metabolic pathway, blocking aromatic amino acid production and synthesis of downstream metabolites with important implications for sensorial profiles of agricultural products (Fuchs et al., 2021b). Plant metabolomes are very sensitive to herbicides, with rapeseed biochemistry being significantly affected by soil concentrations of glyphosate as low as 5 μM (Petersen et al., 2011). Soil (Zhou et al., 2022) and plant associated (Ke et al., 2021) microbes can also be affected by herbicide presence in the soil, with negative effects reported for rhizobial nodulation in legumes, mycorrhizal associations with roots and of nitrogen metabolism by free living microbes (Meena et al., 2020). Conversely, soil microbiomes are able to degrade or detoxify some herbicides such as glyphosate and atrazine, at different rates (Yale et al., 2017; Zabaloy et al., 2022), suggesting a way that herbicide impregnated soils could differently affect plant metabolomes. In one example of this principle, addition of biochar into fomesafen impregnated soil significantly altered the wheat rhizosphere microbiome and reduced herbicide uptake/toxicity (Meng et al., 2019). Similarly, addition of biochar to atrazine contaminated soil reshapes the soybean rhizosphere microbiome, reducing plant stress, improving nodule formation and increasing plant growth (Zhou et al., 2022). Certain synthetic communities of bacteria (including Firmicutes and *Burkholderia*) were able to differentially metabolize glyphosate, impacting the growth rates of *Arabidopsis* (Ramirez-Villacis et al., 2020). Although these case studies prove the concept that microbes can

changes soil levels of herbicide and thus impact plant growth, we were unable to find publications explicitly studying this effect in the context of an agricultural plant's metabolome.

Another way that rhizosphere microbes could contribute to a good terroir is by suppressing pathogens to help maintain the biochemical profile of a healthy plant. Soil pathogens can invade, manipulate (biotrophs) and destroy (necrotrophs) root tissues, inducing a variety of metabolic responses all over the plant (Castro-Moretti et al., 2020). For example, canola roots under attack by *Plasmodiophora brassicae* (clubroot) defend themselves by producing a variety of antimicrobial metabolites (Pedras et al., 2008). Another example, when the soil transmitted necrotrophic pathogen *Ralstonia solanacearum* colonizes tomato roots, it induces production of a range of defensive compounds including antimicrobial quinic acids, flavonoids, polyamines (ie. spermidine) and osmoregulatory hexoses (Castro-Moretti et al., 2020). Elevated levels of glycoalkaloids (toxic to humans) are produced in potato tubers trying to resist root rot pathogens like *Fusarium sulphureum* (Li et al., 2022). In a wonderful example of a soil microbiome preserving a healthy plant metabolome, maize was grown on sterile sand inoculated with soil bacteria that had been filter purified of all protists (predators of bacteria), while some plants were also inoculated with a blend of these bacterial predators: the ciliate (*Tetrahymena pyriformis*), an amoebae (*Acanthamoeba polyphaga*) and a flagellate (*Cercomonas longicauda*). Plants inoculated with protists maintained unstressed metabolic profiles, while plants growing without the influence of the predators experienced significant shifts in their rhizosphere bacterial populations, and accumulated stress induced metabolites (polyols, carbohydrates and phenolic compounds) in their roots and leaves (Kuppardt et al., 2018).

3 Endosphere microbiome contribution to terroir

Changes in the diversity of endophytic microbes living within plant tissues like roots or tubers (eg. potato, ginseng, carrot), stems or shoots (eg. celery, cinnamon, asparagus) or leaves (eg. basil, spinach, tea), may also affect their metabolome. Endophytes are derived vertically through the seed (Johnston-Monje et al., 2021b) or via vegetative propagation (Quambusch and Winkelmann, 2018) as well as horizontally from the external environment (Bulgarelli et al., 2013) however no type of transmission is entirely consistent and invariable. The seed transmitted fungal endophyte *Epichloë* is imperfectly transmitted from 69-99% between different genotypes of host grass (Gagic et al., 2018) and from 0-100% depending on storage conditions; after 18 months at high temperature and humidity, all *Epichloë* in grass seeds are dead (Hume et al., 2013). Different soil conditions, especially pH, alter the makeup of seed transmitted endophytes colonizing rice plants, which would presumably also have an impact on the plant metabolome (Hardoim et al., 2012). In another example, eradicating the seed transmitted microbiome of metal hyperaccumulating plant *Sedum alfredii* significantly lowered plant biomass and heavy metal accumulation, while inoculating these axenic plants with certain vertically transmitted endophytes restored the phenotype (Luo et al.,

2019). It has long been known that vegetative cuttings and tissue cultured plantlets of crops like potato, grape, strawberry, and cassava, do contain vertically transmitted endophytic bacteria and fungi. Propagation method appears to be able to alter the endophytic microbiome: differently propagated sugar cane contains significantly different populations of endophytic fungi and bacteria (Yang et al., 2023), as do different apple scions grafted onto different apple rootstocks (Liu et al., 2018). There is as of yet no knowledge about the impacts these different microbiomes might have on the plant metabolome; however, it is our opinion that vegetatively propagated endosphere microbiomes represent a subset of the normal seed transmitted microbiome and thus deliver only a fraction of the normal seed microbiome's phenotypic benefits to these crops. Because tissue culturing attempts to create sterile plantlets, while vegetatively propagated plants are denied sexual reproduction, the resulting propagules may be nearly devoid of their normal vertically transmitted microbiome and likewise nearly devoid of the accompanying phenotypic benefits that seed endophytes would provide. Because many endophytes are thought to be horizontally transmitted (Johnston-Monje et al., 2021a), environmental variation can also influence microbial diversity in the endosphere. This has been shown in grapes, where the majority of bacterial endophytes in roots were observed to originate and vary in relation to the soil microbiome, which in turn was influenced by soil moisture, carbon, temperature, and geographic location (Zarraonaindia et al., 2015). Another study of grape endophytes found that endophytic yeasts in xylem sap originated from soil, which in turn varied from farm to farm and with relation to soil physio-chemical factors (Liu et al., 2020).

An endophyte could most directly contribute to terroir by producing flavorful, nutritious, medicinal or toxic metabolites which remain inside the agricultural product. The most famous seed transmitted endophytes are *Epichloë* fungi, found in nearly 30% of the Earth's cool-season grasses – these endophytes produce peramines, lolines, ergot, and indole-diterpene alkaloids which are toxic to insects and mammals (Lee et al., 2021). Another example is the antifungal cancer drug Taxol; found in yew trees at concentrations that can vary by up to 125 times (Soliman et al., 2013), it is synthesized by both the tree and its endophytes like *Paraconiothyrium* SSM001 which construct Taxol containing endophytic defenses against invading pathogens (Soliman et al., 2015). Similarly, the anticancer drug maytansine is produced by the endophytic microbial community in roots of *Putterlickia verrucosa* and *P. retrospinosa* plants (Kusari et al., 2014). Numerous other examples of nutritionally, sensorially and pharmaceutically significant substances produced by endophytes have been reviewed elsewhere (Strobel and Daisy, 2003; Newman and Cragg, 2015; Newman and Cragg, 2020; Tilocca et al., 2020; Mathur and Ulanova, 2022); it is usually unclear how significant their contributions might be *in planta*.

Endophytes can alter their host plant's absorption of nutrients by changing the strength of the nutrient sink, for example when leaf endophytes compete for minerals and force the plant to take up more (Venkateswarlu and Visperas, 1987). *Beauveria bassiana* for example, stimulates tomato and wheat to uptake more iron (Sánchez-Rodríguez et al., 2015), while *Neotyphodium coenophialum* increases the concentration of P, Ca, Zn and Cu in

P starved tall fescue (Malinowski et al., 2000). Similarly, *Epichloë gansuensis*-infected grass *Achnatherum inebrians* enjoyed increased plant biomass, and increased leaf accumulation of C, N, P, metals, tryptophan, threonine, serine, proline, phenylalanine, lysine, L-asparagine, glutamic acid, glutamine, glycine, aspartic acid, arginine, and alanine (Liu et al., 2021b). Inoculating tobacco plants with the dark septate fungus, *Acrocalymma vagum*, promoted plant growth and reduced heavy metal content in leaves, theoretically resulting in a healthier cigar (Jin et al., 2018). The ability of bacterial endophytes to enhance micro-nutrient accumulation (eg. Zn, Se, Fe) in plants has been reviewed recently (Kaur et al., 2020).

Endophytes inside roots, stems or leaves might also contribute to terroir by influencing or participating in plant metabolism. Endophytic symbiosis between soil transmitted rhizobia and legumes such as common bean is a classic example where nitrogen fixation within the root results in seeds with significantly elevated levels of protein and starch (Massa et al., 2020). In an example of a growth promoting endophyte influencing the plant metabolome, inoculation of grape roots with endophytic *Paraburkholderia phytofirmans* PsJN, triggered the overexpression of all phenylpropanoid and flavonoid pathway genes, as well as increasing the relative amounts of 32 and 17 different compounds in roots and leaves respectively (Miotto-Vilanova et al., 2019). The root endophyte *Piriformospora indica* stimulates tomato and *Arabidopsis* growth by upregulating host production of putrescine; a polyamine so named for smelling like rotting meat (Kundu et al., 2022). Inoculating pot grown apple trees with a blend of 9 different plant growth-promoting bacterial endophytes isolated from wild black cottonwood and willow trees, increased root growth, delayed leaf senescence, and significantly increased fruit mass and soluble sugar content (Rho et al., 2020). Similarly, inoculating grape vines with 8 different fungal endophytes variously increased the content of reducing sugars, flavonoids, phenols, trans-resveratrol and phenylalanine ammonia-lyase in both fruits and leaves (Yang et al., 2016). Inoculating the medicinal plant *Artemisia annua* with a variety of different bacterial and fungal endophytes, their chemical extracts or elicitors can increase plant growth, stimulate plant defense responses and enhance artemisinin production (Zheng et al., 2021). The bacterial endophytes *Bacillus altitudinis* and *Paenibacillus polymyxa* stimulate growth and medicinal ginsenoside accumulation in roots of ginseng plants (Chu and Bae, 2022). Inoculation of lab grown *Catharanthus roseus* with leaf endophytes *Curvularia* sp. CATDLF5 and *Choanephora infundibulifera* CATDLF6 increased vindoline content by up to 403% although what mechanisms might be involved were unknown (Pandey et al., 2016). Similarly, inoculation and co-culture of tissue cultured grape with different foliar fungal endophytes significantly altered fruit metabolite profiles (Huang et al., 2018). A comparative metabolomics analysis of ryegrass, with or without endophytic *Epichloë festucae*, found the fungus alters the expression of 30% of the plant's genes, triggering a dramatic change in plant metabolism; increasing secondary metabolite accumulation (especially flavonoids and anthocyanins), while reducing primary metabolism (Dupont et al., 2015). Not content to passively

communicate with the plant, soil bacteria *Agrobacterium tumefaciens* and *A. rhizogenes* invade the endosphere and genetically transform plant cells to overproduce auxins and cytokinins resulting in crown gall tumors and hairy roots that produce large amounts of opines; amino acids consumed by the bacteria (Hooymaas, 2000). Many other root endophytes have been documented as being able to alter plant metabolism (Etalo et al., 2018; Korenblum and Aharoni, 2019).

Most studies looking at the influence of an endophytic microbiome on the plant metabolome, establish simple correlations, but do not identify the specific microbes or mechanisms involved. For example in a study of endophytic fungi in different horseradish varieties, 35% of the mycobiome correlated with biochemical variation in the root, but no specific microbes were singled out as responsible (Plaszko et al., 2022). Increased levels of soil organic matter significantly altered the diversity of bacteria living inside roots of the medicinal plant *Echinacea purpurea*, which in turn increased the immunostimulant properties of extracts by more than 400% (Haron et al., 2019). A fascinating experiment where specific causal microbes were identified, inoculated *Arabidopsis* grown on different concentrations of phosphate with a 185-member bacterial synthetic community; shoot levels of orthophosphate correlated negatively with the abundance of the genus *Burkholderia* (Finkel et al., 2019). This correlation was validated through a dropout inoculation experiment, suggesting that under phosphate starvation, *Arabidopsis* can't effectively exclude *Burkholderia* endophytes, which further sequester the scarce nutrient away from the shoots.

4 Carposphere microbiome contribution to terroir

Fruits are enjoyed for their flavor, which consists of mouth perception (sweetness, acidity or bitterness) and aroma, the latter made up of volatile compounds including alcohols, aldehydes, ketones, lactones, terpenoids and apocarotenoids (El Hadi et al., 2013). With an estimated 100 million bacterial cells inside one common apple (Wassermann et al., 2019) and evidence that microbiomes on the surface of fresh fruit and vegetables vary by plant genotype and farming practice (Leff and Fierer, 2013), it is easy to imagine that carposphere microbial terroir might be a thing. Wine grape microbiomes have been variously shown to be influenced by plant cultivar, year, soil, geographic location, vineyard, environmental heterogeneity, agricultural technique and climate (Bokulich et al., 2014; Pinto et al., 2015; Zorraonandia et al., 2015; Stefanini et al., 2016; Chou et al., 2018). It has also been repeatedly shown that grape microbiome makeup correlates directly with differences in the wine metabolome (Bokulich et al., 2016; Belda et al., 2017; Mezzasalma et al., 2017; Liu et al., 2019). Raspberry metabolomes vary in concentrations of anthocyanidin, acids, ketones, aldehydes, and monoterpenes depending on organic versus IPM cultivation (Sangiorgio et al., 2021). These differences were partially explained by changes in fruit associated populations of volatile chemical emitting *Gluconobacter*, *Sphingomonas*, *Rosenbergiella*, *Brevibacillus* and *Methylobacterium*. Experiments

by the same author found that surface sterilization of raspberries significantly reduced volatile aldehydes, monoterpenes, norisoprenoids and other aroma-active compounds, although reinoculating the berry with a previously collected surface microbiome was able to partially restore emission of terpenoids (Sangiorgio et al., 2022). *Methylobacterium* inside strawberries is important in producing the precursors to aromatic furaneol substances (strawberry flavor) such as 2,5-dimethyl-4-hydroxy-2H-furan-3-one (Nasopoulou et al., 2014). When inoculated onto greenhouse grown plants, methylobacteria are able to increase furaneol accumulation in fruit (Verginer et al., 2010b). By metabolically profiling individual bacterial isolates found inside and on the surface of Blaufraenkisch grapes, many of the fruit's aromas were found to be at least partially attributable to these microbes (Verginer et al., 2010a).

Of course, the most important impact of fruit microbiomes on an agricultural product would be on alcoholic fermentation. Many fruits are fermented to make wine and spirits, although grape wine is by far the most popular (Saranraj et al., 2017). At the end of the 19th century, Louis de Pasteur showed that yeasts on the fruit surface were the main microorganisms responsible for wine fermentation (Barata, 2012). Ninety-three different yeast species have been isolated from grapes growing in 22 countries and vary from plant to plant within a farm, by climatic conditions, by grape variety and by agriculture practices (Liu et al., 2017). Yeasts are responsible for alcoholic fermentation of grapes, converting sugars to carbonyl compounds, esters, acids, acetals, and alcohols, of which ethanol can reach 10-16% final concentration, killing many sensitive microbes which might otherwise influence the quality of the final product (Liu et al., 2017). Although wine is a hostile environment for bacteria (low pH, high ethanol concentration and low nutrients) more than 50 species have been isolated from fruits and must, mostly lactic acid producing bacteria including *Lactobacillus*, *Oenococcus*, *Pediococcus* and *Leuconostoc*, acetic acid producing bacteria such as *Acetobacter* and *Gluconobacter*, and others (*Bacillus*, *Enterococcus*, *Enterobacter*, *Pseudomonas*, *Burkholderia*, *Serratia*, *Klebsiella*) with less clear oenological functions (Liu et al., 2017). After alcoholic fermentation by yeasts, lactic acid bacteria begin to de-acidify the wine by converting citrate and malate to lactate, acetate, diacetyl (buttery flavor), acetoin, 2,3-butanediol and carbon dioxide; de-acidification is particularly valuable for acidic, cold climate wines such as those made in Canada (Liu, 2002). Malolactic fermentation by bacteria can result in a range of different compounds with flavors described as spicy, floral, oaky, honey, earthy, nutty, roasted, yeasty, sweaty, vanilla, toasty, smoky, bitter and ropy (Liu, 2002). Acetic acid bacteria are considered unfavorable, spoilage organisms as they produce oxidized compounds with unpleasant vinegar-like flavors such as acetaldehyde and acetic acid (Swiegers et al., 2005). Also present on the grape surface are pathogenic and saprophytic fungi which could create off flavors and toxins; these include downy mildew (*Plasmopara viticola*), powdery mildew (*Erysiphe necator*), grey rot (*Botrytis cinerea*) and saprophytic moulds (e.g. *Cladosporium* spp., *Aspergillus* spp., *Penicillium* spp.). These fungi do not usually survive during well managed wine fermentations (Barata, 2012).

Geographic influences on vineyard soil microbial diversity are more pronounced for fungi, than for bacteria, suggesting a greater role for these microbes in colonizing the carposphere and contributing to wine terroir during fermentation (Coller et al., 2019). Similarly, studies of spontaneously fermented Cabernet Sauvignon grapes in China (Wei et al., 2022b) and 6 geographically disparate Australian Pinot Noir wines (Liu et al., 2020) found that fruit and must mycobiomes were of primary importance to wine flavor and aroma, with bacterial diversity correlating little with variation in wine chemistry. Studying the microbiomes of over 200 California Cabernet Sauvignon and Chardonnay grape musts and fermentations, found regional microbiota signatures that correlated with wine chemical composition (Bokulich et al., 2016). Although a range of different yeast species could be involved in spontaneous wine fermentation (Capozzi et al., 2015) *Saccharomyces cerevisiae* is the most common and important, occurring in soil, varying geographically and being transmitted from soil to fruit to fermentation tank (Mandl et al., 2015). Being the dominant microbe in spontaneous wine fermentations, changes in *S. cerevisiae* strain type or relative abundance can explain the majority of wine flavor differences at a subregional level, when vineyards are separated by less than 12 km (Liu et al., 2021a). Isolating *S. cerevisiae* from six major New Zealand wine regions and inoculating these into the same Sauvignon Blanc juice resulted in wines with significantly different aromas and flavors (Knight et al., 2015). Controversially, many studies have found instability of *S. cerevisiae* strains on grapes and in vineyards over time, while others have found that particular strains of *S. cerevisiae* stably colonize the same winery (building, fermentation tanks, etc) for years, leading to speculation that the latter (known as “winery effect”) is ultimately responsible for most microbial terroir signatures observable in the wine metabolome (Alexandre, 2020). To further confuse the importance of carposphere microbiomes in wine fermentation, most of the world’s wine makers inoculate their grape must with commercial strains of *S. cerevisiae*, inhibiting and overwhelming most fruit surface microbes, eliminating a potentially important source of chemical uniqueness from their fermentations (Alexandre, 2020).

5 Spermosphere microbiome contribution to terroir

Caloriewise, the most important agricultural products are the seeds of cereal grasses like maize, rice and wheat which are often ground into flour for making carbohydrate rich bread, tortillas, arepas and noodles. Infection of cereal seeds with fungi can result in bad odor and taste, but also accumulation of dangerous mycotoxins: the fungus *Claviceps purpurea* (ergot) which infects wheat and rye seeds, produces toxic alkaloids which afflicted tens of thousands of people in Medieval times, causing the disease Saint Anthony’s Fire (Miedaner and Geiger, 2015). Another fungal toxin, deoxynivalenol (also known as vomitoxin) is produced in wheat, barley and corn seeds following infestation by the fungus *Fusarium graminearum* (Pestka, 2010). Fruit seeds like coffee and cacao are also valued human foods, but they are prized for their flavor and secondary metabolites rather than as a staple source of calories. Coffee and cacao seeds develop within a gelatinous mixture of polysaccharides

known as mucilage which is thought to aid in seed dispersal through water and soil, to protect the seed from stomach acids inside animals and to function as a hydrogel, maintaining moisture for germination (Tsai et al., 2021). While some seeds are consumed fresh along with their mucilage (eg. tomato, chia, passion fruit), coffee seeds need to have their mucilage removed before drying to prevent microbial rotting during storage, while cacao seeds need to be fermented before roasting or they will not develop the flavor of chocolate (Schwan and Wheals, 2004; Kadow et al., 2015). To collect and store gel covered seeds for future planting (eg. tomato), mucilage has to be removed before drying and storage. Coffee and cacao are grown in tropical countries, with seed fermentation usually taking place on farm via spontaneous microbiome formation which (depending on the microbial community) can result in the creation of good flavors/aromas/nutrients and the protection against formation of bad ones (Roelofsen, 1958; Lee et al., 2015). The structuring of the seed microbiome appears to depend on the environment in which it was grown: beans (*Phaseolus vulgaris*) sourced from different farms have distinct microbiomes, suggesting that the majority of the seed microbiome is environmentally derived (Klaedtke et al., 2016). Conversely, a recent study also showed that all plant seeds share a core microbiome (Johnston-Monje et al., 2021b), thus it is still unclear what factors are the most important in shaping the spermosphere microbiome.

Cacao seed fermentation begins by manually opening pods and piling seeds up in tanks/heaps/boxes/platforms/baskets where they are left for 2-10 days to spontaneously ferment, then they are moved into the sun or a mechanical oven to dry for 7-21 days, roasted from 5-120 minutes at 120-150°C and milled to produce chocolate (Lima et al., 2011). The fermentation involves an emergent microbiome that consumes the mucilage while producing acids and alcohols that penetrate the seed, killing the embryo and activating endogenous hydrolytic enzymes. The enzyme catalyzed reactions which form the precursors of chocolate flavor and aroma also reduce bitterness (methylxanthines) and astringency (polyphenols) (Schwan and Wheals, 2004). The typical microbiome in a pile of fermenting cocoa beans is initially dominated by yeasts (producing pectinases, heat, ethanol, carbon dioxide, acids, and volatile compounds), which are then replaced after a few hours by lactic acid bacteria (producing lactic acid, ethanol, acetic acid, glycerol, mannitol, carbon dioxide and volatiles), followed by acetic acid producing bacteria (which oxidize ethanol to acetic acid, producing a lot of heat) and finally by species of *Bacillus* and molds (which mop up the remaining acetic acid, lactic acid and mannitol, but can sometimes produce off flavors) (Lima et al., 2011). Controlled incubation experiments with sterile beans show that the most important factors to form the chocolate flavor precursors are acid and heat, and not the microbes per se (Kadow et al., 2015). Inoculating sterile beans with a blend of the yeast species *Saccharomyces cerevisiae* var. *chevalieri*, the lactic acid-producing *Lactobacillus delbrueckii* subsp. *Lactis* and *L. plantarum*, and the acetic acid bacteria *Acetobacter aceti* and *Gluconobacter oxydans* is able to duplicate the quality seen from an average, spontaneous fermentation on a farm (De Vuyst and Leroy, 2020). A number of experiments have shown that through artificial inoculation with

carefully selected strains of yeast and bacteria, it is possible to accelerate the fermentation process, reduce the final acid concentration (acidic beans have weak flavor after roasting), increase production of aromas and reduce off flavor production by bacilli and molds at the end of the process (De Vuyst and Leroy, 2020). A variety of sources explain the provenance of the cacao mucilage microbiome, including workers hands, cutting utensils, fruit flies, earphones, leaves, and baskets, however the most important are the surface of cacao pods (Lima et al., 2011). While the terroir of chocolate is marketed at the national level (eg. Hawaiian chocolate is fruity, Venezuelan is nutty, Papua New Guinean is smoky) (Engeseth and Ac Pangan, 2018) and by individual farms (eg. Akesson's Madagascar estate produces chocolate with hints of raspberries and apricots, while Qantu's Peruvian bars taste like white wine) (Clark, 2021), the scientific community agrees that cocoa quality/flavor is most influenced by plant genotype and the fermentation microbiome (Hernandez and Granados, 2021). Most of the variability observed in spontaneous cacao bean fermentations is as yet unpredictable – a meta-analysis of 60 articles from Brazil, Ivory Coast and Ghana identified more than 1700 microbes that occur in cacao seed fermentations, but was unable to find a correlation between this variation and geographical location or fermentation method (Taylor et al., 2022).

Coffee seeds are also fermented, primarily to remove the mucilage, producing a naked, green bean that can be effectively dried and stored without microbial rotting. Because the fresh bean contains all the precursors necessary to make standard coffee after roasting, enzymatic or mechanical depulping can be used to remove the mucilage; however, if properly managed, microbial fermentation not only removes the mucilage, but can also improve coffee's flavor and aroma (Gonzalez-Rios et al., 2007; Haile and Kang, 2019; Elhalis et al., 2023). In wet, mountainous regions like Colombia, Central America and Hawaii, mature coffee cherries are hand-picked (ensuring consistent maturity/quality), mechanically depulped and then wet-fermented for 24–48 h to remove the mucilage (and create numerous novel aromatic compounds) before drying to stop microbial activity (Lee et al., 2015). In dryer, sunnier climates like Brazil and Ethiopia (and representing 90% of world production) cherries are usually machine-harvested (resulting in various levels of maturity/quality), sundried/fermented as whole fruit for 10–25 days, until finally the fruit/mucilage is flaked off (Lee et al., 2015). Other niche methods to remove coffee seed mucilage include passage through the intestines of the Asian palm civet (Kopi Luwak coffee), the intestines of African elephants (black ivory coffee) and the intestines of the Brazilian jacu bird (Lee et al., 2015); while creating a scarce and expensive product that is chemically distinct from traditionally fermented coffees, these are scored poorly by professional coffee tasters who consider them inferior to traditionally fermented beans (Morison, 2020). In any of these methods, beans that are underfermented can result in coffee with bad flavors (such as potato) because residual mucilage on the seed inhibits drying and facilitates growth of molds, while overfermented beans (one of the most cited problems among coffee producers) accumulate propionic and butyric acids that taste like onion or vinegar (Jackels and Jackels, 2005; Haile and Kang, 2019).

Wet fermentations of coffee seeds are usually spontaneously inoculated, employing the microbiome that is naturally assembled on the farm where cherries are harvested; the microbiology of this fermentation method is difficult to control. Although there are many possible inoculum sources in a spontaneous fermentation including soil, leaf litter, fermentation water and workers hands, there is evidence that fruit surfaces transmit the majority of the coffee seed fermentation microbiome (Figure 3) (da Silva Vale et al., 2021). The same publication describes a core coffee seed fermentation microbiome which includes the dominant microbes *Gluconobacter*, *Leuconostoc*, *Acetobacter* (bacteria) and *Candida*, *Pichia*, *Fusarium*, and *Hanseniaspora* (fungi). Surveying more than 100 studies over the past decades, spontaneous coffee fermentation has been reported to involve a large diversity of microbes including 343 different genera, among these 119 fungi (mostly *Aspergillus*, *Penicillium*, *Fusarium*, *Cladosporium*, *Mucor*, and *Rhizopus*) and 224 bacteria (mostly *Bacillus*, *Leuconostoc*, *Lactobacillus*, *Enterobacter*, *Pseudomonas*, *Klebsiella*, *Pantoea*, *Erwinia*, *Serratia*, *Lactococcus* and *Acinetobacter*) (Vaughan et al., 2015; Duong et al., 2020). A typical wet fermentation sees a pH drop from about 5.6 to about 4.6, while glucose is consumed and lactic acid plus ethanol are produced; these fermentation characteristics vary from farm to farm (Jackels and Jackels, 2005). There is evidence from fermentation microbiome deletion experiments (yeasts were eliminated with the antibiotic Natamycin) that yeasts, which are commonly isolated from coffee bean fermentations around the world, are efficient degraders of seed mucilage, produce significant amounts of flavoring compounds (glycerol, isoamyl alcohol, ethanol, acetaldehyde and ethyl acetate), suppress the growth of mycotoxin producing filamentous fungi and significantly improve coffee sensory scores (Elhalis et al., 2020). Lactic acid bacteria are the most abundant prokaryote in coffee fermentations where they produce lactic and acetic acid (providing acidity to coffee), 2,3-butanedione and acetoin (buttery flavor) and ethyl propionate, ethyl acetate, acetaldehyde, phenyl ethanol, and phenylacetaldehyde (fruity and floral notes) (de Melo Pereira et al., 2020). Inoculating seed fermentations with lactic acid bacteria and yeasts can increase the cupping score of the resulting coffee (Cassimiro et al., 2022). Many other bacteria and filamentous fungi can be found at low levels in coffee fermentations, but it is usually unclear what contributions they might make to coffee flavor (Elhalis et al., 2023). Despite not knowing which particular species are involved, variation in the microbiomes of spontaneously fermented coffee beans can lead to differences in coffee flavor: two farms growing *Coffea arabica* L. var. Acaia in Minas Gerais, Brazil, both conducted wet fermentation of their beans resulting in distinct fermentation microbiomes and contrasting finished products; one cup with citrus and herbaceous sensory characteristics, while the other also contained nutty flavors (Evangelista et al., 2015). Wet versus dry seed processing results in different fermentation microbiomes (Enterobacteria, lactic acid bacteria and *Pichia* yeasts versus acetic acid bacteria and non-*Pichia* yeasts) and different metabolic/flavor profiles (Bruyn et al., 2017).

Fermenting green beans a second time is another way that microbes can modify the biochemistry of coffee. In one example, dry, green coffee beans were inoculated with 3 different commercial

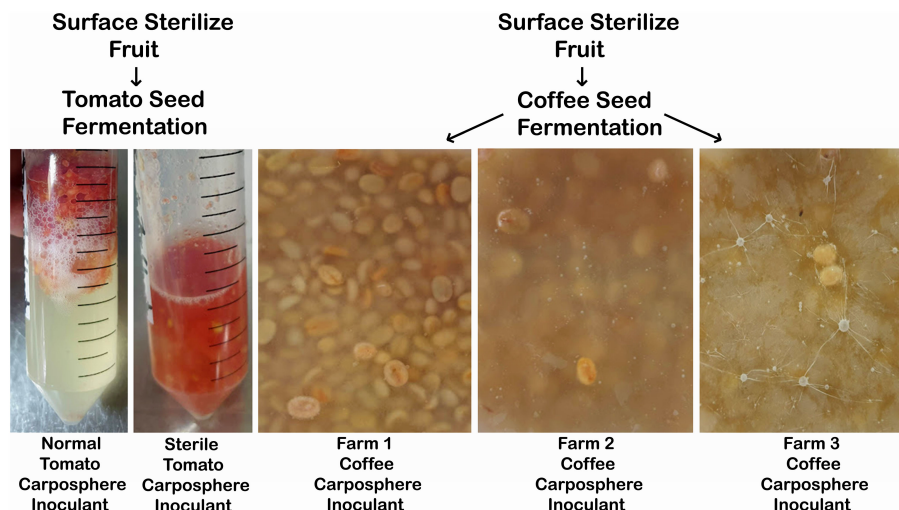


FIGURE 3

Altering the surface microbiome of a fruit influences the nature of its seed fermentation. Tomatoes and coffee cherries were surface sterilized with two 5 minute washes in 70% ethanol, dissected with sterilized utensils and the seeds extracted. Tomato seeds were then incubated for 72 hours after inoculation with either a normal or sterilized fruit surface microbiome (collected by washing the fruit surface with sterile water). Coffee seeds from surface sterilized fruit were inoculated with surface washes of coffee cherries taken from three different farms and incubated for 72 hours at 25°C (Johnston-Monje, unpublished).

strains of *Saccharomyces* and wet fermented for 24 hours before again drying, roasting and conducting chemical and consumer acceptability analysis. The result was a significant increase in antioxidants, polyphenols and flavonoids, but a slightly lower level of consumer acceptance (Kwak et al., 2018). *Rhizopus oligosporus* is widely used as a starter culture in fermented foods such as soy tempeh and when incubated on dry green coffee beans, it significantly improved the aroma precursors that give rise to coffee fragrance during roasting (pyrazines, thiols, furanones, and guaiacols) (Lee et al., 2016). The company Afineur uses a 5 strain synthetic microbiome to ferment green coffee beans sourced from Guatemala, reducing their acidity and bitterness by consuming catechol, caffeine, hydroxyhydroquinone, acrylamide, trigonelline and pyrogallol, while increasing theophylline, theobromine, vitamin B, inositol and antioxidant content (Martin, 2015; Morison, 2020; Afineur, 2023).

6 Anthosphere microbiome contribution to terroir

Flowers are plants' sexual organs and many evolved to attract pollinators; however, humans have also learnt to appreciate them for their beautiful patterns and colors, their fragrance, medicinal value and in some cases, their taste. Roses for example are appreciated for all four – their beauty, their aroma, as soothing teas and as flavors in desserts. Other agriculturally important flowers include chamomile, cannabis, marigold, lavender, jasmine and poppy. Saffron is a colorful spice made from the stigma of *Crocus sativus*, and has been shown to have both a microbiome (Bhagat et al., 2021) and metabolome that varies by climatic region, agricultural practices and post-harvest processing (Gikas et al., 2021). It has been asserted that “variability in microbial presence,

abundance, and composition is a defining feature of the floral microbiome” (Vannette, 2020) suggesting the potential for a variety of different microbiome/metabolome interactions in the anthosphere.

Microbes are present at low levels from the very start of flower formation, but as they bloom and mature, a greater abundance and diversity accumulate (Vannette, 2020). Plant genotype is thought to play a dominant role in shaping both the floral metabolome and microbiome (Wei et al., 2022a), however soil type (Massoni et al., 2021), farm practice (Schaeffer et al., 2023), environmental factors (Johnson et al., 2000; Bartlewicz et al., 2016; Sharaby et al., 2020), and especially visits from pollinators (Ushio et al., 2015), have also been shown to add to or change microbial communities in the flower. Surveying bacterial communities in floral nectar of tobacco trees (*Nicotiana glauca*) growing all over the world, it was found that increasing temperatures and elevation reduced the diversity and evenness, while geographic separation significantly increased dissimilarity (Sharaby et al., 2020). For over a 100 years it has been known that bees transmit fermentative microbes to flowers, and that floral microbiomes remain free of ascomycete yeasts when pollinators are prevented from visiting, (Vannette, 2020). Microbes on stigmas and in nectar compete for limited resources, meaning that early arrivals claim founder effects, locking up resources quickly and modifying the floral environment to be inhospitable to others; both niches have been found to be species poor and usually dominated by a single type of yeast or bacteria (Vannette, 2020). Petals are richer and more heterogenous in distribution of microbial epiphytes, possessing more of the species typical of a phyllosphere (Hayes et al., 2021).

A flower's main purpose is to attract pollinators, but they also need to defend themselves from pathogens. In order to both attract and repel, flowers may modulate their chemistry to influence either type of biotic interaction. Some of the volatile organic chemicals

produced by flowers are in fact antimicrobial: *Arabidopsis thaliana* produces sesquiterpene (E)- β -caryophyllene to inhibit the growth of pathogenic *Pseudomonas syringae* which can damage its stigma (Huang et al., 2012). This volatile and others surge in apple blossoms after infection with fire blight (*Erwinia carotovora*), repulsing honeybees (Cellini et al., 2019). Microbe free *Brassica rapa* flowers emit significantly different fragrance profiles after inoculation with floral bacteria, suggesting that the microbes were inducing different secondary metabolite production in the plant, as well as contributing their own (Helletsgruber et al., 2017). Flowers infected with saffron latent virus produce stigmas containing a significantly different metabolome than uninfected plants (Parizad et al., 2019). Female cannabis flowers produce medicinally important phytocannabinoids in their glandular trichomes, where they are thought to help defend against pathogens and herbivory (Taghinasab and Jabaji, 2020; Tanney et al., 2021) – it is as yet unknown whether interaction with anthosphere microbes can impact cannabis flower metabolomes.

While flowers produce fragrance and food rewards to attract pollinators, microbes can alter their quality and quantity by metabolizing plant compounds and secreting some of their own (Vannette, 2020). Nectar is the best studied aspect of flower microbiology, where yeasts and bacteria metabolize sugars, reducing their concentration by up to 60% (Herrera et al., 2008), sometimes producing significant amounts of ethanol (up to 4% of nectar) (Wiens et al., 2008), amino acids, secondary metabolites and other chemical constituents (Lenaerts et al., 2017; Vannette and Fukami, 2018).

Floral microbiomes can influence fragrance by both contributing volatiles or removing compounds being emitted by the flower (Vannette, 2020). In one example, removing the elderberry flower microbiome using 3 broad spectrum antibiotics resulted in a 66% reduction in terpene emission and the loss of β -ocimene, linalool, epoxylinolool and linalool oxide from the blend (Penuelas et al., 2014). Altered floral metabolomes can smell and taste differently to pollinators, who may change their foraging behavior as a result. Ascomycete yeasts in flowers can produce 2-phenylethanol, while many floral bacteria produce acetoin; volatile compounds which can be attractive to pollinators (Vannette, 2020). Presumably following their nose, bumble-bees prefer flower nectar colonized by nectar yeast *Metschnikowia reukaufi* even though it dramatically reduces sugar concentration (Vannette, 2020).

7 Phyllosphere microbiome contribution to terroir

Leaves are consumed in a variety of different ways including salads (eg. lettuce and spinach), as spices (eg. basil, oregano), for pharmaceuticals (eg. coca, aloe), to make teas (eg. tea, mint) and even to smoke (eg. tobacco). As the primary photosynthesizing organ of a plant, leaves are packed with metabolites involved in light harvesting (ie. carotenoids, antioxidants) and self-defense (eg. alkaloids, waxes). Leaves also absorb carbon dioxide while emitting oxygen, methanol and a variety of volatile compounds (Ameje et al., 2018). The leaf and its encompassing area is called the

phyllosphere, which represents the largest biological surface on Earth, containing innumerable microbes whose impact on plant physiology is often unknown (Morris and Kinkel, 2002). Phyllosphere residents are mostly Alphaproteobacteria, Gammaproteobacteria, Bacteroidetes, Actinobacteria and hyperdiverse fungi (Vorholt, 2012). These microbes can come from the seed or the soil, travelling through the vasculature until reaching the leaf. It is also possible that they reach the leaf surface through the air, contact with other plants, water drops or visitation by insects and other organisms. The leaf surface is a relatively inhospitable environment with limited access to water, carbon and nitrogen, and constant exposure to fluctuating temperature, humidity and solar radiation. Phyllosphere microbes could theoretically affect the leaf metabolome by altering plant metabolism, by consuming plant produced biochemicals or by contributing their own metabolites (Bringel and Couée, 2015). Bacteria on a leaf surface can usually be found in the seams between epidermal cells or clustered around trichomes, where they form aggregates of a few thousand cells (Vorholt, 2012). Microbes can also be found colonizing the leaf endophytically and intracellularly, where they can interact with the plant in other ways.

Phyllosphere microbiomes are significantly shaped by plant genotype, so that different species have distinct microbial populations on their leaves (Bringel and Couée, 2015); this makes sense, since that it has been established that the dominant members of the juvenile shoot microbiome are in fact vertically transmitted and not dependent on a commonly available environmental inoculum (Johnston-Monje et al., 2021b). In fact, certain plant phyllosphere mycobiomes can be overwhelmingly made up of species specific seed transmitted microbes, for example *Sarocladium zeae* which can make up 99% of the maize shoot mycobiome, or *Penicillium* endophytes which can make up 99% of the rice shoot mycobiome (Johnston-Monje et al., 2022). It has been observed in some plants that a significant amount of the phyllosphere microbiome is shared with roots, as various endophytic participants in the rhizophagy cycle can also be found in trichomes and on leaf surfaces (White et al., 2019). Soil could also be an inoculum source for the phyllosphere: about half of all *Arabidopsis* phyllosphere bacteria have been experimentally estimated to derive from soil (Massoni et al., 2021); soil was concluded to be a key source of grape phyllosphere bacteria (Zarraonaindia et al., 2015); oak seedlings grown on 3 different soils developed distinct populations of phyllosphere bacteria and fungi (Wolfgang et al., 2023). Bacteria and yeasts can be absorbed into roots (Paungfoo-Lonhienne et al., 2010) and a subset of these root microbes are translocated through vascular tissues, xylem and phloem, from roots to shoot meristems (White et al., 2014; Liu et al., 2020; Benito et al., 2022; Micci et al., 2022). Filamentous fungi, such as *Fusarium* spp., can also enter roots, growing systemically throughout the plant, eventually colonizing shoots and leaves (Lofgren et al., 2018; Rodriguez et al., 2009). Plants do not passively sponge up fungi and deliver them directly to the leaf, apparently filtering them and only allowing certain species through; *Bromus tectorum* or maize grown on microbially distinct soils nevertheless develop analogous phyllosphere mycobiomes

(Nebert, 2018; Ricks and Koide, 2019). Bacteria that travel through vasculature and arrive at nutrient rich shoot meristems can often be observed forming biofilms on the surfaces of developing leaves and intracellularly colonizing dividing meristematic cells (White et al., 2014). As bacterially colonized plant cells mature and differentiate into epidermis or trichomes, they begin to produce superoxides while intracellular endophytes secrete ethylene and reduced forms of nitrogen (ie. ammonia, nitric oxide) which serve as antioxidants (Chang et al., 2021). This nutrient exchange process in plant cells has been termed the 'nutrient trap mechanism' because once begun, bacteria cannot cease nitrogen secretion without being damaged by superoxides (Chang et al., 2021). A range of plants from sphagnum moss to tomatoes have been observed to have trichomes, nodules or epidermal cells manifesting this endophytic nutrient trap (Kox et al., 2020; Micci et al., 2022). Of the structures involved in this association, glandular trichomes are especially relevant to mention – they have long been known to contain a diversity of terpenoids, phenolics, antioxidants and other secondary metabolites thought to be involved in defense (Feng et al., 2021). Trichomes have now also been shown to be sites of significant nitrogen fixation by intracellular bacteria (Micci et al., 2022). Bacteria are seen to emerge from the lateral pits or ruptures in trichome walls, accumulating at the bases of the trichome and spreading out onto the leaf surface, thus contributing to the phylloplane microbial community and explaining how soil or seed derived endophytes might make it all the way there (Micci et al., 2022).

Although many phyllosphere microbes come from the seed or soil, leaf surfaces also become colonized by bacteria and fungi that vector through the air, splash from other plant surfaces and are brought in by insects or other organisms (Gong and Xin, 2021). Established leaf microbiomes can be altered by their proximity to other plants, temperature, precipitation, exposure to sand storms and foliar pesticide application (Bringel and Couée, 2015; Cernava et al., 2019). Some of these environmentally transmitted, leaf surface colonizers are the shadow yeasts (*Sporobolomyces* spp.) that arrive as airborne spores to colonize the endosphere and phyllosphere of many plants (Ling et al., 2020). Many other fungi such as *Alternaria* spp. and *Cladosporium* spp., are also known to colonize leaf surfaces (Bao et al., 2022). These fungi are typically epiphytic, but can sometimes enter plants as endophytes and later transition into saprophytes as leaves begin to senesce (Rodriguez et al., 2009).

However they arrive, phyllosphere microbes can impact the leaf metabolome by influencing plant metabolism, by consuming plant produced biochemicals or by contributing their own metabolites. Using quantitative nuclear magnetic resonance and imaging high-resolution mass spectrometry to visualize *Arabidopsis* leaf surface metabolites, colonization with organoheterotroph *Sphingomonas melonis* or the phytopathogen *Pseudomonas syringae* pv. *tomato* dramatically altered carbohydrate production, arginine metabolism and phytoalexin biosynthesis (Ryffel et al., 2016). In grasses, Ascomycete fungal endophytes of the genus *Epichloë* grow on and within shoots where they increase plant production of phenolics and other antioxidants (White and Torres, 2010; Xia et al., 2018) while secreting their own alkaloids (peramines, lolines, lolitrems and ergolines); reducing palatability and impacting the feeding behavior of herbivores (Bharadwaj et al., 2020). Leaf endophytes

of the genus *Paenibacillus* isolated from leaves of *Leucojum aestivum* produce a range of alkaloids (e.g., galanthamine, lycorine, ismine, lycoramine, haemanthamine, tazettine, galanthine, homolycorine, and hippeastrine) that were characteristic of the plant (Ptak et al., 2022); reinoculating these bacteria back into axenic plants increased their alkaloid, chlorophyll and carotenoid content. Foliar spraying of tea (*Camellia sinensis*) with *Bacillus amyloliquefaciens* reduced polyphenol, catechin, and caffeine levels, while increasing amino acids and theanine in harvested leaves (Huang et al., 2022). Removing the *Sambucus nigra* phyllosphere microbiome using antibiotics reduced the phyllosphere concentration of lactate, citraconic acid, acetyl-CoA, isoleucine, and several secondary metabolites including terpenes and phenols (Gargallo-Garriga et al., 2016). A similar experiment with *Brassica nigra* found that using antibiotics to remove bacteria did not change the emission of volatile compounds from the leaf; however, applying fungicides to remove fungi triggered emission of four new compounds (cyclohexanone, cyclohexyl cyanide and 2 unknown) suggesting the microbes had previously been consuming the molecules (Saunier et al., 2020). In experiments using Korean perilla (*Perilla frutescens*), the reduction of phyllosphere microbes by rigorous seed surface sterilization resulted in plants producing markedly less mint oils and totally lacking aroma, compared to control seedlings bearing the full microbiome (Linsey Park and James White, unpublished). Glandular trichomes are found on leaves of many dicots, e.g., hemp (*Cannabis sativa*), tomato (*Solanum lycopersicum*) and mints (family Lamiaceae), and they contain terpenoids, phenolics and oils (Schilmiller et al., 2008). We believe that because at least some of these compounds are important in fostering nitrogen fixation by endophytic microbes, that their production by the plant is tightly correlated with the presence, diversity and activity of the phyllosphere microbiome.

8 Conclusions

Plants are holobionts that host a great diversity of microbes within their tissues and on their surfaces. These microbes can influence the plant to change its metabolism, they can intercept, consume and alter plant metabolites and they can secrete metabolites of their own into the phytosphere. If these microbial populations vary (ie. by location, by environment, by agronomic practice) so too their impact on the plant metabolome can vary. In the rhizosphere, microbial populations can help the root acquire and absorb nutrients, they can secrete compounds which induce the plant to alter its metabolism, or they can modify the soil to mitigate biotic or abiotic root stress, maintaining an unstressed metabolic state in the plant. Inside the plant, endophytes can produce agronomically desirable molecules, they can induce the plant to increase its production of desirable metabolites, and they can alter source-sink relationships to make the plant increase nutrient absorption or redistribute molecule storage. In the phyllosphere, microbes can modify volatile emissions and produce their own metabolites, while inside trichomes they participate in a nutrient trap where they produce reduced forms of nitrogen and the plant produces superoxides, terpenes, phenolics and lipids. Microbes in flowers can alter floral scent by emitting volatile compounds themselves or

inducing the plant to change what it is releasing. Anthosphere microbes can also influence nectar chemistry, often by consuming sugars therein. In fruits, the most metabolically important microbes are found on the surface where they either emit volatile compounds themselves or they induce plant metabolism to create them. Microbes on the fruit surface also seem to be the most important members of the spontaneous fermentation microbiome which is important for making wine and fermenting coffee/cacao seeds to remove the mucilage, while providing chemical precursors which increase quality of the product. The impact of microbes on the flavors, aromas, nutritional or medicinal value of agricultural products is often studied under controlled conditions, for example by killing particular strains with antibiotics or by inoculating new microbes onto the plant and watching for changes in the plant metabolome. In reality, most agricultural production occurs under the unpredictable conditions of a farm where proof of microbial influence on the plant metabolome usually can't get any better than observing a correlation. In a lab or in a controlled factory environment where plant microbiomes can be washed away and replaced (ie. washing grapes and inoculating them with alcoholic yeasts), terroir engineering may become increasingly possible, but out in the field with unpredictable environmental variation and biotic interactions, achieving an optimal microbial terroir may continue to depend on a blend of the environmental stability, producer's savoir faire and good luck.

Author contributions

DJ-M conceived of, designed and wrote most of the paper, made **Figures 1 and 3**, and also conducted the seed fermentations pictured in **Figure 3**. LV reviewed literature and wrote part of the sections on seed and fruit microbiomes. JLM reviewed literature and drew **Figure 2**. JW reviewed literature and wrote the section on

phyllospheres. All authors contributed to the article and approved the submitted version.

Funding

The writing of this review was funded by The University of the Valley. Publication fees provided by the Max Planck Society.

Acknowledgments

We are grateful for open access funding provided by the Max Planck Society. Thank you to the reviewers for their thoughtful comments which helped make this a much better paper.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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