An Introduction to Flavor and its Evaluation for Crop Scientists – A Review to Inform Discourse and New Methods

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Abstract: Flavor and eating qualities of vegetables, fruits, grains, and value-added products are becoming increasingly important for consumers. This is especially true in local food and organic sectors where good flavor is expected and prioritized. With sensory qualities becoming more relevant factors in purchasing and eating decisions, growers, plant breeders, and crop researchers need ways to evaluate flavor and eater preference for crops and crop varieties. Traditional sensory science relies on the descriptions and evaluations of trained panels made up of purported expert tasters. But these methods are not accessible nor necessarily appropriate for the purposes and goals of crop research and breeding. Still, formal sensory science approaches remain the theoretical epitome of flavor research despite their shortcomings. Critical assumptions like food homogeneity may not hold in agricultural contexts, which gives reason for more methodological discourse on evaluating flavor in crops and cultivars. This review focuses on the biological and psychological factors surrounding flavor development in plants and the perceptions and preferences of human eaters as a foundation for crop researchers engaging in these conversations.

Introduction

In 1825, one of the world's original gastronomes Jean Anthelme Brillat-Savarin said, "smell and taste are in fact but a single composite sense, whose laboratory is the mouth and its chimney the nose."[1] Somewhat remarkably, modern scientists still use similar descriptions. Sensory scientists employ a psychophysical understanding of flavor defining it as the "biological response to chemical [stimuli] by the senses [that is] interpreted by the brain in the context of human experience."[2] In truth, while chemical understanding of flavor has expanded tremendously since Brillat-Savarin, a complete and integrated comprehension of flavor development, perception, and preference still remains elusive[3-5].

Despite incomplete understanding of the complexities underlying flavor, there is still much interest in measuring the trait as part of the plant breeding and trialing process, but agreement on appropriate methods in crop sciences is lacking. Traditionally, sensory science uses a highly trained, expert panel of judges to assess and describe flavor qualities. In some cases, crop research programs have replaced these tasting experts with breeder experts instead (P. Simon, personal communication). Others have begun to apply rapid sensory evaluation methods, which rely on untrained or semi-trained tasters (ex: a field harvest crew) and/or professional end-users like local chefs, bakers, and brewers[6-8]. Appropriate and reliable methods for sensory evaluation that are applicable to plant breeding and agricultural research are still being debated and evaluated, and new approaches will likely emerge. Using humans to evaluate crop or cultivar flavor is inherently difficult due to the complexities of the biology and psychology underlying flavor development, perception, and preference. This review focuses on these particulars with hopes of providing baseline knowledge for plant scientists engaged in these conversations.

Talking About Flavor

In everyday English, the terms taste and flavor are used interchangeably, but human physiologists would say the two are not the same. Taste, referred to by itself, implies the five basic tastes – sweet, sour, salty, bitter, and umami (the meaty or delicious sensation associated with mushrooms, soy sauce, and parmesan cheese) – which are perceived by specific receptor cells located in taste buds on the tongue[5]. When it comes to flavor, however, taste is only one part. Aroma is another critical component; in fact, volatile odor molecules are what give fruits and vegetables most of their distinctive flavors[9]. Others consider mouthfeel or a food's texture vital to overall flavor[10], and there is certainly some truth to eating with the eyes first, so appearance matters too[11,3,12]. While taste is one crucial element, the term flavor encompasses much more of the eating experience by considering taste, appearance, smell, and texture. If plant breeders and researchers are going to evaluate flavor using humans, common terms and clear definitions are necessary. The previously mentioned definition[2] provides a good starting point, but additional details on human taste physiology might be informative.

Whether evaluating a raw vegetable or formulated recipe, it helps to conceptualize food as a type of matrix. Consider a tomato (*Solanum lycopersicum*) fruit for example. Generally speaking, it is made of cells that contain sugars, acids, salts, aromas and other molecules that contribute to flavor, i.e. the chemical stimuli referred to in definitions. Understanding food as a matrix is useful when considering different crops or plant organs and how they might develop or release flavor molecules differently (ex: tomato versus broccoli). In vegetables, most volatiles are synthesized after cells are damaged from cutting or chewing, which exposes enzymes to their substrates[13,3].

When a slice of tomato is chewed, its cells are crushed, spilling the contents into the mouth. Taste receptor cells are clustered in taste buds along the tongue's epithelium, and their membrane receptors bind the molecules involved in sweetness, sourness, umami, saltiness, and bitterness as they are released from the tomato tissue[5]. Saliva and the fruit's liquid create an aqueous solution that coats the tongue and taste receptors with their chemical stimuli[14]. As the tomato tissue breaks down further, warm air circulating in the mouth and nose wafts the freed tomato aroma molecules (volatiles) so they bind to the receptors of olfactory cells lining the back of the throat and nasal cavity[15,9]. The tongue and mouth are also equipped with other types of nerve cells involved in flavor perception. The trigeminal nerve for example is responsible for sensing the cooling sensation of menthol in mint (*Mentha* spp.), the drying astringency of tannins in wine and tea, and the spicy burn from capsaicin in hot peppers (*Capsicum* sp.)[16,3,5]. Some sensory nerves are involved in tactile perception and assess a food's texture[17]. Importantly, there is substantial variation in the taste and flavor-sensing machinery among humans, which must be considered when using humans as flavor evaluators[16-18].

Multiple ligands (chemical stimuli) can bind to the same receptor. For example, the membrane proteins on sweet-sensing taste cells can bind sucrose, fructose, glucose, sucralose, and a host of different sugars with varying affinities[5]. Odor molecules are the same. The volatile safrole for instance was previously used to flavor root beer, toothpaste, and chewing gum because of its “candy shop” aroma[19,20]. Safrole binds to multiple types of olfactory receptors simultaneously[19] explaining its complex and enticing smell. Unfortunately, safrole was later found to be carcinogenic, and therefore banned by the FDA as a product additive[20].

Taste and smell have evolutionary explanations. They give humans (and other animals) the ability to find nutrients and evaluate what they consume. For the most part, the taste and odor receptors involved in flavor detection are G-protein coupled receptors (GPCRs), which when bound to an appropriate ligand, result in signal transduction and development of an action potential[15,21,22]. This electrical signal travels to the brain for processing. Sensory nerves mostly lead to the brain’s thalamus, which communicates with the frontal lobe – the brain’s control panel – and, ultimately, this is where the psychological experience of flavor is created[15,21,23]. Additionally, smell signals activate parts of the brain that control memory and emotions before they are integrated with other sensory information like taste, appearance, and texture. The brain (or perhaps mind) is responsible for “touching up the final percept” and integrating all the signals, so flavor is experienced as a unified sensation and not as individual, disparate parts[24]. While this makes for an enjoyable experience as an eater, for researchers, the role of the brain/mind interaction complicates matters.

Altogether, the brain/mind takes information from the senses about food we consume and puts it into context with the body’s nutritional needs, cultural identity, the surrounding environment, and past experiences and memories to come up with each individual’s experience of flavor. To be clear, flavor perception and preference are not solely determined by any inherent quality about the food or eater themselves, but rather the amalgamation of sensory, biological, socio-cultural, historical, and environmental information. Since much of this information is unique to each individual, the same fruit or vegetable sample can evoke different impressions and responses. Understandably, this poses challenges for scientists using humans to investigate flavor qualities in fruits, vegetables, and grains.

Evolutionary History of Flavor

While sometimes framed as part of the modern “Good Food Movement”[25], human interest and selection for flavor traits has been relevant since domestication. As humans noticed and replanted desirable plant phenotypes, they inevitably had an impact on flavor and its underlying genes. A typical feature of plant domestication syndrome is a reduction in secondary metabolites, particularly those perceived as toxic or bitter. Some propose there was little intentional selection for the reduction of these bitter or harsh compounds and emphasize that humans were quite adept at finding ways to reduce unpalatable characteristics via cooking or processing[26]. In fact, cooking, processing, and preserving can completely alter the building blocks of flavor, so it should not be assumed that early humans deliberately rogued bad-tasting individuals.

Domestication's main features have shown to have relationships with flavor-related traits, so intentional selection for other traits may have had indirect consequences. For example, the loss of natural dispersal mechanisms such as non-shattering seed and non-deciduous fruit has been linked to changes in fruit texture in both tomato and pepper[27]. Recessive alleles of a single gene promote ripe fruit remaining on the plant and increased pericarp firmness, a legacy that persists today in American preferences for firm tomatoes and crisp sweet peppers[12,28]. Additionally, during domestication humans selected against plant mechanical protections like the prickles displayed by wild Solanaceae relatives[29], which surely improved their mouthfeel.

Selection for larger plant tissues whether roots, tubers, fruit, leaves, or stems also had an effect on flavor because chemical flavor components become increasingly diluted as size increases. For example, declining tomato flavor can be traced back to the earliest stages of human intervention and selection for larger fruit[18]. Additionally, genes linked to alleles conferring larger fruit size significantly altered fruit metabolite profiles, including the regulation of many volatile compounds[30,31]. Selection driven by culturally important traits has shown to also have flavor side effects. Zhu et al.[30] found that pink tomatoes (popular in Asia), which resulted from a single gene change, had over 100 significantly modified fruit metabolites, some of which are known flavor contributors. Furthermore, selection for traits unassociated with the plant organ of interest, like more even and rapid seed germination, could also have impacted flavor during the domestication process[26]. For example, many bitter-tasting and toxic compounds inhibit seed germination[32], so as humans selected for earlier sprouting seeds, they may have effectively and unconsciously selected against more acrid flavor phenotypes.

The history of crop flavor and humans is long, and it is important to recognize flavor has a functional and evolutionary role for plants, too. Seed distribution is imperative to survival. Brightly colored and tasty fruits, or at least those more palatable, might have enticed more seed dispersing animals than poor or off-tasting counterparts. Evolution of volatiles and olfactory receptors in animals would have allowed long range signaling of ripe fruit to seed dispersers[9]. Plant breeders should consider that evolutionary and natural selective forces have worked alongside humans and random chance to shape a vast genetic potential for flavor within crop species and their wild relatives[13]. But while flavor diversity in plants developed over millennia, it seems humans have done an incredible job of reducing that diversity in the last century, albeit in some crops more than others[9]. The growing consumer focus on eating qualities and subsequent breeding for better flavor is largely a response to this decline in perceived flavor quality[18].

Tomato acts as a posterchild for efforts to improve flavor in fruits and vegetables because consumers are acutely aware of their poor flavor due to both genetics and the methods associated with industrial production (i.e. harvesting when green, cool storage, ethylene ripening)[33,34,18]. Tomato was domesticated approximately 80,000 years ago, and there begins its flavor story[33,34]. During domestication and subsequent improvement phases, tomato underwent several major bottleneck events[13]. While the plant is native to coastal deserts of South America, domestication is believed to have occurred in modern-day Mexico after birds deposited seeds during seasonal migrations[33,34]. As part of the Columbian Exchange, tomato seeds were brought to Europe in the 15th Century[35]. During this time tomato fruits were mostly gold-colored and reportedly "small and sour," but they gradually gained eating popularity in Spain, Italy, and France as a way to flavor food without expensive spices[34,35]. Nonetheless, settlers brought their own cultivars when they colonized the modern-day United States. Altogether considered, much genetic diversity has been lost from tomatoes as people (and birds) moved them around the world.

In the mid-1800s United States, Alexander Livingston was a farmer, scientist, and seedsman with an affinity for tomatoes[34]. He began crossing varieties brought from Europe to wild tomatoes in the Americas and eventually developed some of the most popular varieties in the country that were notably larger and sweeter[36,33]. Livingston is credited with popularizing the persisting cultural ideals of what tomatoes should look and taste like in the United States (round, red and sweet) while also promoting their culinary use among the country's chefs[36,34]. While tomato has undergone a massive narrowing of genetic diversity, Livingston began the process of reincorporating some of this diversity by making new crosses. In Livingston's lifetime, farmers produced most seed on their farms and selected varieties that both produced well and fit the eating quality expectations of their local customers[33]. Many of today's heirloom varieties serve as a reminder of a pre-industrial time when good flavor was considered necessary for a variety's success. But the rise of the global food system has indeed greatly changed breeding priorities.

Instead of looking for varieties that are locally well-adapted and tasty to local eaters, both breeders and growers have been forced to prioritize traits for the industrial food system. In tomatoes, marketable yield, disease resistance, shelf life, and shipping ability have all been breeding goals[33,34]. Perhaps unexpectedly, Gao et al.[31] used a pan-genome to find that the genetic diversity in modern tomato varieties is larger than in heirlooms, so the regaining of genetic material started by Alexander Livingston in the 1800s has continued. A key difference, however, is that little genetic material related to flavor has been recovered. Introgression of genes for abiotic stress tolerance and disease resistance were hallmarks of tomato breeding throughout the 20th Century[34,31], which greatly benefited grower yields. But improving sensory qualities has largely been ignored until more recently[9,18,31].

The story of tomato is not necessarily unique, and all crops have their own histories and challenges. Tomato flavor, or lack thereof, has become a top complaint of consumers[33,18]. But brassica breeding has resulted in stronger-tasting cauliflower (*Brassica oleracea*) cultivars that are linked to decreased consumption[37]. For most domesticated food crops, the tradeoff is a narrowing of genetic diversity, but priorities in the industrial food system have exacerbated the loss in flavor because of over-focus on a few traits[33,9]. Of course, better genetic understanding of flavor in crops means little if it is not integrated with insights about human flavor perception and preference, which is why more work is needed on approaches to flavor evaluation within agricultural contexts.

The Short History of Formal Sensory Science

While flavor's evolutionary relationship between plants and people has gone on for millennia, formal sensory science is not yet a century old. Prior to the 1930s, the methods and technology to evaluate food and sensory qualities had not been standardized[38]. The first sensory science experiments looked at acceptance of military rations by enlisted troops with a goal to reduce the number of soldiers who skipped meals[39,40]. By 1937, the American Chemical Society presented its first panel on "Flavor in Foods," and the field was poised for rapid expansion[40,38].

Just like in agriculture and plant breeding, the early 20th Century was a time of rapid industrialization, segmentation, and specialization for the food industry. As economies of scale increased, sensory science emerged from business interests aimed at gaining larger market shares by consistently appealing to as many consumers as possible[4,38]. An executive of a baking company, W. Platt in 1931 said, "all our millions ... depends on that little sensation which our products make upon the tongues of our customers"[39]. According to Elaine Skinner in Lawless and Heymann[41], sensory science is the "child of industry," and its insight is to safeguard the "meeting of consumer expectations and a greater sense of marketplace success," not to inform anything fundamentally true about food. In other words, the needs of the global food industry have driven both research and methods in sensory science. They have added much to the understanding of food properties but little applicable value for flavor evaluation in plant sciences and non-industrial contexts. Despite problems with sensory science's origins, assumptions, and methodologies, their descriptive methods are still largely used as benchmarks of scientific validity and rigor for flavor evaluation.

Sensory science is a unique field because it has never concerned itself with developing a body of theoretical knowledge[16,42,4], which typically plays a foundational role in a scientific discipline. Instead, sensory science has historically borrowed existing theories from physiology and psychology that interpret human behavior and experiences as responses to an objective reality[42]; it left little room for social and/or cultural influences.

Formal sensory scientists understand that biochemical parts of food act as stimuli to induce a psychological experience called flavor. But their paradigm has sought to bring the whole process under experimental control[4]. For example, tasters are isolated from one another or must evaluate samples under red light so they cannot be influenced by appearance or other opinions. Results are only considered meaningful if they are statistically significant and done in a controlled environment[39,43], which in effect means a flavor component only becomes tractable when it is somehow amenable to this type of experimentation. One has to wonder if this approach transfers well into real-life eating situations with much more complex stimulation. Formal sensory science assumes flavor and human perception can be reduced to its constitutive parts[44,18], and these parts are separable from the eating context making them portable and predictable in others[4]. But in fact, it seems clear that flavor is an emergent phenomenon, where the whole is greater than the simple sum of its parts.

While formal sensory scientists typically hold that flavor is an intrinsic property of food and eaters are passive receivers of both these stimuli and the psychological experience of flavor[41], there are some social scientists who believe taste is a property inherent to eaters instead[45]. The reality is likely somewhere in between, as Lahne and Trubek[46] write, there appears to be an "active and reflexive" process between objective properties of food, the way they are processed in each individual's brain, and extrinsic factors too[47,48].

The socio-cultural factors that affect flavor perception and preference are considered biases by formally trained sensory scientists. In fact, central to formal sensory science is attempting to separate the objective truths about food from the inner experiences of tasters and other "biasing" stimuli[41]. Importantly then, the field makes two critical assumptions. First, their standard practices and methods are valid and robust for finding these objectively true sensory properties[4]. Second, they assume that physical and chemical properties are sensorially relevant by default even though their correlations with perception might not be as strong as expected[44,49,18,11].

To their credit, sensory science has recognized some of its own shortcomings and begun to reflect on their assumptions. More recently, the field's attention has turned toward examining its ecological validity and links to consumer experiences[48]. Much of this has been driven by a realized "mismatch [between] perceived requirements [for] rigorous sensory science research and empirical reality"[4]. As their popularity with consumers skyrockets, artisanal products like cheese and beer are examples where application of traditional sensory methods appears to fall short. This is because artisanal products are not homogenous (in fact, variability in this context is valorized), and they have extrinsic values that are perceptible to eaters too[46,48]. In Lahne and Trubek[46], eaters said an artisanal Vermont cheddar tasted good partly because it was produced in small batches with a particular care for the livestock, people, and land. These factors are clearly influential in human discernments about flavor and preference[47,48], but they are largely ignored by sensory scientists despite the embedded nature of producers, eaters, and food in society. These realizations have led some sensory scientists to compare formal sensory methodologies to an overfit statistical model[4]. In other words, sensory science is so reliant on the information and imperatives imposed by the industrial food system that their application is not feasible in alternative contexts.

These are relevant considerations for plant breeders and researchers looking to evaluate or improve flavor. Harker et al.[50] note the natural heterogeneity of fruits and vegetables will often overwhelm detection of significant differences in triangle tests with trained sensory experts. Admittedly, traditional methods may not be the best, but neither are they useless. They remain one tool in a toolbox. At the same time, there appears immense opportunity for plant scientists to apply and develop new tools, particularly those geared toward non-industrialized contexts. Dawson and Healy[8], for example, wrote a review for plant breeders on rapid sensory evaluation methods that eliminate or reduce training obligations, although rapid methods are often critiqued for not being rigorous enough. While research groups like the Seed to Kitchen Collaborative at the University of Wisconsin have started working with these tools to examine their utility and reliability, the tendency for plant scientists to try and mimic formal sensory analysis techniques still remains widespread.

Flavor Development in the Plant

A plant's genotype plays a fundamental role in the synthesis and accumulation of flavor-related compounds. Many studies have shown variety (genotype) has a significant effect on taste-related traits like amounts of sugar and titratable acidity, which are thought to be strongly correlated with perceived sweetness and acidity, respectively. In some species, specific genes involved in flavor metabolism have been identified, but at least in tomato, there is no obvious genetic clustering of good versus bad-tasting cultivars[49]. This underscores the complexity of untangling chemical stimuli and relating them to people's preferences. Table 1 shows some examples of genetic, environmental, and cultural effects on flavor traits but is by no means a complete list.

Sugar content, while a seemingly straightforward proxy of sweetness, is a quantitative trait itself[49]. It is impacted by other gene pathways and products like those controlling pigment synthesis and storage. Pigments underlie important visual characteristics that can influence people's preferences (discussed later). In Table 1, for example, the uniform ripening mutation (*u*) in tomato causes changes in the accumulation and distribution of fruit chloroplasts, which eliminates green shoulders but ultimately leads to lower sugar content than in non-mutants[64]. Some pigment molecules - like anthocyanins in grape (*Vitis vinifera*) and bitter melons (*Momordica charantia*) - have shown to be perceived as bitter[66]. In fact, some anthocyanins are among a group of molecules that have the ability to bind to multiple types of sensory receptors including taste (bitter), trigeminal receptors (astringency), and odor receptors[17,66,58].

For some, the prospect of increasing sugars or reducing bitter compounds in fruits and vegetables to improve their taste is enticing. Many breeders, however, recognize the fundamental metabolic tradeoffs between increasing sugar and decreasing yields, which is why so many are focusing on improving volatiles[49,9]. In attempts to predict consumer liking for fruits and vegetables, studies have found the most successful models utilize volatile measurements[3], but the resources needed to quantify volatile organic compounds are similarly cost prohibitive as employing formal sensory evaluation with trained tasters. Klee and Tieman[18] say it is possible to identify genes regulating the synthesis of flavor volatiles as well as alleles of those genes that promote a more flavorful composition. While some researchers advocate strongly for genetic approaches to improving flavor, the process of relating chemical stimuli to human preferences and perceptions is awash with complexity[49,9,18]. Still, these types of key flavor genes and desirable alleles have been identified in tomato and strawberry (*Fragaria x ananassa*) as ones lost during domestication[13,31].

Even if relevant flavor genes and alleles can be identified, the flavor phenotype is still highly influenced by the environment. For some flavor-associated traits like titratable acidity in tomato, studies have calculated relatively high heritability (87%), while estimates for other traits such as lycopene are much less (16%)[13,60,18]. The ways in which growing environment can affect flavor-related chemicals in plants seem endless in the literature. Perhaps obviously, large amounts of water can dilute flavor of fruits and vegetables, but temperature and light both have tremendous impacts on organoleptic qualities, too. Higher light intensities have shown to increase levels of sugar, ascorbic acid, and dry matter in certain crops, while colder growing temperatures have shown to affect the texture, taste and smell of others[52,58].

The environment's effect on flavor includes cultural techniques used by the grower and field-specific factors like soil composition and nutrients. Protected culture, fertilization regimens, and the color of plastic mulch are examples from Table 1 where growing decisions affect flavor. Even plant stress responses can act to influence flavor-related chemicals like in leafhopper tea, so named because the distinctive flavor imparted to leaves after being bitten by leafhoppers[57]. With the great diversity in farm practices and locations, this presents another layer to the study and evaluation of crop flavor.

While it may be possible to identify key genes and alleles involved in flavor development, there remains questions about the expression of those genes in various environments and under different growing conditions. Naturally, this is made more complicated by gene x environment (GxE) interactions which are also common in the literature. Hassan et al.[59], for example, found a significant GxE effect on allicin content in 104 garlic (*Allium sativum*) accessions grown in Egypt and China. Scientists clearly have their work cut out for them trying to regain lost flavor in crops, since not only are the underlying genetics complex, their expression is highly mutable to a seemingly limitless stream of environmental and horticultural factors.

Flavor Perception by Humans

While genetic, environmental, and horticultural factors can impact the production and accumulation of plant flavor compounds, human perception of these stimuli is not equal. In fact, Reed and Knaapila[17] say, "perhaps no single human trait has as much person-to-person differences as abilities to taste and smell," and human genetic differences are at least partially responsible for differences in perception of the same tasting sample[58]. Table 2 contains examples of known genetic and environmental factors that influence flavor perception and preferences in humans. Roper and Chaudhari[5] report the number and distribution of taste buds, receptor cells and variants of receptors are all under genetic control. Such observations have led comparative physiologist to describe each person as living in their own "individual taste world"[5]. For example, taste and odor thresholds – the minimum amount of a stimulus to result in a perceptible sensation – vary widely from person-to-person, and the combinatory nature of receptors and ligands can easily elicit a response at sub-threshold levels[5,17,18].

The term "super taster" is ubiquitous in the sensory science literature, and in fact, further stratification can be found that differentiates tasters, non-tasters, medium tasters, and super tasters[40,18]. Super tasters are so named because of their high sensitivity to two bitter compounds – 6-n-propylthiouracil (PROP) and phenylthiocarbamide (PTC) – neither of which are found naturally in food[17,58]. The sensitivity to these two chemicals lies in the *TAS2R38* gene, one of at least 25 in the *TAS2R* bitter receptor gene family[21]. The relationship between PROP, PTC and *TAS2R38* has been intensely studied, but these studies give relatively little insight into the impact of genetics on final bitter sensitivity, since the "nontaster" form of *TAS2R38* still might be able to taste other bitters[21].

For perception of other tastes, like sweetness, there is a better understanding of the role of genetics. For example, Table 2 lists the promoter-region of sweet receptor gene *Tas1r3*, which has good ability to predict a person's sensitivity to sweet stimuli[74]. There is evidence that sour perception also has a genetic component, but little research has sought to investigate specifics, and scientists have yet to untangle the physiological machinery of salt perception let alone any potential underlying genetics[5,17,74].

Both sweetness and bitterness perception can be modified by the presence of certain volatiles[9,58,76], but this requires appropriate odor receptors to be present in the nose and throat. In the human genome, the family of olfactory receptor (*OR*) genes is one of the largest and has shown to contribute to variation in abilities to smell certain odorants. There are nearly 400 functional human *OR* genes along with an equivalent number of pseudogenes, and about 60 others found with both functional and nonfunctional variants[15,18]. As described earlier with safrole, ORs work combinatorially and are broadly tuned to respond to a wide range of volatile ligands[18,70]. By themselves, single allele changes in an *OR* gene have relatively small effects[15].

Using 26 families in Finland, Knaapila et al.[22] came to interesting conclusions when they examined the heritability of olfactory-related traits. They estimated very low heritability for the ability to perceive lemon and chocolate aromas, but high heritability for pleasant responses to cinnamon smells[22]. Genetics do not explain the entirety of human flavor perception. Age, education, occupation, socio-economic level, health and smoking history are some of the many characteristics that can modify responses to sensory stimuli[11,47,68]. Education, for example, can dictate which and how many words a person uses to describe and understand a food's properties, while the language itself can have bearing too. In Japanese, there are more than 400 words used to describe food texture, while only about 100 in English[77]. Reed and Knaapila[17] say the average human can differentiate over 1 trillion smells, but surely there are not enough words in any language to distinguish each one separately!

Sensitivity to bitterness in cauliflower has been linked to consumption amount[58], and plant-based foods enhance the expression of bitter receptor genes[73]. In fact, sensory cells, especially olfactory receptor cells, are regularly replaced throughout life. The types and distribution of receptor cells can change in orders of several magnitude over time, which has recently been proposed as an adaptive mechanism to changing chemosensory environments[70]. In other words, human gene expression changes in response to chemical signals from the environment – including in food – to alter the types and distribution of sensory cells. This explains why systematic and repeated exposure to odorants can increase sensitivity[17,70,76].

If the cellular machinery involved in flavor perception changes regularly, then surely this has implications for its evaluation in crops. It also gives rise to more questions about formal sensory analysis training and calibration protocols. The training of panelists in sensory science is supposed to reduce the amount of variation attributable to differences in individual taste perception, but few studies have been published on the effect of training, and several have shown inconsistencies of professional tasters over time[4,10]. Even with the use of trained sensory experts, the effect of taster is still frequently statistically significant, and convention has been to place blame on the abilities of tasters rather than the methods[10,16,39]. This is all the more reason for researchers in the plant sciences to explore and describe new approaches to flavor evaluation in contexts other than industrial food production.

Human Flavor Preferences

Ultimately, improving flavor in crops is fundamentally related to human preferences, so understanding how preferences are formed will be helpful for plant scientists in these endeavors. Perhaps unexpectedly, there are genetic components to human smell and flavor preferences, some of which are related to receptor variation[74]. For example, variation in the OR6A2 gene has been correlated to dislike of cilantro (*Coriandrum sativum*) because of perceived soapiness[75]. There are a wide range of influences that affect human preferences and aversions, and the historic approach of using averages and consensus metrics in sensory science can belie the importance of different preference criteria[3,16,39].

Preference development has been shown to begin *in utero* as nutrients and volatiles from a mother's food are passed to the baby[13], but overall, humans are born with relatively few innate preferences[68]. Newborns show a preference for both sweet and fatty stimuli as well as mildly salty solutions but show aversions for bitter and sour tastes[17]. Preferences and aversions retain a great deal of plasticity throughout lifespans because they are sensitive to modification from lived experiences, which sometimes work unconsciously[78].

Volatile compounds are largely derived from essential nutrients like fatty acids, amino acids, and antioxidants like glucosinolates and carotenoids that are beneficial for human health[3,9]. In that sense, Goff and Klee[13] say plant volatiles can be thought of as "positive nutrient signals that communicate health benefits." While not completely untangled yet, there appears to be a type of backdoor communication between the body and brain about nutrients consumed in food, and this can be a mechanism by which people learn to prefer certain foods and flavors over others[13]. Myers and Sclafani[78] refer to this as "flavor-nutrient conditioning," which is sensed post-ingestion, and there are plenty of documented instances where animals seemingly prefer more nutrient dense foods over others[79]. The relationship with flavor, however, is at this point unclear.

Food preferences can be affected by a variety of learning mechanisms and environmental factors like dietary habits, personal experiences, culture, religion, and physiology[11,47,48,58,68,80]. Numerous studies have pointed out an exposure effect – the more times a person has encountered a food or flavor is positively correlated to acceptance and liking[11,78]. Generally, humans exhibit innate neophobia, although openness to new things has been linked to both geography and culture[16,80]. Preferences and aversions can also arise from other associations and conditioning besides nutrients. For example, rewarding or distracting children with candy can give rise to preferences for particular flavorings and more intense sweetness[74,81]. Likewise, an aversion can easily develop from a bout of food poisoning or toxicity[78].

Another factor affecting liking is whether a food meets expectations, which also relates to a person's history of use and experience[11,16,48]. This is largely where novel colors, shapes, and the appearance of fruits and vegetables can drive eaters to reject them. For example, in a roundtable at the 2019 Organic Vegetable Production Conference (Madison, WI), organic farmers lamented many customers complained about tomato flavor but were also unwilling to buy any non-red tomatoes because their unfamiliar color. This is a popular criterion in US markets. Using preference mapping, Oltman et al.[12] identified the largest consumer segments had strong priorities for red tomatoes and a firm, crisp texture with few seeds. American partialities for red and firmer tomatoes are one example of how culture can affect preferences.

While the senses have evolved for humans to assess their environments, food is also a way that humans indulge themselves, connect to others, and search for identity through consumption[45,47,80]. Individual and cultural food preferences are inextricably linked to art, design, media, and marketing that all signal what food should look and taste like as well as who should be eating it[48]. Beginning in the 1980s, French sociologist Bourdieu wrote several papers on how food was used to advertise class and social standing throughout history[80], and Finn[25] has extended this idea to the modern "Good Food Movement" in the United States. She and others argue that the development of connoisseurship is a way that people attempt to assert status in light of concentrating money and political power[25]. As Bourdieu famously said, "taste classifies, and it classifies the classifier"[80]. Food preferences have been used as a way to characterize people in different social strata, too. For example, throughout the 19th Century in Britain, having a sweet tooth was associated with the working class because they did not possess the prowess to elevate their tastes beyond the visceral pleasures of sugar[80]. Indeed, at least part of the impetus for current breeding work that prioritizes better flavor is socially based, so clearly more than just physical and chemical properties of plant parts are involved.

Laudan[35] retells world history from the perspective of cuisine, and how food has been used to assert power and dominion over others as various empires set out to conquer the world. She writes much about religion and how it has shaped regional cuisines and cultural food preferences. For example, the rise of Protestantism in Britain created widespread disavowal of sensual pleasures including from food, which led to the relatively unadorned boils and roasts that characterize much of British cuisine[35,80]. And the arrival of Buddhism in Japan created an emphasis on simple, mildly flavored and vegetable-focused dishes[35]. Even though this is ancient history, these factors still influence people's food preferences and their liking of different crop cultivars. Historical events have helped form the traditions and foodways that at least partially inform individual identities. As new foods – or new crop cultivars – are tasted, the interaction between brain and mind cannot help but compare them to past memories and experiences which inevitably tug on emotions. Anecdotally for example, at a public tomato tasting event in 2019 (Farm to Flavor, Madison, WI), one taster pointed out their favorite tomato and explained it was because the texture reminded them of tomatoes in their home country of Brazil. This poses a problem for understanding flavor as an objective measurement for plant scientists because it appears there may be no such thing.

Pangborn et al.[68] were some of the first to study differences in aroma preferences across the globe. Perhaps expectedly, they found that different geographic areas had preferences for some smells over others, and the preferred smells differed distinctly by region[68]. Advancements in science and nutrition have further complicated understanding how people develop preferences[48]. In a meta-analysis of consumer liking studies in kiwifruit, Harker et al.[50] found preference differences for eaters in Japan versus those in New Zealand, who were overall more accepting of soft fruit. The authors found an interesting subsection of New Zealand consumers who preferred blander and less sweet kiwifruits whom they hypothesized ate the fruit for its health benefits rather than its sensory properties[50]. Cervellon and Dabe[81] found similar results in their comparisons of food and flavor preferences between French and Chinese eaters. While both cultures have a strong emphasis on food, French preferences were almost entirely driven by affective reasoning, or in other words, they were driven mostly by "sensations, feelings, and emotions"[81]. The results for Chinese eaters indicated that preferences and food choices were based on a balancing of affective and cognitive reasons such as health benefits[81].

Altogether, there are a wide variety of factors that inform which foods and flavors are preferred. While these are surely relevant considerations for plant breeders and researchers, their implications on flavor evaluation methods remain unknown. Food preferences may be described as highly flexible, but plant breeders should consider that some of the determinants of preference are deeply rooted and sensitive topics. For example, when tomato cultivars are geared toward American preferences for firm, sweet, and red, this is a way in which immigrants, refugees, and other marginalized groups are forced to assimilate. Meaningful plant breeding and efforts to evaluate flavor must consider these factors as methods are introduced, improved, and discussed.

Conclusion

The quest to recover and maintain better flavor and sensory qualities in crops is undoubtedly a daunting task for breeders and researchers. While genetics play a role in laying the foundation for good flavor, the growing environment and cultural techniques have a big impact on their manifestation[18]. Human perception of flavor is fickle. As genetically unique individuals, everyone's sensory machinery is different and constantly changing in response to the environment[17,70]. And still neither of these tells the full story. While sensory and plant scientists alike describe flavor as the "sum of [sensory] inputs that informs the brain what we are eating,"[18] it is clearly more than that. Reflexively and unavoidably, everything tasted is put into the context of past experiences, expectations, histories, and identities. Flavor doesn't just tell us what we're eating, it reminds us about who we are and where we come from, too.

Yet somehow, in spite of all that makes studying flavor so complex, it has been assumed that the formal sensory science methods are the best. Certainly, these traditional sensory methods have value and a continue place in flavor research, but the inability to mimic descriptive analyses with professionally trained panelist is often lamented by plant scientists. Attempts are made to proxy their methodologies with the use of expert breeders, while rapid sensory methods and alternatives that utilize professional end-users are automatically relegated as inferior. It seems unlikely that the approaches in traditional sensory evaluation are objectively better at coping with the realistic complexities of assessing flavor especially in non-industrial contexts where food also has extrinsic value[48]. With sensory evaluation being the "child of industry"[41], their methodologies have not been described, critiqued, and refined in the same way as other scientific disciplines. In fact, studies investigating the impact of training on reducing taster variability or its effect over time are practically absent in the literature[4,16,50]. Presumably some of this information exists, but it is outside the public domain and proprietarily owned by major food companies who use formal sensory science to guard market shares. Likewise, it can easily become problematic when one group of people (trained sensory panelists) is making decisions about what they think is best for others (all eaters), especially when the group in power doesn't accurately reflect the people they are making decisions for. With these things considered, plant scientists should be wary of valorizing traditional methods, and room needs to be made for discourse that recognizes the historic shortcomings of applied flavor research. Instead, plant scientists must see the situation as an opportunity to go back to the drawing board and come up with new approaches that are better suited to non-industrial and agricultural contexts. This should be the future of plant science that works on improving flavor.

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