Bitter taste perception of TAS2R38-PAV and CA6-A genotype individuals suppresses aroma and flavour perception when consuming "salad" rocket (Eruca vesicaria subsp. sativa)

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Original Article

Bitter taste perception of *TAS2R38*-PAV and *CA6*-A genotype individuals suppresses aroma and flavour perception when consuming "salad" rocket (*Eruca vesicaria* subsp. *sativa*)

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Abstract

Many nutritious leafy vegetables that should be eaten as part of a healthy diet are shunned by consumers who perceive them to be bitter. Through a combination of sensory, genetic, and analytical chemistry methods we show that individuals with "taster" genotypes for a bitter taste receptor (*TAS2R38*) and high taste bud density (*Carbonic Anhydrase VI*, *CA6*; gustin) encoding genes cannot perceive the aroma and flavour traits of the leafy vegetable rocket (*Eruca vesicaria* subsp. *sativa*) as strongly as "non-tasters," due to heightened perception of bitterness. In addition, we associated sensory data with *Eruca* phytochemical and transcriptome data from growing locations in Italy and the United Kingdom. We observed that several genes were consistently associated with mustard, pungency, tingling, numbing, and warming attributes (*MYB28c*, *SDI1a*, *BCAT4*, *MAM1b*, *CYP79F1*, *CYP83A1*, *MBP2b*), and which are in turn associated with the biosynthesis of glucosinolates and their hydrolysis into pungent compounds such as isothiocyanates.

Keywords: flavour, taste receptor, genotype, glucosinolates, bitterness, sensory analysis

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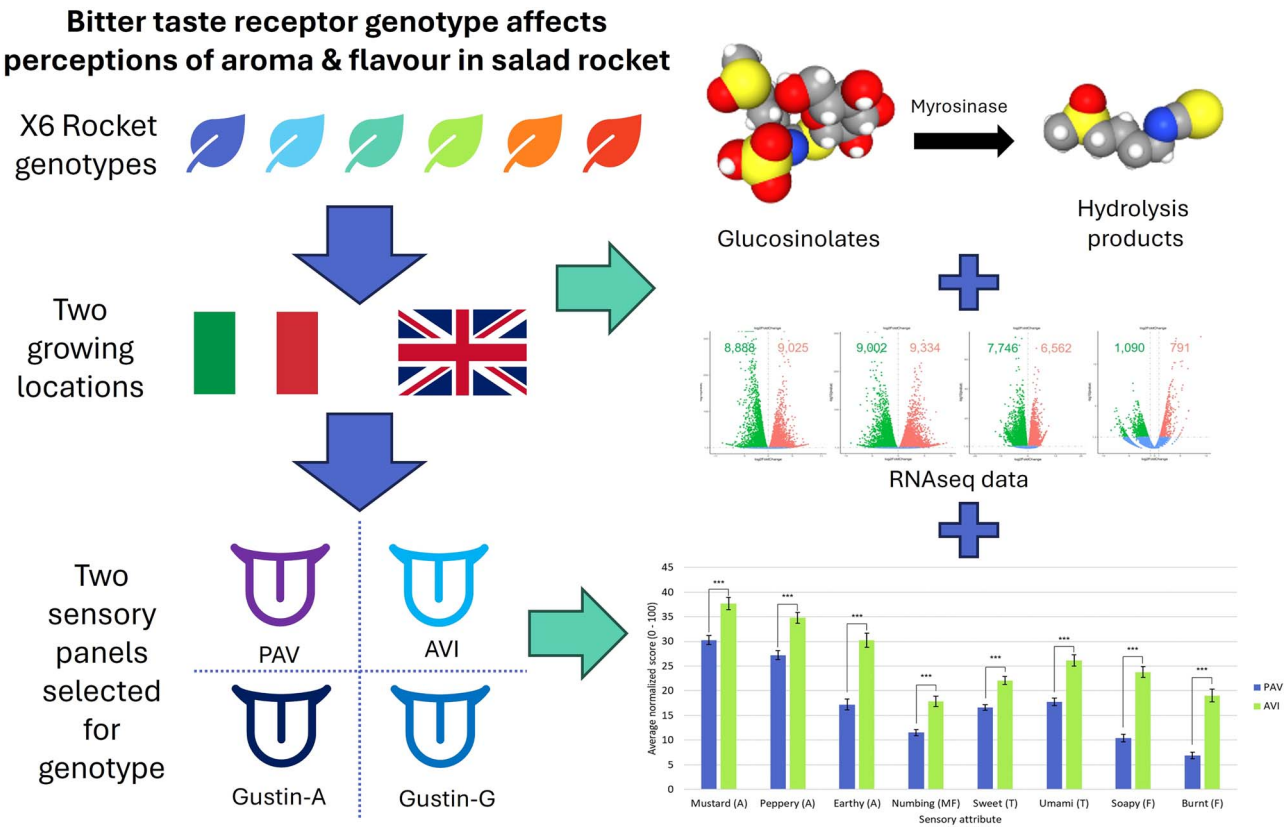
Graphical abstract



Introduction

Leafy vegetables, consumed raw, are a recommended component of healthy diets, providing fibre, minerals, vitamins, and health beneficial plant phytochemicals (Brouwer-Brolsma et al., 2020). Despite a myriad of healthy eating guidelines published in different countries, the majority of citizens in the global north fail to eat adequate amounts of vegetables in their diets (Kalmpourtzidou et al., 2020). The reasons underpinning these food behaviours are complex, but a dislike of the taste, flavour, and other sensory properties is most frequently cited as the reason these healthy foods are avoided (Drewnowski, 1997). In our work, we have focused on a salad crop, since these are usually consumed without cooking, and offer high concentrations of health-related compounds. However, they also suffer from a lack of consumer acceptance due to strong taste and flavours. One of the most divisive crops in terms of consumer acceptance is "salad" rocket (*Eruca vesicaria* subsp. *sativa*; also known as arugula and rucola); a member of the Brassicaceae Family that is widely consumed across the world as a leafy vegetable, and has become naturalised on every inhabited continent (Tripodi et al., 2021). It has a sensory and phytochemical profile similar to that of "wild" rocket (*Diplotaxis tenuifolia*) and watercress (*Nasturtium officinale*) with leaves that are known for their characteristic peppery flavour, pungent aroma, and bitter taste (Bell et al., 2017a). The intensity of these attributes is closely linked with the cultivation environment (Bell et al., 2020b). Our previous research has shown that high growth temperatures are associated with increased concentrations of defensive phytochemicals called glucosinolates (GSLs; Jasper et al., 2020). These compounds are hydrolysed by endogenous myrosinase enzymes and cofactors to produce volatile organic chemical (VOC) hydrolysis products such as isothiocyanates (ITCs; Blažević et al., 2019). ITC compounds are associated with beneficial health effects in humans (Bell & Wagstaff, 2017), but some impart bitterness and pungency that a large proportion of consumers find repellent (Bell et al., 2017b; Oloyede et al., 2021), posing a barrier to consumption of these nutritious crops. Previous research on the sensory properties and consumer acceptability of *Eruca* leaves has found that most consumers prefer sweet, peppery leaves, with low levels of pungency and bitterness (Bell et al., 2017b). Given that these attributes are responsive to cultivation practices and growth conditions it is challenging to produce crops with consistent and acceptable sensory attributes between growing regions and across cultivation seasons.

Taste and flavour quality of "salad" rocket is further complicated by human taste receptor genotypes. Depending on the combination of bitter taste receptor genotype and fungiform papillae density (FPD) on the tongue (thought to correlate with overall taste receptor density; Melis et al., 2013), people experience the taste of foods differently (Dinehart et al., 2006). What is overpoweringly bitter for one individual may not be perceived as bitter at all by another. Many studies on isolated compounds have demonstrated that there are associations between specific alleles of TAS2R bitter taste receptors and the intensity of bitterness perceived (Tepper, 2008). Those capable of detecting bitterness at low concentrations are often described as "supertasters," and those who cannot perceive certain compounds as "non-tasters." These differences in perception have been well demonstrated for individual compounds (Drayna, 2005), but the patterns of taste perception and intensity are not as clear in complex food matrices such as fruits and vegetables (Louro et al., 2021).

GSLs found within vegetables like *Eruca* contain a thiocyanate moiety (-N-C=S) which is known to predominantly activate a human bitter taste receptor called TAS2R38 (Wieczorek et al., 2018). Allelic diversity in the *TAS2R38* gene results in variation in sensitivity to bitter compounds (Behrens et al., 2013). As a result of genetic recombination and inheritance, three common diplotypes are present within the human population: PAV/PAV homozygotes ("supertasters"), PAV/AVI heterozygotes ("medium-tasters"), and AVI/AVI homozygotes ("non-tasters"; Bell et al., 2017b). The *TAS2R38* haplotypes arise because of functional single nucleotide polymorphisms within the gene sequence that encode amino acid substitutions: proline alanine valine (Pro-Ala-Val; PAV), the dominant (sensitive) variant, and alanine valine isoleucine (Ala-Val-Ile; AVI), the recessive (insensitive) one (Calò et al., 2011).

FPD is associated with the CA6 (Carbonic Anhydrase VI, also known as gustin) trophic factor for taste bud development. A single nucleotide polymorphism within this gene (rs2274333; A/G) modifies the binding structure of the protein, conferring a structural change that affects zinc binding and full functionality. The A/A genotype is associated with fully functioning protein and a high FPD, whereas the G/G genotype is associated with disruption of the protein and a lower FPD (Calò et al., 2011). As taste receptors are contained within papillae, it is considered that high FPD is related to higher taste sensitivity; therefore, gustin genotype has similarly been associated with "supertaster" and "non-taster" bitterness genotypes in the literature, but does not itself confer taste perception. The literature provides conflicting results with regard to the role of *CA6* in taste perception, and its interactions with specific bitter taste receptor genotypes. Previous research has indicated that *CA6* genotype is linked with *Brassica* vegetable intake, with the G/G "non-taster" genotype being more likely to prefer these crops because of the association with reduced numbers of TAS2R38 receptors on the tongue (Melis et al., 2013; Shen et al., 2016). However, other studies have not found conclusive associations between *CA6* and *TAS2R38* in the perception of bitterness from propylthiouracil (PROP; see Diószegi et al., 2019 for a complete review). The genes for *TAS2R38* and *CA6* are not genetically linked, with *CA6* located on Chromosome 1 and *TAS2R38* on Chromosome 7 (Kent et al., 2002). It is therefore possible for an individual to be a *TAS2R38* PAV/PAV "supertaster" and a gustin G/G "non-taster." The reductionist view that people are either "supertaster" or "non-taster" for bitterness sensitivity is therefore inaccurate when multiple genotypes are considered. The nature of genetic recombination means that levels of perception are on a "spectrum" from low to high sensitivity and depend greatly on the combinations of taste receptor genotypes an individual has, and the specificity of compounds which bind to those receptors.

Previous studies of *Eruca* have demonstrated perception and liking are not only related to nonvolatile tastants (such as GSLs), they are also affected by VOCs; some which can be perceived both as aroma (via olfactory receptors, ORs) and as trigeminal sensation (via trigeminal nerve sensations in the mouth and nose; Bell et al., 2017a, 2017b, 2020b). ITCs have been shown to activate the TRPA1 ion channel within mammalian cells which induces inflammatory response and the induction of heat and pain sensations (Jordt et al., 2004). When ingesting pungent foods such as rocket, mustard (*Brassica juncea*), or wasabi (*Eutrema japonicum*), the intensity of this activation can be highly unpleasant and result in lachrymose reactions. In low concentrations ITCs give rise to a range of flavours, variously described as sulphurous, musty, mustard, vegetative, radishy, acrid, green, and fragrant (Bell et al., 2018). It is unknown if specific ORs are involved with perception of ITCs and other volatile GSL hydrolysis products, but is likely that genetic variation of ORs also plays a role in an individual's sensitivity (Keller et al., 2007).

The effect of differences in taste sensitivity on the interaction of aroma/flavour perception with taste perception is relatively unexplored within the literature. Given the complexity of *Eruca* sensory attributes, the aim of this study was to identify the role of *TAS2R38* and *CA6* genotypes in the sensory perception of rocket and if this results in any effects on the ability to perceive aroma and flavour from this crop. *TAS2R38* and *CA6* are two of the best studied genes in relation to taste perception, and were selected because of the body of existing research specifically related to crops of the Brassicaceae family (such as *Eruca*). We hypothesised that individuals with a PAV and A allele copy, of *TAS2R38* and *CA6* respectively, would perceive bitter taste and mouthfeel traits associated with trigeminal sensation more intensely than their "non-taster" AVI-G homozygous counterparts. We conversely hypothesised that AVI-G homozygous individuals would perceive aroma, nonbitter tastes, and retronasal flavour more strongly, as their palates are not as dominated by high intensity bitter sensations conferred by functional genotypes (PAV and A). In terms of *Eruca* genotype, we hypothesised that specific sensory perceptions would be associated with differential expression patterns of genes involved with sulphur assimilation, GSL biosynthesis and hydrolysis, sugar metabolism, and abiotic stress response pathways in leaves, giving rise to differences in aroma, taste, and flavour.

Materials and methods

Plant materials, phytochemical analyses, and transcriptome sequencing

Details of the cultivation locations, weather conditions, genotypes, chemical analysis methods (including sulphur, GSLs, hydrolysis products, VOCs, and sugars), transcriptome sequencing, and bioinformatics are described in Bell et al. (2023). Samples used for sensory panel assessments came from the same plant materials and sample time points as described in that study. See Supplementary Table 1 for a full sampling and replication diagram of samples used in sensory, chemical, and transcriptome analyses.

Sensory panel selection, training, and genotyping

To have trained sensory panellists that varied in bitter taste genotype, we recruited two sensory panels to assess *Eruca* leaf samples. Panel #1 consisted of trained individuals from the University of Reading Sensory Science Centre (Reading, UK). The same Panel #1 individuals were present for both the Italy ($n = 11$) and U.K. trial sessions (one additional member recruited; $n = 12$). Panel #1 members were trained in accordance with ISO 8586:2012 standards and subject to performance monitoring according to ISO 11132:2012 standards. Panel #2 was recruited from the Reading area and consisted of individuals who had previously participated in sensory studies and given consent to be contacted. Panel #2 underwent training for 15 sensory tasks (Supplementary Table 2) to ensure they were able to recognise, describe, and discriminate in accordance with Panel #1. Within Panel #2, $n = 10$ individuals were present for the Italy trial sessions; six of whom were present again for the U.K. trial sessions, with a further three people recruited (following screening and training) to replace those who dropped out ($n = 9$). In both panels individuals were trained in leaf assessment over 11, one-hour sessions using supermarket produce (such as bagged rocket leaves, green peppers, pepper corns, condiment mustard, and dried garlic) and food grade

Table 1. Sensory panel genotypes of individuals assessing "salad" rocket leaves cultivated in Italy and the UK.

Panel (country of sample cultivation)	Gender	*TAS2R38*		*CA6*		Total
		PAV/PAV or PAV/AVI	AVI/AVI	A/A or A/G	G/G	
Panel 1 (Italy)	Female: 91% Male: 9%	9	2	7	4	11
Panel 2 (Italy)	Female: 70% Male: 30%	3	7	5	5	10
Panel 1 (UK)	Female: 92% Male: 8%	9	3	8	4	12
Panel 2 (UK)	Female: 44% Male: 56%	5	4	4	5	9

compound standards (1-octen-3-ol, quinine, and allyl ITC; Merck-Sigma, Gillingham, UK).

Panellists from both panels gave consent for their *TAS2R38* and *CA6* genotyping data to be used in the study. Buccal swabs of participants were taken in duplicate and sent to Biosearch Technologies—LCG Group (Hoddesdon, UK) who performed all DNA extractions and genotyping. Panels #1 and #2 were genotyped for *TAS2R38* and *CA6* using Kompetitive Allele Specific PCR markers: *hTAS2R38*—A49P (rs713598), A262V (rs1726866), V296I (rs10246939), and *hCA6* A90G (rs2274333) (Melis et al., 2013). Panellist genotypes are summarised in Table 1. A favourable opinion for conduct of all sensory work and collection of panellist tissue sample and genotype data was given by the University of Reading Research Ethics Committee (UREC 18/23) and samples held in accordance with the Human Tissue Act (2004).

Vocabulary development and sensory analysis

Both panels conducted independent vocabulary development over three half-hour sessions using commercially available bagged rocket leaves and use of standards (bagged rocket leaves, green peppers, pepper corns, condiment mustard, dried garlic, sugar, 1-octen-3-ol, quinine, and allyl ITC) prior to the Italy trial. Assessors discussed, with the aid of a facilitator, the various sensory attributes associated with the odour, mouthfeel, taste, flavour, and aftereffects of leaf samples. Each panel devised a consensus vocabulary, after which similar terms were amalgamated by the facilitator in discussion with the two panels, and the final list of sensory terms and their definitions is provided in Table 2. Before the U.K. sessions, panellists were refamiliarised with the vocabulary, attending two additional half-hour sessions. This was done to ensure consistency of responses. Newly recruited members of Panel #2 underwent additional training and familiarisation sessions as described above.

First time point sample (D0) sensory evaluations took place on the day following sample delivery to the University of Reading. All samples were stored at 4 °C overnight. Day five (D5) samples were evaluated five days later under identical conditions. Sensory descriptors were entered into Compusense (Guelph, Ontario, Canada) software and assessors were asked to score each attribute on unstructured, 20 cm, line scales (anchored "nil" to "extreme"). Panellists were not given explicit training on the extremes of each attribute. This scale was therefore relative to each assessor's own personal experience. Evaluations were conducted under artificial daylight conditions in a plain, air-conditioned room in isolated sensory booths. Samples were presented with three-digit random codes in duplicate with a balanced presentation order over two, one-hour sessions (a.m. and p.m.). Three leaves were selected from bags at random for presentation and placed onto transparent petri dishes. Samples were delivered to participants through hatches adjoined to booths in order to limit interactions with researchers during the assessments. Panellists were instructed to first break leaves with their fingers and assess the aroma. Next they were instructed to place leaves in their mouths and chew, assessing mouthfeel, taste, and flavour. Upon completion of these attribute evaluations each panellist was asked to swallow the leaves and wait 30-s before scoring aftereffects every 30-s for 2 min (T0–T3). Rocket cultivars 21 and 25 were withdrawn from the U.K. second cut analyses due to visible deterioration in quality that could have posed a health risk to the assessors. Panellists were provided with cold water and natural yogurt for palate cleansing between samples (Bell et al., 2017a).

Statistical analysis

Sensory data for each panellist were individually normalised across four scoring sessions in each respective trial (Italy and UK; XLStat v.2021.3.1.1190, Addinsoft, Paris, France). To check panellist performance in the sensory assessments, responses were analysed using Senpaq (version 6, Qi Statistics, Kent, United Kingdom). Criteria for evaluation included assessors' ability to discriminate between cultivars, and their repeatability between replicates (compared to the panel average). As we were investigating the effect of differences in genotype that influence taste perception we were cautious to exclude panellists based on interaction, however this was considered within genotype groups. For the Italy trial all assessors met the criteria for inclusion in the subsequent statistical analyses. For the U.K. trial, two individuals had their responses removed from the dataset for not meeting these criteria, and additionally one panellist was removed for being absent for >70% of the scoring sessions. For full panellist performance statistics see Supplementary Table 3.

Data from each trial were then collated and tested for normality distribution using Shapiro–Wilk tests. Attributes fitting a normal distribution were analysed using ANOVA with protected Tukey's HSD pairwise comparison tests. Interaction effects between country (Italy and UK), *Eruca* cultivar, cut number, storage duration, *TAS2R38*, and gustin genotypes were fitted.

A split-level ANOVA was performed (XLStat) to account for the unbalanced genotype composition of the two panels. TAS2R38, gustin, and the TAS2R38 × gustin interactions were treated as nested effects, with manual *F*-values calculated. This was done by dividing the nested effect and panel–sample interaction (sample × TAS2R38 × gustin) mean squares values. The Microsoft Excel FDIST function was then used to calculate a manual *p*-value from

Table 2. List of sensory terms and definitions used in the evaluation of "salad" rocket leaves grown in Italy and the UK.

Sensory attribute	Definition
Aroma	
Pungent	A sharp aroma; associated with perceived strength and eliciting a tingling sensation in the nostrils (provided as a standard of condiment mustard)
Mustard	Potent aroma associated with crushed condiment mustard (provided as a standard)
Peppery	Pungent aroma associated with ground peppercorns (provided as a standard)
Green	Aroma(s) associated with cut grass and freshness (provided as a standard of green peppers)
Earthy	Resembling or suggestive of earth or soil (provided as a standard)
Mouthfeel	
Crisp	Brittle sensation on the teeth or tongue when biting leaves
Crunchy	The physical and audible sensation perceived when chewing leaves
Firmness	Degree of ease with which leaf stems can be broken and chewed by the teeth
Moistness	Associated with the water content of the leaf samples ingested
Taste	
Bitter	Taste associated with quinine (provided as a standard)
Sweet	Taste associated with sucrose solution (provided as a standard)
Umami	Taste associated with monosodium glutamate solution (provided as a standard)
Flavour	
Peppery	Flavour associated with ground peppercorns (provided as a standard)
Green	Flavour associated with cut grass and freshness (provided as a standard of green peppers)
Soapy	Flavour associated with soap and medicinal products
Mustard	Flavour associated with the potency of condiment mustard (provided as a standard)
Burnt	Flavour associated with overcooked burnt foods; reminiscent of burning rubber
Aftereffects	
Warming (mouthfeel)	A persistence of the sensation of heat/temperature within the mouth after swallowing (provided as a standard of condiment mustard)
Tingling (mouthfeel)	Persistence of a tingling sensation upon the surface of the tongue after swallowing (provided as a standard of condiment mustard)
Green (flavour)	Persistence of a grassy, fresh flavour (provided as a standard of green peppers)
Drying (mouthfeel)	Persistence of an astringent sensation in the mouth after swallowing
Numbing (mouthfeel)	Persistence of a loss of physical sensation in the mouth and on the tongue after swallowing (provided as a standard of condiment mustard)
Bitter (taste)	A persistence of bitter taste after swallowing (provided as a standard of quinine solution)

the manual *F*-value, nested effect degrees of freedom (df = 1), and the panel × sample interaction degrees of freedom (df = 15). For all other non-nested effects, the *F*-values were calculated against the baseline error. Type II sum of squares values for all variables are given except where a significant interaction was observed, in which case, the Type III sum of squares value was used for interpretation (Supplementary Table 4).

Sensory data that did not fit a normal distribution were analysed using Mann–Whitney *U* test (country, cut number, storage duration, TAS2R38, and gustin) and Kruskal–Wallis one-way analysis of variance (cultivar). As interaction effects cannot be determined using nonparametric tests the *p*-values generated for these variables do not account for the imbalance in genotype numbers; therefore, these data were also analysed using the same split-level ANOVA with Tukey's HSD approach as for normally distributed data. The results of this analysis were not used in the interpretation and are only used as a comparator to the nonparametric test results (Supplementary Table 4).

Principal component analysis (PCA) with Pearson's correlation analysis ($n-1$) was performed on sensory data for the Italy trial, with the addition of sulphur content, phytochemical (GSL, hydrolysis product, and sugar) concentrations, VOC abundances, and RNAseq gene expression (FPKM) data (Bell et al., 2023) as supplementary variables. Two hundred and fifty-eight *Eruca* genes were selected based on genome annotation data (Bell et al., 2020a) and their putative identifications. These included genes associated with sulfur metabolism, GSL biosynthesis, GSL hydrolysis, cell redox homeostasis, GSL transport, defence response, VOC synthesis, and sugar metabolism. This analysis was performed using normalised average AVI-A, AVI-G, PAV-A, and PAV-G sensory responses from the Italy trial (which represents a complete dataset). This was done to elucidate differences between genotypes and understand the factors driving differences in individuals' perceptions.

Results

Country of cultivation, pre-, and post-harvest handling impacts on perceived sensory attributes of *Eruca*

The sensory properties of six *Eruca* recombinant inbred lines derived from a mapping population (Bell et al., 2022) were determined after growing commercial-scale crops in Italy and the UK, by using two trained panels of assessors (Supplementary Table 5). These lines were identified in our previous work as having very different GSL profiles (Bell et al., 2022). Italy-grown samples developed a significantly more peppery flavour than U.K.-grown equivalent lines and line 68 was significantly more peppery than lines 21, 25, and 72 (Figure 1; Supplementary Table 4). As repeated harvests (cuts) from the same plants are known to intensify pungency in the leaves, the first and second cuts were evaluated from each location. Warming mouthfeel was scored significantly higher (on average) in second cut samples compared to first (Figure 1) which is linked to increased GSL and hydrolysis product formation (Bell et al., 2023). Comparison of the crop between the day of harvest (D0) and five days later (D5), the time that corresponds to

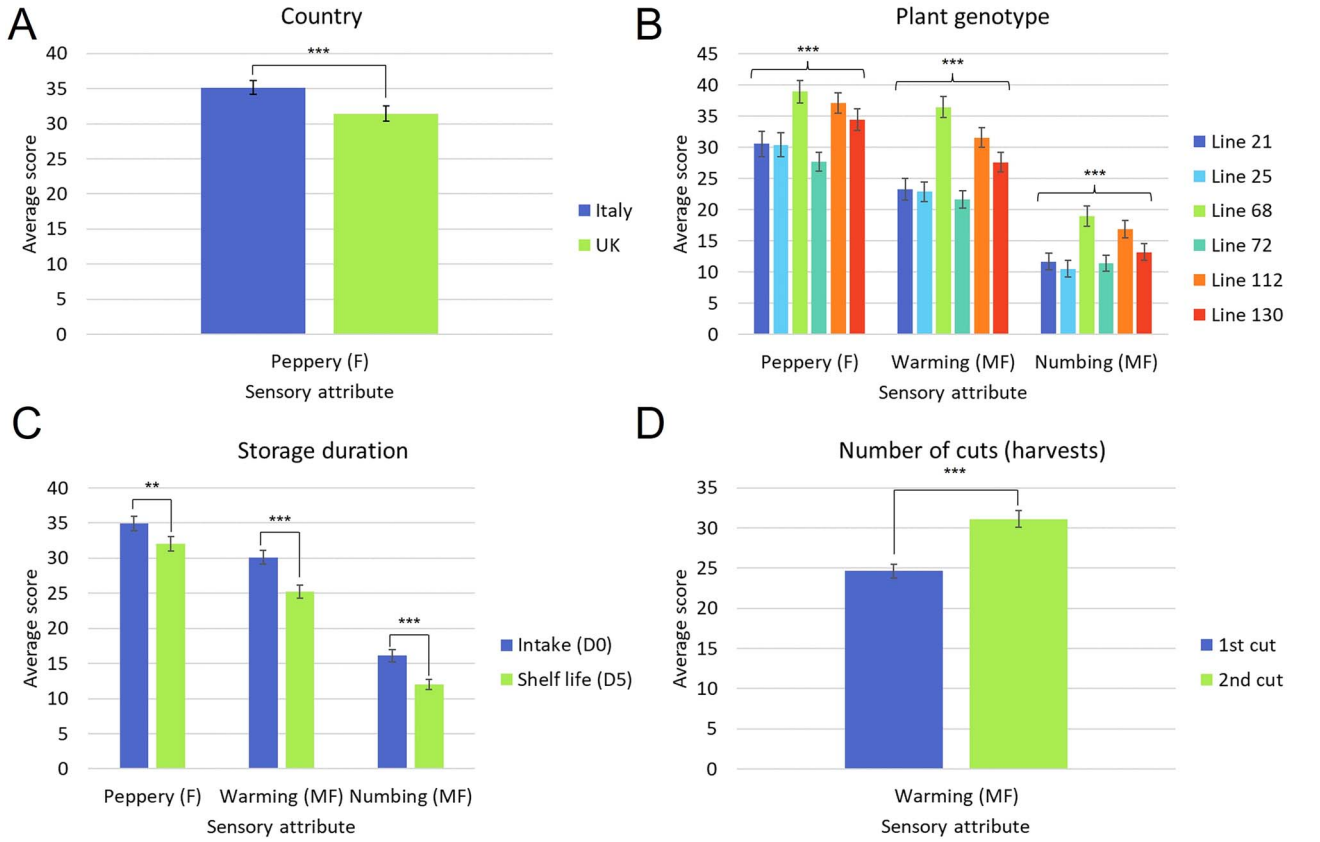


Figure 1. Differences between sensory attributes of tested *Eruca vesicaria* subsp. *sativa* extreme lines. (A) Average scores of *Eruca* peppery flavour in Italy and the UK ($p \leq .0001$). (B) Average scores of peppery flavour ($p \leq .0001$), warming mouthfeel ($p \leq .0001$), and numbing mouthfeel ($p \leq .0001$) between six *Eruca* extreme lines. (C) Average scores of peppery flavour ($p = .003$), warming mouthfeel ($p \leq .0001$), and numbing mouthfeel ($p \leq .0001$) between intake (D0) and (D5) of *Eruca* shelf-life storage. (D) Average scores of warming mouthfeel between first and second cuts of *Eruca* ($p = .000$). Error bars represent standard error of the mean. Asterisks denote level of significant difference: $^{**}p < .01$; $^{***}p < .001$; ns = not significant. See Supplementary Table 4 for a summary of statistical analyses.

when most people would eat *Eruca* purchased through supermarket retailers, showed that bitterness, peppery flavour, warming, and numbing mouthfeels all significantly declined over this shelf-life period. On average, bitterness was scored 1.5-fold higher at D0 compared with D5 across all samples (Supplementary Table 5).

Human taste receptor genotype affects more than just taste perception of *Eruca*

Eruca samples were evaluated by two sensory panels who were genotyped for their *TAS2R38* and *CA6* taster status. Significant differences between PAV (summarised as individuals that were either PAV/PAV or PAV/AVI) and AVI (i.e., AVI/AVI) genotypes were observed at T1 (1 min after swallowing) and T2 (1.5 min after swallowing) for bitter taste aftereffects. The average scores across the aftereffect time course for PAV and AVI individuals (black solid and dotted lines; Figure 2) indicate a clear separation between genotypes and reflects previous observations that PAV individuals are more sensitive to bitterness (Shen et al., 2016). The sensitivity of PAV individuals was also observed to extend to mouthfeel aftereffects, such as tingling and numbing sensations (Figure 3). PAV individuals scored samples significantly higher at T2 and T3 for tingling and T1–T3 for numbing as well as other attributes (Supplementary Table 4).

When responses for aroma, mouthfeel, nonbitter tastes, and flavour from PAV and AVI individuals are scrutinised, there is a clear, significant trend, which shows AVI individuals score higher (on average) than those with a PAV allele (Figure 4) for these nonbitter sensations. This same observation was found for *CA6* G-allele individuals compared with those with at least one A allele (Figure 4). When considering *CA6* alone, significant effects were observed in responses for mustard aroma ($p \leq .0001$), peppery aroma ($p = .006$), earthy aroma ($p \leq .0001$), sweet taste ($p = .000$), soapy flavour ($p \leq .0001$), burnt flavour ($p \leq .0001$; Figure 4), tingling aftereffects ($p = .05$), drying aftereffects ($p \leq .042$), and numbing aftereffects ($p = .006$; Supplementary Table 4).

PCA of sensory data illustrated that the perceived intensities of aroma, flavour, and mouthfeel attributes are strongly affected by individual's *TAS2R38* and *CA6* genotypes. The effect of *TAS2R38* and *CA6* genes (or lack thereof in null-genotype individuals) therefore extends far beyond only bitter taste perception (Figure 5). Sensory responses cluster clearly according to the *TAS2R38-CA6* genotype of individuals and align with responses for specific traits. For example, aroma (earthy, peppery, mustard), flavour (soapy, burnt, peppery), and mouthfeel (numbing, warming) attributes of *Eruca* leaves associate with the responses of AVI-G individuals (*TAS2R38* "non-tasters," low FPD) and in opposition to responses from individuals with a PAV allele (Figure 5, group I). AVI-A individuals were intermediate in their responses, clustering between AVI-G and PAV-A individuals. This supports the hypothesis that taste receptor and FPD genotypes form a "spectrum" of sensitivity to sensory traits (not just bitter taste). Conversely, responses from individuals with a PAV allele (PAV-A and PAV-G) are strongly associated with bitter taste perception and aftereffect mouthfeel sensations (Figure 5, indicated by arrows II, III, and IV).

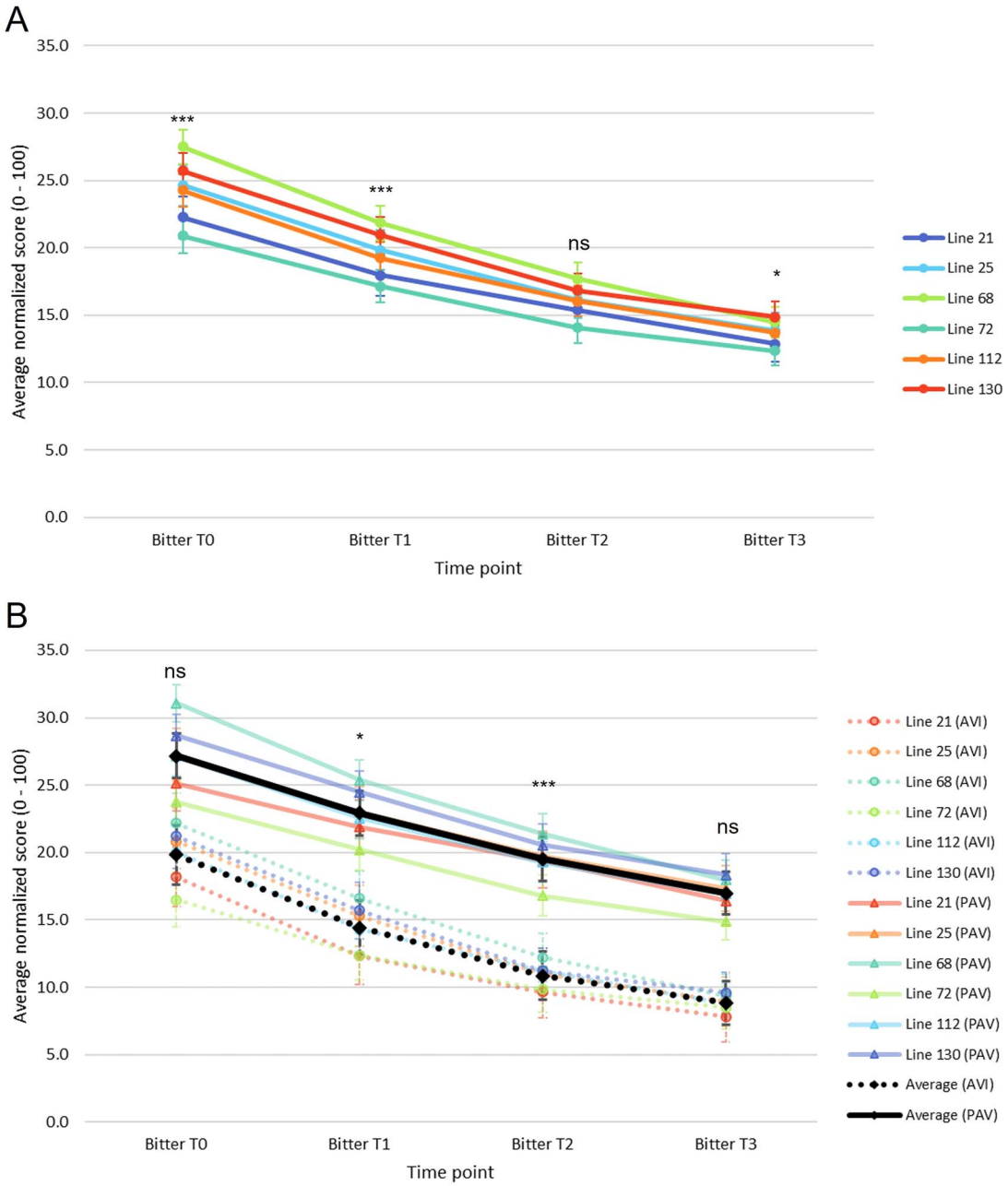


Figure 2. Bitter taste aftereffect scores in *Eruca* according to (A) plant genotype (T0, $p \leq .0001$; T1, $p \leq .0001$; T2, $p = .244$; T3, $p = .02$), and (B) *TAS2R38* taste receptor allele status (T0, $p = .052$; T1, $p = .044$; T2, $p \leq .0001$; T3, $p = .114$) across Italy and U.K. field trials. Time points correspond to 30-s intervals postswallowing. Error bars represent standard error of the mean. Asterisks denote level of significant difference within the time point: $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$; ns = no significance. See Supplementary Table 4 for a summary of statistical analyses.

The sensitivity of individuals with a PAV allele to bitterness is well established, however the trade-off with sensitivity to aroma, flavour, mouthfeel, and (some) other nonbitter tastes has not been established in complex foods such as *Eruca* leaves before. There is a clear trend for aftereffect mouthfeel sensations to persist in individuals with a PAV allele, and intriguingly, it is PAV-G (*TAS2R38* "supertaster," low FPD individuals) that were found to be most sensitive to bitterness and its persistence on the palate over the aftereffect time course (Figure 5, arrow II). This is contrary to established theory and is indicative of previously unreported synergistic effects between *TAS2R38* and *CA6* genotypes in complex food matrices.

From these data, sensory perceptions of *Eruca* leaves are primarily driven by the duration of mouthfeel aftereffects, rather than initial taste, flavour, or aroma upon ingestion for PAV-A individuals. This is underpinned by differences in expression of specific plant genes and the relative abundances of GSLs and VOC hydrolysis products they form (Bell et al., 2023). Conversely, the opposite is true for AVI-A genotype individuals who perceive the initial sensory attributes more intensely, and which then fade quickly. Correlation analyses of sensory responses, *Eruca* leaf metabolites, and gene expression data (Bell et al., 2023) revealed that our observations are underpinned by differences in GSL and VOC abundance, and in turn the expression of specific gene copies within leaves (Supplementary Table 6). Sensory attributes such as aroma (peppery, earthy, green), mouthfeel (warming), flavour (peppery), and bitter taste are associated with concentrations of total GSLs, total GSL hydrolysis products, and the VOC

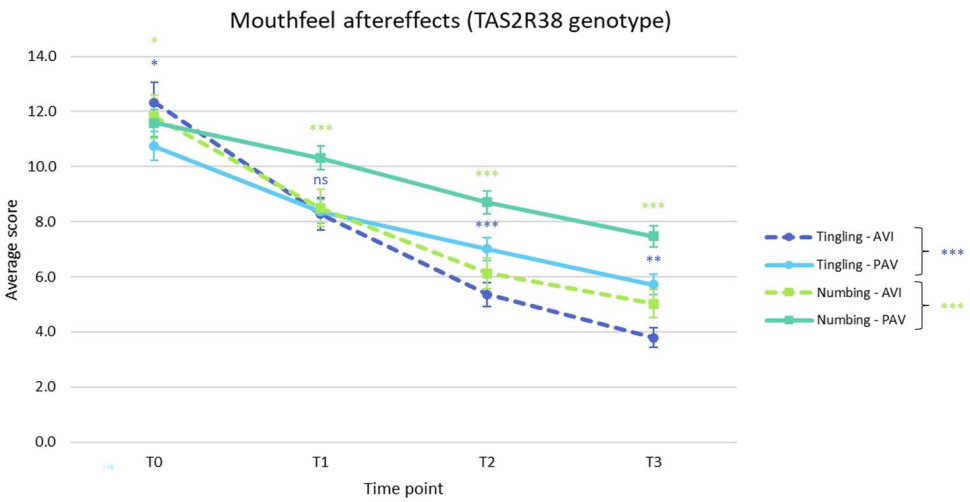


Figure 3. Differences between sensory aftereffects of tested *Eruca vesicaria* subsp. *sativa* extreme lines over a 2-min period (T0–T3) postswallowing. Average scores of *Eruca* mouthfeel aftereffects according to assessor *TAS2R38* PAV and AVI allele status (tingling: T0, $p = .044$; T1, $p = .892$; T2, $p = .001$; T3, $p = .003$; numbing: T0, $p = .05$; T1, $p \leq .0001$; T2, $p \leq .0001$; T3, $p \leq .0001$) across Italy and U.K. field trials. Error bars represent standard error of the mean. Asterisks denote level of significant difference: $*p < .05$; $**p < .01$; $***p < .001$. See Supplementary Table 4 for a summary of statistical analyses.

tetrahydrothiophene. The association of PAV-allele individuals with bitter sensitivity corresponds to expression of plant genes relating to sulphur metabolism (*APK3*), GSL biosynthesis (*MAM1b* and *CYP79B2c*), GSL hydrolysis (*MBP2b*), GSL transport (*GTR1c* and *GTR1d*), glutathione metabolism (*GPX8* and *GSTU20*), and sucrose biosynthesis (*SUS5*, *SUS6a*, and *SUS6b*). Across all *TAS2R38-CA6* genotypes several *Eruca* genes were consistently associated with mustard, pungency, tingling, numbing, and warming attributes (*MYB28c*, *SDI1a*, *BCAT4*, *MAM1b*, *CYP79F1*, *CYP83A1*, and *MBP2b*; Supplementary Figures 1–4). The GSLs which are synthesised by these genes can therefore be perceived by all assessed human genotypes, and our evidence suggests that null-genotypes may be the most sensitive of all to aroma and flavour-related compounds such as ITCs.

Discussion

Study limitations

A limitation of the presented experiment is the numbers of participants used for drawing comparisons between genotypes. Greater numbers of participants would increase the statistical power of the data, however the numbers of participants used here per panel and overall are in line with other sensory analyses in the literature (Bell et al., 2020b; Chodur et al., 2018; Kang et al., 2023; Turner et al., 2021), and is within the ISO standards for a trained panel of 8 to 12 panellists (ISO 13299:2016). Genotypes across the two panels used in this study were consciously balanced in order to avoid biasing responses, and robust statistics were used to account for Type I errors and unbalanced genotypic interactions.

Age, ethnicity, and gender were not considered as contributory variables in this experiment, but which are likely to be linked with sensory perceptions of *Eruca*, and have interactions with taste receptor and FPD genotypes/frequencies. Future research should build upon this work to determine the significance (if any) of these factors, within the context of a larger population consumer study rather than within the trained panel approach taken here.

Expression of specific plant gene copies are associated with *Eruca* sensory attributes

Ensuring that plants are nutritious, attractive, and pleasurable foods to eat is essential to promoting consumption as part of a healthy diet. Here we revealed that individuals with differing *TAS2R38* taste receptor and gustin genotypes perceive phytochemical profiles of *Eruca* leaves in distinctive ways. We took a novel approach to identifying how expression of specific plant genes translates into sensory perceptions in humans. PCA of *TAS2R38-CA6* sensotypes (Supplementary Figures 1–4) revealed a subset of genes consistently associated with characteristic *Eruca* attributes (mustard, pungency, tingling, numbing, and warming). Increased expression of *BCAT4*, *CYP79F1*, *CYP83A1*, *MAM1*, and *MYB28* is associated with increased GSL biosynthesis and is well documented in the literature (Banerjee et al., 2016; Zhang et al., 2016). This study is the first to demonstrate quantitatively the links between expression of these genes and increased perception of their associated sensory phenotypes in humans.

Our data have generated novel insights into the potential transcriptional regulation of metabolites associated with organoleptic phenotypes. Genes encoding myrosinase binding proteins (MBPs) had a strong association with aroma and flavour traits (Supplementary Figures 1–4). Myrosinase-binding proteins are involved in complex formation of isoenzymes, but transgenic experiments have proved inconclusive in terms of their relationship with generation of ITCs. They may act as a means of regulating GSL hydrolysis by modifying the structure of myrosinase (Eriksson et al., 2002), but this has not been robustly tested. Our data show that it is expression of specific gene paralogs in the *Eruca* genome which are associated with sensory phenotypes. This highlights the importance of assessing expression patterns across gene paralogs, and not assuming each has the same function or are expressed at the same ontogenic stage in the plant.

Human TAS2R38 PAV genotype confers increased sensitivity to aftereffects, but reduced sensitivity to aroma, nonbitter tastes, and flavour attributes

A key finding of this study was that assessors with at least one *TAS2R38* PAV allele perceive some aromas and flavours significantly less than AVI/AVI "non-tasters" (Figure 4). Our observations appear to be a distinct phenomenon in sensory perceptions of the complex food matrix of *Eruca* leaves. We hypothesise that the heightened sensations of bitterness

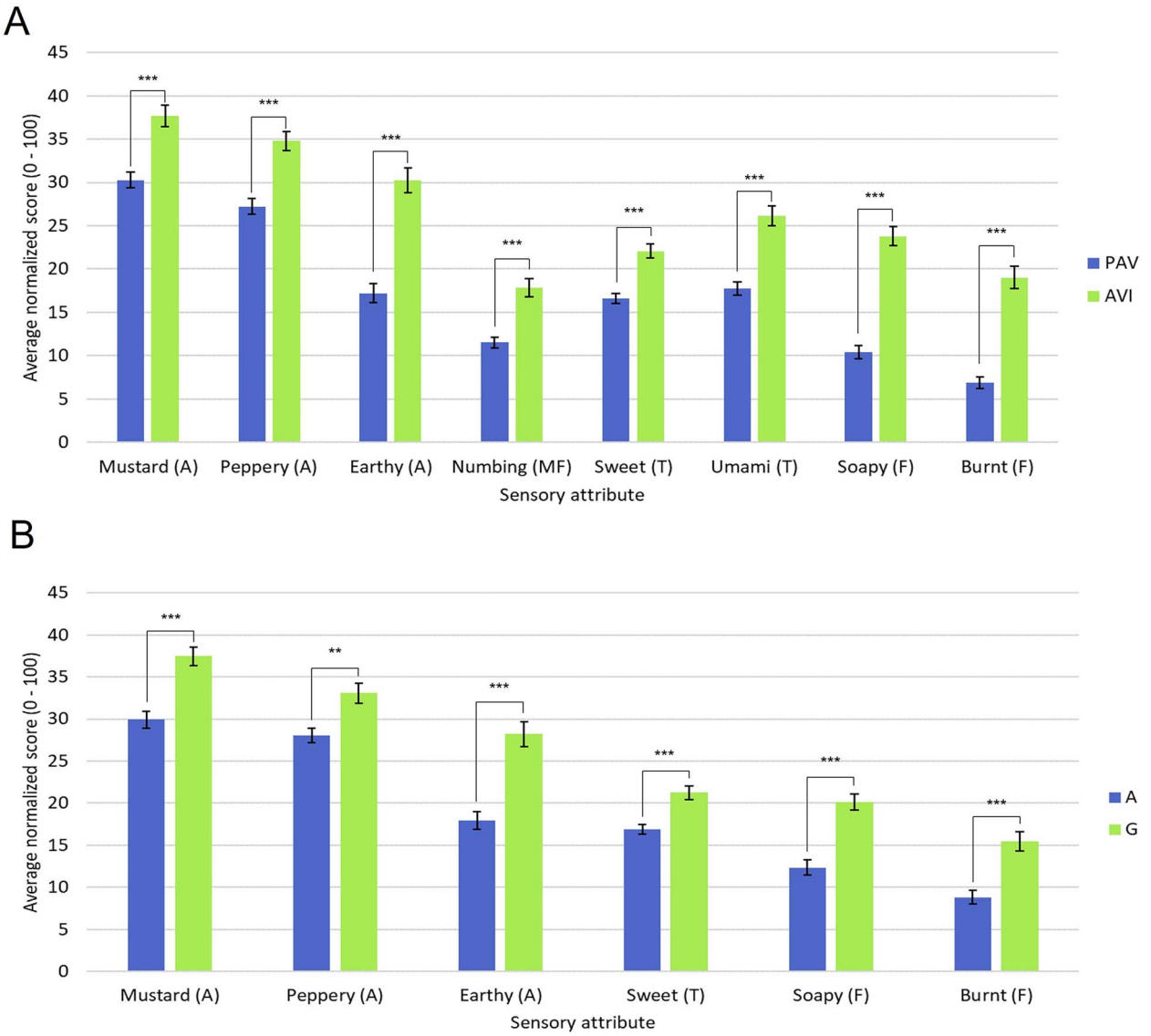


Figure 4. Scores for sensory attributes of *Eruca* extreme lines according to (A) *TAS2R38* taste receptor allele status (summarised as PAV for PAV/PAV or PAV/AVI, and AVI for AVI/AVI genotypes,) and (B) *CA6* (gustin) allele (A/G) status across Italy and U.K. field trials. (A) *TAS2R38* scores differed significantly for mustard aroma ($p \leq .0001$), peppery aroma ($p \leq .0001$), earthy aroma ($p \leq .0001$), numbing mouthfeel ($p \leq .0001$), sweet taste ($p \leq .0001$), umami taste ($p \leq .0001$), soapy flavour ($p \leq .0001$), and burnt flavour ($p \leq .0001$). (B) *CA6* scores differed significantly for mustard aroma ($p \leq .0001$), peppery aroma ($p = .006$), earthy aroma ($p \leq .0001$), sweet taste ($p = .000$), soapy flavour ($p \leq .0001$), and burnt flavour ($p \leq .0001$). Error bars represent standard error of the mean. Asterisks denote level of significant difference: $^{**}p < .01$; $^{***}p < .001$. See Supplementary Table 4 for a summary of statistical analyses. Abbreviations: A = aroma; MF = mouthfeel; T = taste; F = flavour.

(Figure 2) and mouthfeel traits such as tingling and numbing (Figure 3) in PAV allele individuals "drowns out" the neurological signals produced by ORs. The phenomenon of sweet-tasting compounds masking bitter taste perceptions is well documented (Ley, 2008), however we are unaware of any previous reports demonstrating that the strength of bitter perception an individual experiences reduces their ability to perceive aroma and flavour. An analogy might be a band playing in a room crowded with people—the collective noise from the crowd (e.g., aromas and flavours) is drowned out by the increased volume of drums and amplifiers (e.g., PAV allele bitterness). If the band were to play without amplifiers (analogous to the AVI/AVI genotype) the crowd would be much easier to hear and dominate the sensory profile to a greater extent, making it harder to perceive the band clearly.

This analogy also extends to the gustin *CA6* genotype. Similar observations provide evidence that members of the assessment panels with an A-allele (propensity for higher FPD) perceived aromas (mustard, peppery, earthy), flavours (soapy, burnt), and sweet taste significantly lower than G/G genotype (propensity for lower FPD) individuals (Figure 4). As this study only considered two genes involved in taste perception it is possible that confounding effects from other untested taste receptor genotypes could be influencing the observations. Genes and genotypes which could be considered in future research include other bitter taste receptors such as: TAS2R2 (a recently and newly described bitter receptor; Lang et al., 2023) to better determine its function in response to foodstuffs; and TAS2R14 and TAS2R39, that are thought to bind to flavonoids, and of which *Eruca* contains high concentrations (Roland et al., 2013). Nevertheless, this study has shown that taste and flavour perceptions of complex food matrices such as *Eruca* are not reflective of effects seen when only isolated compounds (such as PROP) are studied.

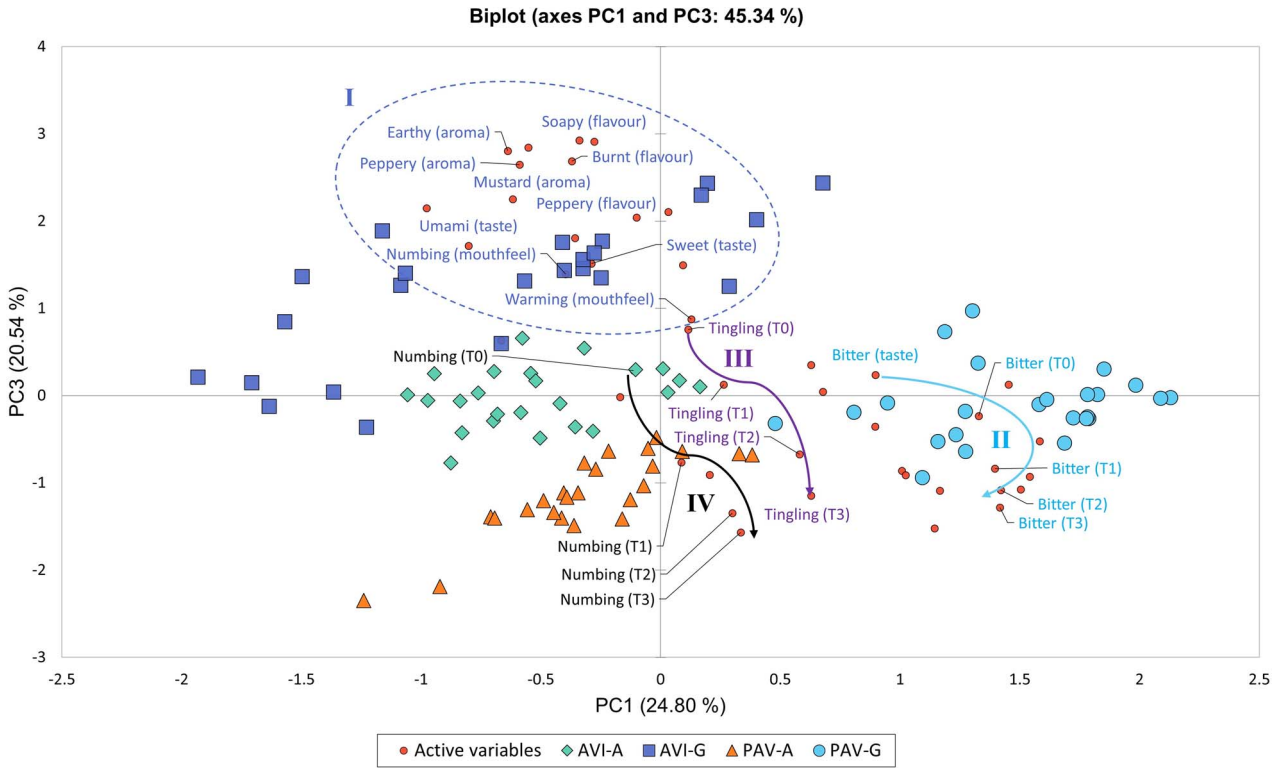


Figure 5. Principal component analysis (PCA) biplots for Italy-grown *Eruca vesicaria* subsp. *sativa* extreme line sample sensory analysis scores of individuals according to their *TAS2R38-CA6* allele genotype (refer to Table 1). PC1 and PC3 were selected for presentation and explain 45.3% of the observed variation. Circle I (indigo) highlights the sensory attributes associated with responses from individuals with the AVI-G genotype. Arrow II (light blue) highlights the progression of bitter taste and aftereffects (T0–T3), descending into the lower right quadrant, and associated with responses from individuals with the PAV-G genotype. Arrow III (purple) highlights the progression of tingling mouthfeel aftereffects (T0–T3), descending into the lower right quadrant, and associated with responses from individuals with at least one PAV allele. Arrow IV (black) highlights the progression of numbing mouthfeel aftereffects (T0–T3), descending into the lower right quadrant, and associated with responses from individuals with at least one PAV allele.

Our data suggest there may be evolutionary trade-offs for being a "supertaster"—an individual may have a heightened ability to detect potentially harmful (bitter) compounds in foods but may suffer a corresponding deficiency in their ability to perceive other nonbitter tastes and aromas. The implications of this study are therefore wide ranging, beyond crop improvement and the chemical basis for taste and flavour in *Eruca*. The data are indicative of effects extending to the evolution of human taste and olfactory perception which are worthy of detailed investigation in that context. Considering the results of this study we propose that sensory panels be inclusive of a wider range of taste receptor genotypes, and to include null genotypes when evaluating complex foods. This will allow researchers to obtain a broader range of perceptions which might otherwise be missed if only "supertaster" individuals are used. In recognizing the contribution of human genetic diversity in relation to the sensory perception of food, we can ensure that groups of people with different genotypes can all have access to foods that are both good for their nutrition and which are pleasurable for them to consume.

It should be acknowledged that not all researchers have the capability or access to perform taste receptor genotyping. This of course would be a barrier to our proposal, though other proxy phenotype indicators, such as PROP sensitivity or FPD counts, could be used in such cases. This approach itself is however not accurate or definitive. As we have shown in examples here, FPD count is not linked with the *TAS2R38* gene, and it is possible for someone to have the AVI/AVI-A/A genotype conferring high FPD but low bitter (thiourea) taste perception. Indeed it is also possible that other taste receptor genes "restore" the function of the AVI/AVI diplotype, such as *TAS2R4* (Nolden et al., 2024). This may partly explain why AVI/AVI individuals can still perceive and report bitterness in *Eruca* leaves.

Practical applications

Crop improvement

The identification of specific genes associated with sensory traits in rocket leaves can be used to breed new varieties with improved taste and flavour profiles. This could lead to increased consumer acceptance and consumption of this nutritious leafy vegetable. Utilization of the data in this study will allow breeders to accelerate the selection of flavour-related traits by targeting specific genes for their relative expression. We have identified several such genes that could be used in this way, as they are consistently associated with sensory perceptions across taste receptor genotypes.

Personalised nutrition

The findings on the influence of taste receptor genotypes on bitterness perception and other sensory attributes in rocket leaves could be used to develop personalised dietary recommendations. This could help individuals make informed food choices based on their genetic predisposition and preferences. Information on individuals' taste receptor genotype could be coupled with information on their metabolic genotype, such as *GSTM1* (Houghton et al., 2013), for example. In this way, an individual's ability to metabolise health beneficial ITCs (such as sulphoraphane) can

be determined and combined with their disposition towards bitter perception and flavour sensitivity.

Sensory panel selection

Given the results of this study, it is perhaps more prudent to be aware of genotypes and/or taste sensitivities than it is to strictly control their selection in experimental designs. As observed in here, panellist performance is not necessarily linked to genotype, because each individual is perceiving taste and aroma sensations differently based on many different interacting genetic and experiential factors. This study highlights two concerns for trained sensory panel research. Firstly, considering "insensitivity" as a reason to screen out potential panellists could be ill advised in some situations. Here, the panellists more sensitive to bitterness were less able to detect other aroma and taste attributes in rocket and less able to discriminate between the rocket samples; and yet their profile of perception will reflect that of a subpopulation of consumers. Secondly, in evaluating trained panel data there is often the aim to reduce assessor-by-sample interaction rather than to investigate it; the interaction can be due to true differences in perception that warrant further investigation.

Evolutionary studies

The data presented could be used to investigate the evolutionary trade-offs associated with taste perception in humans. This could shed light on the complex interplay between genetics, sensory perception, and dietary choices. It may also better elucidate why null alleles for taste receptors persist within populations, and whether they confer a selective advantage more broadly across food types and populations.

Conclusion

This study highlights the importance of considering genetic diversity in taste receptor genes when evaluating the sensory attributes of foods, using *Eruca* leaves as a case study. It reveals that individuals with different TAS2R38 and gustin genotypes perceive the plant's phytochemical profiles in unique ways. Key findings include the association of specific gene expressions with sensory traits such as bitterness, aroma, and mouthfeel. Notably, "supertasters" with the PAV allele of *TAS2R38* and the A-allele of *CA6* exhibit heightened sensitivity to bitter tastes, potentially at the expense of perceiving other flavours and aromas. These insights suggest that the sensory experience of consuming rocket leaves is complex and influenced by multiple genetic factors. We propose including a wider range of taste receptor genotypes in sensory panels to account for the diverse dietary preferences and nutritional needs of different individuals in populations. Perhaps more simply and fundamentally, the ability of panellists to generate robust and reliable data with "real" foodstuffs (regardless of genotype) should be given a greater amount of consideration. Having an AVI/AVI genotype for *TAS2R38* bitterness perception does not mean that an individual is not sensitive to other sensations. Likewise a PAV/PAV-A/A individual may have a reduced ability to detect and describe aroma and flavour, as evidenced here. It may be that the approach for selecting assessors is food/drink specific, as some matrices are more complex than others, and it is clear that there is no "one-size fits all" approach for every foodstuff. This more considered approach can help ensure that foods are both nutritious and enjoyable for everyone, and acknowledge the evolutionary trade-offs in human taste perception that exist within populations.

Supplementary material

Supplementary material is available at *International Journal of Food Science and Technology* online.

Data availability

The datasets supporting the conclusions are included within the article (and its additional files). *Eruca* transcriptome data can be accessed and downloaded from the University of Reading Research Data Archive (https://doi.org/10.17864/1947.000458). *Eruca* reference sequence and annotation data are available via the European Nucleotide Archive (project PRJEB50993, accession number GCA_932364175). Additional *Eruca* genome, transcriptome, and annotation information is available from LB upon request.

Author contributions

Luke Bell (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Funding acquisition [supporting], Investigation [equal], Methodology [equal], Supervision [supporting], Validation [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Martin Chadwick (Data curation [supporting], Formal analysis [equal], Investigation [equal], Supervision [supporting], Writing—original draft [supporting], Writing—review & editing [equal]), Manik Puranik (Data curation [supporting], Formal analysis [equal], Investigation [supporting], Writing—review & editing [supporting]), Anne Hasted (Data curation [supporting], Formal analysis [supporting], Software [supporting]), Richard Tudor (Project administration [supporting], Supervision [supporting]), Lisa Methven (Conceptualization [equal], Data curation [supporting], Formal analysis [supporting], Funding acquisition [supporting], Investigation [supporting], Methodology [equal], Supervision [supporting], Validation [supporting], Writing—original draft [supporting], Writing—review & editing [supporting]), and Carol Wagstaff (Conceptualization [equal], Funding acquisition [lead], Project administration [lead], Supervision [lead], Writing—review & editing [supporting])

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Conflicts of interest

The authors declare the following interests/personal relationships which may be considered as potential competing interests: L.B. reports resources were provided by Bakkavor Ltd. (Spalding, UK) and Cultiva Europe Ltd. (Rome, Italy). R.T. is an employee of Elsoms Seeds Ltd. The other authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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