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Fresh tomato specific fluctuations in the composition of lipoxygenase-generated C6 aldehydes

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Abstract

Linoleoyl and α-linolenoyl fatty acyl groups are converted to hexanal and hexenal ((Z)-3-hexenal and (E)-2-hexenal), respectively, on the maceration of tomato fruits. These C6 aldehydes greatly contribute to the mix of volatile compounds which determines the flavour of the tomato. Cherry and standard fresh tomatoes were used to study the relationship between fatty acid composition of the intact fruit and the C6 aldehydes produced on maceration. The cherry tomato (var. Cherry Belle) had approximately twice as much α-linolenic acid as the standard tomato (var. Solairo). The enrichment of α-linolenic acid in the cherry tomato compared to the standard tomato was not evenly distributed between the major lipid classes (neutral lipids, glycolipids and phospholipids) but was prominent in the neutral fraction. The linoleic/α-linolenic acid ratio in the cherry and standard tomatoes was 1.75 and 4.1, respectively; this was reflected but not matched by the hexanal/hexenal ratio on macerating these tomatoes (0.1 and 0.27, respectively). Analysis of volatile compounds on macerating tomato fruits was extended to 14 other commercially available varieties which were nominally split into 'cherry' (50 g average fruit weight and below) and 'standard' (average fruit weight above 50 g) tomatoes. Hexanal/hexenal ratios were remarkably different between 'cherry' (0.05–0.1) and 'standard' (0.14–0.27) tomatoes. The concept of increasing α-linolenic acid levels in tomatoes to increase desirable flavour is discussed.

Keywords: Lipoxygenase; Hexanal; Hexenal; Tomato flavour; Lipids; Linoleic acid; α-Linolenic acid

1. Introduction

Volatile molecules derived from lipoxygenase (LOX) activity during tomato fruit maceration are recognised as important factors in determining the flavour quality of the fruit (Buttery, Teranishi, & Ling, 1987). The amounts generated vary substantially between individual tomato fruits (Brauss, Linforth, & Taylor, 1998). These are real differences as they have been reported by several authors (using different methods) and the variation is outside experimental error. This variation in volatile production is sufficiently large to cause a variation in flavour perception and therefore it becomes a consumer issue. What is less clear is the cause of this variation in the LOX-generated volatiles. The pathway for the production of LOX-generated volatiles is well established; therefore causes of tomato specific variations can be postulated. If the cause could be identified then steps could be taken to produce tomatoes with consistent flavour qualities.

During tomato fruit maceration, linoleic acid and α-linolenic acid derived from glycerolipids are converted to the C6 aldehydes, hexanal and (Z)-3-hexenal, respectively. The latter can be isomerised in situ to (E)-2-hexenal and so a mix of these aldehydes and the corresponding alcohols, formed from the aldehydes by the action of alcohol dehydrogenase (ADH), often exists. Work by Kazeniac and Hall (1970), using crude tomato fruit homogenates and exogenous α-linolenic acid, established that this tri-unsaturated fatty acid was the precursor of (Z)-3-hexenal and (E)-2-hexenal. This observation was confirmed when Stone, Hall, and Kazeniac (1975) injected radio-labelled α-linolenic acid into the stems of tomato plants and followed the generation of radio-labelled volatiles on fruit homogenisation 24 h later. These workers used the same experimental strategy to identify the volatile compounds generated from linoleic acid and concluded that hexanal was the major product.

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Two years later, Galliard and Matthew (1977) combined elements of both of the previous studies when they added radio-labelled linoleic and α-linolenic acids to tomato fruit homogenates and followed the production of radio-labelled volatile compounds. The previously described precursor/product relationships were confirmed; furthermore, intermediate hydroperoxides of the radio-labelled fatty acids were identified. Both polyunsaturated fatty acids were converted to 9- and 13-hydroperoxides but only the latter appeared to be converted to volatile aldehydes. The net result is a predominance of C6 aldehydes over C9 aldehydes on macerating tomato tissue. In the same year Galliard, Matthew, and Fishwick (1977) completed an overall picture of the generation of C6 aldehydes from tomato fruit tissue when they followed the change in endogenous lipids which occurred on the maceration of tomato fruit tissue. Although their method of lipid analysis was crude, they observed that glycoglycerolipid and glycerophospholipid levels were reduced, together with a measurable drop in total polyunsaturated fatty acid levels on macerating tomato fruit tissue. Their proposed scheme for the production of LOX-generated flavour volatile compounds from tomato fruits is shown below.

Recent attempts to increase our understanding of this pathway in tomatoes have used molecular biology to: study the role of alcohol dehydrogenase (ADH) (Prestage et al., 1998), change the level of unsaturated fatty acids by altering the activity of the Δ^9-desaturase enzyme (Wang et al., 1996), and to alter the expression of lipoxygenase genes (Kausch and Handa, 1997). Biochemical studies on lipoxygenase (Regdel, Kuhn, & Schewe, 1994) and lipoxygenase/hydroperoxide lyase (Riley, Willemot, & Thompson, 1996) have also been reported.

From Fig. 1 several sources of variation in the volatiles generated from LOX activity can be postulated: e.g. substrate concentration; physical state of the fatty acid substrate (monomeric or micellar); and activity of the various enzymes. The work described in this paper tests the importance of tomato fruit fatty acyl composition in predetermining the composition of the C6 aldehydes produced on tissue maceration.

2. Materials and methods

2.1. Selection of tomato varieties

Fresh tomatoes (16 varieties) were provided by Sainsburys: Yellow cherry; Favorita; Gardeners delight; Sungold; Cherry Belle; 8900; Manhattan; Flavia; Colbridge Pronto; Vitador; Evn Pronto; Plum; Ferrari; Solairo; Momotara; Beef Trust. The average fruit weight ranged from 8 g (Yellow cherry) up to 249 g (Beef Trust). Tomatoes with an average weight below 50 g were classified as 'cherry' tomatoes.

2.2. Lipid extraction

Tomatoes (70 g) were cut in half, the seeds removed and then heated in a microwave oven (600 W) on full power for 3.5 min to minimise the action of lipid metabolic enzymes during lipid extraction. A portion of the treated tomato tissue (2 g) was then homogenised with internal standard (0.2 mg methylpentadecanoate) in an Ultraturrax blender (Ika) with methanol (20 ml) for 30 s. Chloroform (40 ml) was then added and the homogenisation process continued for a further 2 min. The mixture was then filtered and washed (×2) with chloroform/methanol (2:1, v/v; 60 ml). Filtrates were

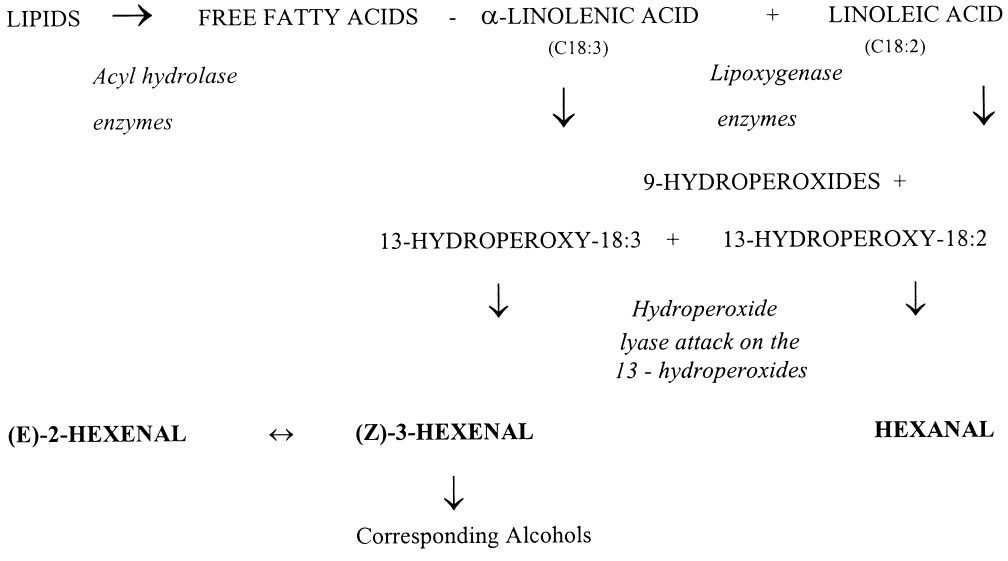

Fig. 1. Pathway for the generation of C6 aldehydes during tomato fruit maceration.

combined and 0.88% KCl added (one quarter of the total filtrate volume). This mixture was vigorously shaken and allowed to settle for 10 min. The lower layer (containing the lipid material) was recovered and washed with a water/methanol (1:1) mix (one quarter of the lower phase volume). The lower layer was recovered and washed again. Finally, the lower lipid-containing layer was reduced to 1 ml using a stream of nitrogen and stored under nitrogen at −20°C until required for analysis.

2.3. Lipid separation

The extracted lipids were fractionated on Sep-Pak silica cartridges (Waters Association) into neutral lipids, glycolipids and phospholipids (Glass, 1990). Two cartridges (both washed with 15 ml chlorofrom) were connected in series and the lipid extract (dissolved in 2 ml chloroform) carefully loaded onto the solid phase extraction matrix with a Hamilton syringe. Eluting solvents were then delivered to the cartridges through a 10 ml syringe at a constant flow rate (2 ml min^{-1}) through a syringe pump system. Major lipid classes were eluted in sequence as follows: neutral lipids (20 ml of chloroform); glycolipids (20 ml of chloroform containing 15% methanol); and phospholipids (20 ml methanol).

2.4. Fatty acid analysis

A portion of the total lipid extract or the fractionated lipids was dissolved in $CHCl_3$ (7 ml) and 2.5 ml of methanolic HCl, 0.5 ml of 2,2-dimethoxypropane and 0.2 mg of heptadecanoic acid (internal standard) were added. The sample was left overnight and $NaHCO_3$/Na_2CO_3/Na_2SO_4 (2:1:2; 1 g) was added. After 30 min, the solution was filtered. A 2:2:0.8 ratio of $CHCl_3$:CH_3OH:H_2O was required; therefore 4.5 ml of CH_3OH and 2.8 ml of water were added and left for at least 30 min. A portion of the lower organic layer (250 μl) was concentrated to 50 μl under nitrogen and 1 μl was injected into the GC–FID for fatty acid analysis.

2.5. Headspace sampling

Fruit (100 g) was macerated in a stomacher machine (Seward M50-110, London) with internal standard (2.5 μg of 2-octanone in 100 μl water) for 2 min. After maceration, headspace was collected onto a Tenax trap, (CHIS, SGE, Milton Keynes, UK) at 75 ml min^{-1} for 20 s using a vacuum pump. The trap was then removed and the volatiles analysed by GC–MS as described below.

2.6. Chromatographic conditions

Tenax traps were desorbed in a headspace injector (CHIS, SGE) connected to a Hewlett–Packard 5890 Series II gas chromatograph (column head pressure 18 psi, helium carrier gas). The volatiles were desorbed from the traps (3 min, 240°C) and cryofocused onto a 400 mm region of the column (BP-1, 25 m×0.22 mm ID, 1 μm film thickness; SGE). After desorption, the column was held at 40°C (2 min), then temperature-programmed from 40 to 106°C at 4°C min^{-1} and from 106 to 145°C at 15°C min^{-1}. Compounds were detected using a MD 800 mass spectrometer operating in the scan mode over the m/z range 30 to 250 (Fisons Scientific, Manchester, UK).

2.7. GC–MS data analysis

The relative amounts of compounds were determined by integrating peak areas for characteristic ions of the volatiles of interest at the appropriate LRI values. This method allowed quantification of low levels of volatile as the characteristic ions chosen gave the best signal to noise ratio. Peak areas were corrected for chromatographic and sampling variation by reference to the Internal Standard (IS) according to the equation below. Peak areas were therefore expressed as a percentage of the IS per 100 g fresh weight:

$$\frac{\text{Peak area} \times 50 \times 100 \text{ (normalisation factor)}}{\text{Peak area of internal standard} \times \text{actual weight of fruit (in g)}}$$

2.8. Data analysis

Unless otherwise stated, average values were obtained from four replicates and the standard error on the means calculated. Unpaired t-tests were used to measure the significant difference between results obtained from cherry and standard tomatoes.

3. Results and discussion

3.1. Total fatty acid (fatty acyl) analysis from standard (var. Solairo) and cherry (var. Cherry Belle) tomatoes

Total fatty acyl concentration values obtained in this study (Table 1) are similar to previously quoted values (Galliard et al., 1977). Statistical analysis of the data (unpaired t-test) gives $p = 0.32$. H_0 (the null hypothesis, i.e. there is no difference in the total concentration of fatty acyl groups in the cherry and standard tomatoes) is retained. This indicates that the total masses of fatty acyl groups per unit fresh weight within cherry and standard tomatoes are comparable and so justifies the use of percentage values when comparing the levels of individual fatty acyl groups in both tomatoes (Fig. 2). From these data it can be seen that, in both cherry and

Table 1
Concentration of fatty acyl groups in cherry (var. Cherry belle) and standard (var. Solairo) tomatoes

Tomato type	Total fatty acyl amount (mg kg^{-1}) fresh weight (±SE)
Cherry (var. Cherry Belle)	621 (±63.5)
Standard (var. Solairo)	513 (±77.0)

Table 2
Relative composition of the major fatty acids in (var. Cherry Belle) and standard (var. Solairo) tomatoes

Tomato type	Average % 18:2	Average % 18:3	Average ratio 18:2/18:3 (±SE)
Cherry	32.3	18.8	1.75 (±0.15)
Standard	43.5	11	4.1 (±0.39)

standard tomatoes, the relative composition of the major fatty acids is 18:2 > > 16:0 > 18:3 = 18:1 > > 18:0. Despite these similarities in the overall pattern of fatty acid composition, α-linolenic acid levels are greater in cherry tomatoes, and the standard tomato contains higher levels of linoleic and stearic acids.

Differences in the amounts of linoleic and α-linolenic acids between the cherry and standard tomatoes are further highlighted in Table 2. Statistical analysis of the data (unpaired *t*-test) gives $p = 0.0015$. H_0 (the null hypothesis, i.e. there is no difference in the ratio of linoleic to α-linolenic fatty acids between cherry and standard tomatoes), can be rejected. Clearly there is a significant difference in the ratio of linoleic: α-linolenic acids between cherry and standard tomatoes.

3.2. Fatty acyl composition of major lipid groups in cherry and standard tomatoes

Lipids were extracted and fractionated from cherry (var. Cherry Belle) and standard (var. Solairo) tomatoes and the major lipid groups separated by solid phase separation. Fatty acyl groups were derivatised, then resolved and quantified by GC. Relative levels of total fatty acyl amounts in the major lipid groups are shown in Fig. 3. Statistical comparisons of the levels of total fatty acyl amounts in each major lipid group revealed no significant differences. A similar pattern of fatty acyl levels between the major lipid groups in both cherry and standard tomatoes is therefore evident; neutral lipids contained the most fatty acyl moieties, followed by phospholipids and then glycolipids.

Further analysis of these fractions (Table 3) revealed some evidence that α-linolenic acid was enriched in the neutral lipid fraction and oleic acid in the phospholipid fraction in cherry tomatoes compared to the equivalent fractions in the standard tomato. In addition, standard tomatoes were enriched with linoleic acid in the

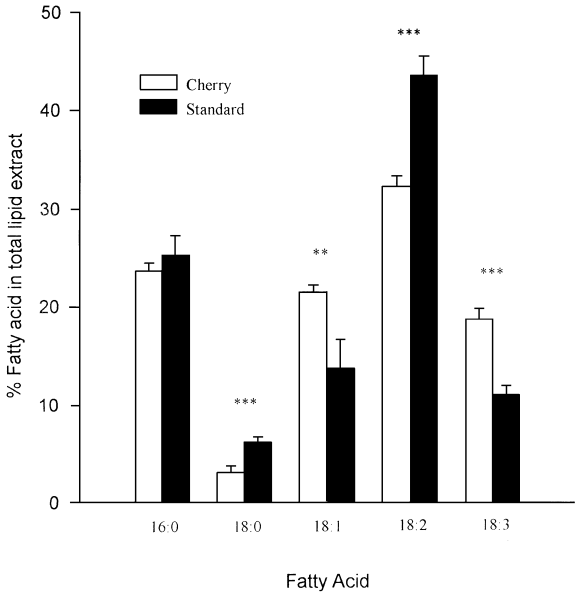

Fig. 2. Relative composition of the major fatty acids in cherry (var. Cherry Belle) and standard (var. Solairo) tomatoes. ** Significant at the 5% level; *** significant at the 1% level.

phospholipid fraction compared to the same fraction in cherry tomatoes.

A comparison between results from the present work and results from Galliard et al. (1977) shows a similarity in the total acyl mass present (50–60 and 48 mg 100 g^{-1} Fwt, respectively). Relative amounts of neutral lipid (N), glycolipid (G) and phospholipid (P) classes are, however, different. Care is required when making these comparisons because Galliard et al. (1977) quote total lipid masses whereas the current work deals with the relative amounts of fatty acyl moieties found in each lipid class. This notwithstanding, it can be calculated that the ratio of G:P fatty acyl groups from Galliard is 1:3 compared to 1:2.3 in the present study. A comparison between the neutral fractions is less straightforward, but if one assumes that our neutral fraction is made up of sterols, acylated sterols, cerebrosides, TAG and DAG (as shown in the more detailed lipid analysis of cucumber tissue by Fishwick, Wright, & Galliard, 1977) then one might expect to observe 1:2.2 fatty acyl groups (N:P) compared to our result of 3.5:2.3 (or 1:0.66). Guclu, Paulin, and Oudain (1989) show, clearly, that the level of phospholipids falls dramatically over a short period (1–3 days) on entering the ripe phase. We should therefore not be surprised to observe variability in lipid compositional data in published work.

3.3. Comparison between the levels of (Z)-3-hexenal, (E)-2-hexenal and hexanal generated on macerating a wide range of tomatoes

If there is a simple direct correlation between the composition of precursor fatty acids and the C6 volatile

Table 3
Percentage fatty acyl composition of the major lipid groups in cherry (var. Cherry Belle) and standard (var. Solairo) tomatoes

Major lipid group	Tomato type	Average % fatty acyl composition (±SE)				
		16:0	18:0	18:1	18:2	18:3
Neutral	Cherry	20.2 (±1.8)	7.3 (±2.6)	29.5 (±4.4)	33.0 (±4.1)	10.0 (±2.0)**
	Standard	19.3 (±1.7)	10.8 (±2.8)	24.8 (±2.3)	42.0 (±3.2)	4.0 (±0.4)
Glycolipid	Cherry	28.3 (±3.5)	14 (±2.0)	18.8 (±3.5)	21.5 (±2.4)*	16.8 (±2.8)
	Standard	26.0 (±3.7)	12.3 (±2.0)	19.7 (±2.7)	28.3 (±2.4)	15.3 (±1.8)
Phospholipid	Cherry	25.5 (±1.0)*	7.1 (±2.0)	21.5 (±1.2)***	33.8 (±2.8)**	14.0 (±2.8)
	Standard	27.8 (±0.5)	5.1 (±1.8)	11.3 (±1.7)	43.0 (±2.4)	13.0 (±1.0)

* Significant at the 10% level; ** significant at the 5% level; *** significant at the 1% level.

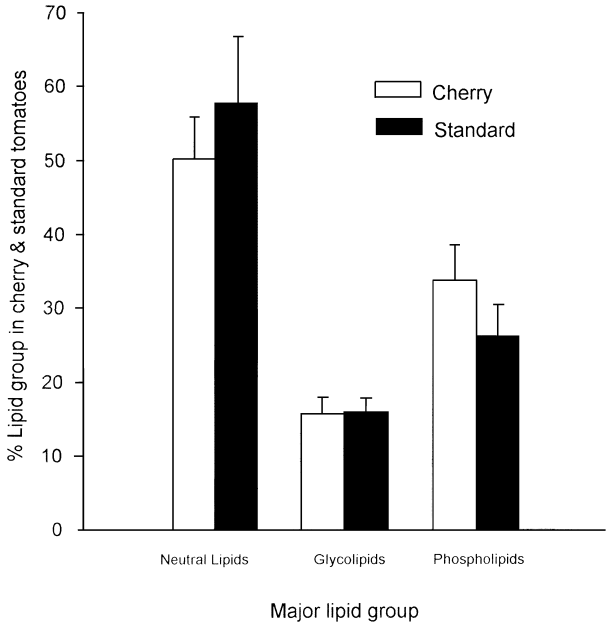

Fig. 3. Relative composition of the major lipid groups in cherry (var. Cherry Belle) and standard (var. Solairo) tomatoes

Table 4
Relationship between tomato fruit fresh weight and the ratio of C6 aldehydes produced on tissue maceration

Tomato variety	Average mass (g)	Ratio of C6 aldehydes (hexanal/hexenal)
Yellow Cherry	8	0.09
Favorita	10	0.10
Gardener's Delight	10	0.06
Sungold	12	0.10
Cherry Belle	14	0.10
89001	15	0.05
Manhattan	19	0.10
Flavia	30	0.08
Colbridge	59	0.17
Vitador	75	0.27
Evn Pronto	76	0.21
Plum	76	0.17
Ferrari	77	0.19
Solairo	85	0.27
Momotara	228	0.14
Beef Trust	249	0.28

Fruit (100 g) was macerated in a stomacher machine for 2 min and the headspace volatiles analysed by GC–MS.

molecules produced on tomato fruit maceration, then one would expect the ratio of linoleic acid:α-linolenic acid to be equivalent to the ratio of hexanal:hexenal ((Z)-3-hexenal + (E)-2-hexenal). A comparison between the fatty acid ratios (Table 3) and the C6 aldehyde ratios (Table 4), for Cherry Belle and Solairo tomatoes, reveals that such a correlation does not exist.

Further inspection of these data does, however, reveal a relationship between the relative sizes of these ratios. The standard tomato has approximately twice the fatty acid ratio and three times the C6 aldehyde ratio as the cherry tomato. In short, the relative amounts of hexanal and hexenals produced in macerated tomato fruits crudely reflects (but does not match) the relative composition of their precursor fatty acids, linoleic and α-linolenic acids, respectively.

In total, 16 varieties of tomatoes were homogenised in the headspace analysis investigation. The tomatoes were grouped into cherry and standard varieties on the basis of weight (over 50 g is classified as a standard tomato). A striking difference in the hexanal:hexenal ratio can be observed (Table 4). Furthermore, the majority of the predominant hexenal portion in the headspace is composed of (Z)-3-hexenal (5–14×more concentrated than (E)-2-hexenal). Statistical analysis of the data (unpaired *t*-test) gives $p = 0.000021$. H_0 (the null hypothesis, i.e. there is no difference in the ratio of C6 aldehydes produced from cherry and standard tomatoes) can be rejected. Clearly there is a difference with standard tomatoes producing on average a hexanal:hexenal ratio which is 2.5×greater than that produced by cherry tomatoes.

When the data are plotted in terms of the amount of C6 aldehyde released compared to the mean weight of each tomato fruit variety (Fig. 4a–c) a further observation can be made. The concentration of both hexenal isomers, (Z)-3-hexenal and (E)-2-hexenal, in the headspace, increases with decreasing tomato size/mass.

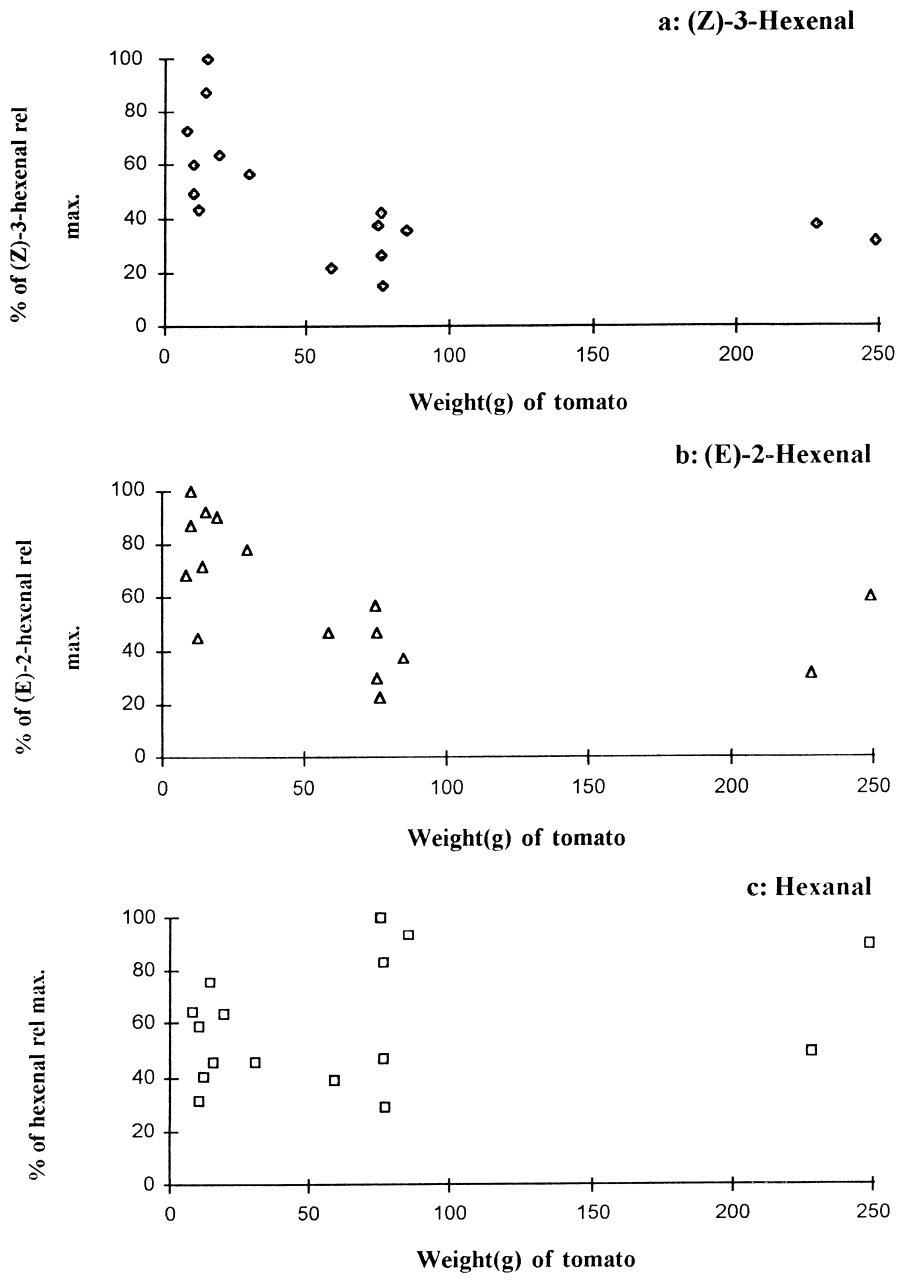

Fig. 4. Relationship between the amount of C6 aldehydes generated on maceration and the average fresh weight of the tomato fruit. All 16 varieties of fruit (100 g) were each macerated in a stomacher for 2 min and the headspace volatiles analysed by GC–MS. Percentage C6 aldehyde values were calculated relative to the maximum amount of that C6 aldehyde measured over the range of tomatoes studied.

Hexanal production appears to be less clearly related to tomato mass.

The fact that there is no equivalent overall increase in all of the lipid degradation products suggests that the lipid degradation pathway is specific, showing that there are differences in the metabolism of the linoleic and α-linolenic fatty acids. It has been reported that, during chilling of tomato fruits, certain acyl hydrolase enzymes preferentially cleave more highly unsaturated fatty acyl groups from lipid backbones (Whitaker, 1993; L'Heureux, Bergevin, Thompson, & Willemot, 1994). The action of these or similar enzymes during tomato fruit tissue maceration is suggested from the work by Galliard et al (1977). They reported similar acyl compositional data as reported here for the cherry tomatoes; on tissue homogenisation (duration not clear) almost 2.7× as much α-linolenic acid was lost compared to linoleic acid (current authors calculations).

The difference in the acyl composition between the cherry and standard tomatoes is not distributed evenly throughout the lipid classes (Table 3). Instead a specific

enrichment of α-linolenic acid in the neutral lipid fraction of cherry tomatoes was observed. On the other hand, the variation in the levels of oleic and linoleic acids are accentuated in the phospholipid fraction. It is possible that acyl hydrolase enzymes are stimulated during tomato fruit maceration, which are not only selective for highly unsaturated fatty acyl groups, but are particularly active with neutral lipid substrates. Galliard et al. (1977) reported that the neutral lipids, sterol lipids and cerebrosides remained intact during tomato fruit homogenisation but that the amount of triaclyglycerol (when present) was dramatically reduced.

4. Conclusion

A comparison of the ratio of linoleic acid:α-linolenic acid, present in the intact fruit of cherry (var. Cherry Belle) and standard (var. Solairo) tomatoes, to the ratio of hexanal:hexenal, generated on macerating these fruits, revealed a significant difference. Relative to their corresponding fatty acyl precursors, hexenal production was favoured over hexanal production in both tomato types. Assuming the absence of any interconversion between hexenals and hexanal, a selective lipid metabolic route must exist which preferentially metabolises α-linolenoyl moieties over linoleoyl ones.

Cherry (var. Cherry Belle) tomatoes contained approximately twice as much α-linolenic acid as standard (var. Solairo) tomatoes. The distribution of this increase in α-linolenic acid was not equivalent across the major lipid classes but was particularly apparent in the neutral lipid fraction. Although the direct increase in α-linolenic acid composition of tomatoes may be a strategy to increase the flavour quality of tomatoes in general, as has been suggested by Wang et al. (1996), one must also consider the importance of directing the α-linolenic acid into specific complex lipids so that the selective metabolic pathway(s) is (are) provided with the precise substrates required.

Further work, to characterise the action of selective acyl hydrolase enzymes in ripened tomato fruit and to analyse the detail of acyl composition and distribution between individual lipid molecules, would provide crucial information for any genetic modification strategies designed to enhance the flavour of tomatoes.

References

Brauss, M. S., Linforth, R. S. T., & Taylor, A. J. (1998). Effect of variety, time of eating and fruit-to-fruit variation on volatile release during eating of tomato fruits (*Lycopersicon esculentum*). *Journal of Agricultural and Food Chemistry*, *46*, 2287–2292.

Buttery, R. G., Teranishi, R., & Ling, L. C. (1987). Fresh tomato aroma volatiles: a quantitative study. *Journal of Agricultural and Food Chemistry, 35*, 540–544.

Fishwick, M. J., Wright, A. J., & Galliard, T. (1977). Quantitative composition of the lipids of cucumber fruit (*Cucumus sativus*). *J. Sci. Food Agric., 28*, 394–398.

Galliard, T., & Matthew, J. A. (1977). Lipoxygenase-mediated cleavage of fatty acids to carbonyl fragments in tomato fruits. *Phytochemistry, 16*, 339–343.

Galliard, T., Matthew, J. A., & Fishwick, M. J. (1977). The enzymic breakdown of lipids to volatile and non-volatile carbonyl fragments in disrupted tomato fruits. *J. Sci. Food Agric., 28*, 863–868.

Glass, R. L. (1990). Separation of phosphatidylcholine and its molecular species by high performance liquid chromatography. *Journal of Agricultural and Food Chemistry, 38*, 1684–1686.

Guclu, J., Paulin, A., & Soudain, P. (1989). Changes in polar lipids during ripening and senescence of cherry tomato (*Lycopersicon esculentum*): relation to climacteric and ethylene increases. *Physiology of Plants, 77*, 413–419.

Kausch, K. D., & Handa, A. K. (1997). Molecular cloning of a ripening-specific lipoxygenase and its expression during wild-type and mutant tomato fruit development. *Plant Physiology, 113*, 1041–1050.

Kazeniac, S. J., & Hall, R. M. (1970). Flavour chemistry of tomato volatiles. *Journal of Food Science, 35*, 519–530.

L'Heureux, G. P., Bergevin, M., Thompson, J. E., & Willemot, C. (1994). Molecular species of phosphatidylcholine, phosphatidylethanolamine and diglycerides of tomato pericarp during ripening, chilling and subsequent storage. *Journal of Plant Physiology, 143*, 699–703.

Prestage, S., Linforth, R. S. T., Taylor, A. J., Lee, E., Speirs, J., & Schuch, W. (1998). Volatile production in tomato fruit with modified alcohol dehydrogenase activity. *J. Sci. Food Agric.* (submitted).

Regdel, D., Kuhn, H., & Schewe, T. (1994). On the reaction specificity of lipoxygenase from tomato fruit. *Biochim. Biophys. Acta, 1210*, 297–302.

Riley, J. C. M., Willemot, C., & Thompson, J. E. (1996). Lipoxygenase and hydroperoxide lyase activity in ripening tomato fruit. *Postharvest Biology and Technology, 7*, 97–107.

Stone, E. J., Hall, R. M., & Kazeniac, S. J. (1975). Formation of aldehydes and alcohols in tomato fruit from U-14C-labeled linolenic and linoleic acids. *Journal of Food Science, 40*, 1138–1141.

Wang, C. L., Chin, C. K., Ho, C. T., Hwang, C. F., Polashock, J. J., & Martin, C. E. (1996). Changes of fatty acids and fatty acid-derived flavour compounds by expressing the yeast (9-desaturase gene in tomato. *Journal of Agricultural and Food Chemistry, 44*, 3399–3402.

Whitaker, B. D. (1993). Lipid changes in microsomes and crude plastid fractions during storage of tomato fruits at chilling and non-chilling temperatures. *Phytochemistry, 32*, 265–271.