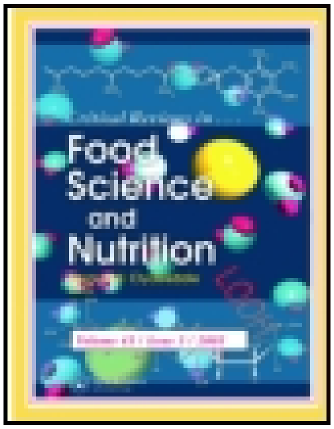

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Multi-Scale Biomechanics of Tomato Fruits: A Review

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Multi-scale biomechanics of tomato fruits: A review

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Abstract

Bruising and other mechanical damage to fruit caused by external forces during and post-harvesting is manifested at the macro scale but is ultimately the result of failure of cells at the micro scale. However, fruits have internal structures and cells from different tissue types react differently to application of an external force. Not much is known about the effects of such forces on single cells within tissues and one reason for this is the lack of multi-scale models linking macro- (organ or whole fruit), meso- (tissue) and micro- (cell) mechanics. This review concerns tomato fruits specifically as this is an important crop and is an excellent exemplar of past and proposed research in this field. The first consideration is the multi-scale anatomy of tomato fruits that provides the basis for mechanical modeling. The literature on experimental methods for studying multi-scale mechanics of fruit is then reviewed, as are recent results from using those methods. Finally, future research directions are discussed, in particular the combination of work over all scales. It is clear that a bottom-up approach incorporating single cell mechanics in finite element models of whole fruit assumed to have internal structures is a promising way forward for tomato fruits but further method developments may be needed for these and other fruits and vegetables, in particular recovery of representative single cells from tissues for mechanical characterization.

Keywords: Tomato fruits; Anatomy; Multi-scale biomechanics; Mechanical damage; Biomaterial

1 Introduction

The fruits of tomato (*Solanum lycopersicum*, with common synonyms *Lycopersicon esculentum* and *Lycopersicon lycopersicum*) are important in the human diet, as shown by data from the Food and Agriculture Organization of the United Nations that world production of tomato fruits was more than 120 million tons in 2010 (FAOSTAT, 2012). Harvesting, packaging and transport of tomato fruits are essential processes between crop production and sales to consumers but immediate and latent damage resulting from such processing can cause a rapid reduction in quality such as visible bruising (Van linden *et al*., 2008). Mechanical damage to fruit, manifested at the macro scale, is caused by failure of cells at the micro scale, although cells from different tissue types react differently to external forces. Thus, an apparently simple damage process is closely related to the macro- (organ or whole fruit), meso- (tissue) and micro- (cell) mechanics of the fruit (Fig. 1).

There have been some reviews in this field. For example, Bruce (2003), Pelling *et al*. (2008) and Geitmann *et al*. (2009) reviewed the measurement and mathematical modeling of plant cell mechanics. Genard *et al*. (2007) and Mebatsion *et al*. (2008) proposed a general system of organization for a virtual fruit and reviewed how fruit micro-structures might be modeled. Ho *et al*. (2013) overviewed the current paradigm of multi-scale modeling and numerical techniques for multi-scale analysis in food engineering. More, specifically, Dominguez *et al*. (2011) reviewed plant cuticle biomechanics during growth. Overall, however, it seems that not much is known about how to relate the mechanics of tomato fruits across the scales and therefore how external forces applied to tomato fruits cause damage to single cells within the tissues. Therefore, investigating the multi-scale mechanical behavior of tomato fruits is clearly an important issue. The objective of this paper is to review the literature on multi-scale anatomy and mechanics of tomato fruits and to discuss future research requirements.

2 Multi-scale anatomy of tomato fruits

2.1 Macro- and meso-anatomy

Botanically, a tomato fruit is the ovary of a flowering plant and as a fleshy fruit produced from a single ovary, it is technically a berry. Although the size and weight of tomato fruits increase during their development (at different rates for different varieties), typical sizes might be exemplified by data from Li *et al.*, 2011a in which the height, diameter and volume of tomato fruits (variety *Jinguang*28) at the light-red ripening stage varied from about 57 to 71 mm, 64 to 83 mm, and 120 to 215 cm^3, respectively. The sphericity varied from 90 to 99%.

Cultivated tomato fruits always have 3 to 8 locules (Li *et al.*, 2011b); a locule is a chamber within an ovary full of liquid and seeds. Three and four locular tomato fruits are most common and are always chosen for investigating fruit mechanics. Examples can be seen in Fig. 2. Three locular tomato fruits represent those having an asymmetric internal structure (odd number of locules) whilst four locular tomato fruits represent internally symmetric fruits. Each tomato fruit is a hierarchically structured material at the macro scale, consisting of different types of tissue i.e.

the exocarp, mesocarp, endocarp and locular gel tissue at the meso scale. The fruit shoulder corresponds to exocarp tissue over the locule. The valley between two adjacent fruit shoulders on the fruit surface, which spreads obviously from stem base to blossom end, corresponds to exocarp tissue over the cross wall (Li *et al*., 2010).

2.2 Micro-anatomy

Each tissue in a tomato fruits is a highly structured arrangement of cells at the micro scale. For instance, the exocarp (skin) tissue is mainly composed of 2 or 3 hypodermal cell layers in which the cell wall is thick (0.66 to 4.40 εm has been reported for five different tomato cultivars by Borowiak and Habdas (1988)). This is covered with a non-living layers of waxes and lipids called the cuticle (Lopez-Casado *et al*., 2010; Kosma *et al*., 2010). Although different in different varieties (Matas *et al*., 2004), the thickness of these exocarp cell layers does not change significantly during fruit development and is about 36 εm (*L. esculenlentum* Mill. *wild type* & *flacca*; Rancic *et al*., 2010). Fruit exocarp is a protective tissue and its main functions include moderating gas exchange between fruit tissues and the surrounding environment and protecting internal tissues from excessive water loss, mechanical injury and attack by external weather, diseases and insects (Diaz-Perez *et al*., 2007). Inside the exocarp is the mesocarp which is made from large thin walled cells and vascular tissue. The number of mesocarp cell layers is constant during fruit development at about 15 or 16 layers but cell growth results in great increases in mesocarp thickness (Rancic *et al*., 2010), providing most of the edible flesh of the tomato fruit.

For ripe tomato fruits (*L. esculentum* variety *vf*36), the mean value of the height of ñinnerò pericarp (i.e. mesocarp) cells was found to be 372 ± 7 εm with a mean ratio of height to width of 0.81 (Wang *et al.*, 2006). As is easily observed, tomato fruits gradually become red during ripening. It has been found that during most of the ripening period (from mature-green to red), chlorophylls drastically decreased in both exocarp and mesocarp whilst lycopene increased significantly and ϐ-carotene, ɔ-carotene and lycopene-epoxide increased slightly (Carrillo-López & Yahia, 2012), causing the color changes.

Inside the mesocarp is the endocarp, which is a unicellular layer bounding the locular cavities. Cell growth also results in increasing endocarp thickness (cell size) but overall increases in pericarp thickness during fruit development are mainly due to the changes in the mesocarp mentioned earlier. Together the mesocarp and endocarp are the nutritive tissues of tomato fruits and that is their main function. Chambers within the mesocarp called ñlocular cavitiesò contain the seeds in a gel.

Representative scanning electron micrographs of tomato exocarp, mesocarp and locular gel tissues at the light-red ripening stage are shown in Fig. 3. These show that the cell size is the smallest and the cell arrangement most compact in exocarp tissue while the cell size is largest in locular gel tissue. As discussed later, the resistance of exocarp tissue to external forces is much larger than that of the inner tissues because the cells in the former are so compact (*L. esculenlentum* Mill. *Harzfeuer* & *Vanessa F*1 & *Roma*, Bargel & Neinhuis, 2005; *Solanum* *lycopersicum Jinguang*28, Li *et al*., 2012a). In contrast, pericarp cells at the ripening stage are not only large and variable in size and shape but are only loosely attached to one another, so mechanical separation by a gentle process is feasible (Wang *et al*., 2004).

3 Multi-scale mechanics of tomato fruit

3.1 Determination of multi-scale mechanics

Whole fruit mechanics are generally determined by compression testing (Sirisomboon *et al*., 2012). In this method, a fruit is compressed to rupture between the metal base plate and the moving parallel plate of an instrument such as a texture analyzer. Force-deformation curves are recorded in real time during loading (Babarinsa & Ige, 2012). Mechanical parameters such as peak force, rupture energy and compressibility can be extracted directly from the curves (Li *et al*., 2011a). Other parameters such as (whole fruit) elastic modulus and failure stress can be calculated by applying Hertz Theory, assuming the fruit is an elastic homogeneous sphere. The Poisson ratio of three (cherry) tomato varieties (e.g. *Mosaica F*1, *Zucchero F*1, 1018 *F*1) has also been calculated from height and diameter changes during deformation and the result varied from 0.22 to 0.35 (Kabas & Ozmerzi, 2008a). The Poisson ratio of tomato exocarp tissue (variety *Admiro*) was determined using uniaxial tensile test and the result showed from 0.45 to 0.47 at 21℃ (Gladyszewska *et al*., 2011).

At the meso-scale, a tomato fruit should regarded as a multi-tissue system (Matas *et al*., 2004; Matas *et al*., 2005), as shown clearly in Fig. 2. Because it is difficult to prepare realistic samples for biaxial testing, it is common for tissue samples to be excised from fruits and to be subjected to uniaxial tests. Standard tissue specimens of known dimensions are made according to ASTM D5379, E8, E9 and E290 standards (Alamar *et al*., 2008) and the mechanics determined by compression, tension, shear and bend testing using a texture analyzer (Li *et al*., 2012a). Force-displacement curves for the tissue specimens are recorded in real time and the standard mechanical parameters calculated. Typical values are shown in Table 1.

At the micro-scale, there have been few attempts to characterize the mechanical properties of single tomato fruit cells. However, single cell mechanics of isolated pericarp cells have been determined using high strain-rate micro-compression testing (Blewett *et al*., 2000). Force-deformation data were modelled to find cell wall material properties, assuming the cells could be considered to be liquid filled spheres filled with water and that water loss during the (very fast) compressions could be neglected. The cell walls yielded at about 2% wall strain and at lower strains the elastic moduli of the cell walls were found to be 30 to 80 MPa (Wang *et al*, 2006). This method can only be applied successfully to cells isolated from tissues (or suspension cultured cells, which do not represent fruit cells well). So far, such isolation has only been possible for mesocarp cells from ripe fruits (Wang *et al*, 2006).

Values of multi-scale mechanical parameters of tomato fruits from the literature are presented in Table 1.

3.2 Discussion of multi-scale mechanics

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There are some significant points that may be drawn from the data in Table 1 (although it must be accepted that the number of studies is small). Firstly, tomato fruits exhibit multi-scale mechanical characteristics. Some researchers have focused on macro-mechanics with the laudable aim of providing direct help to fruit handlers in choosing effective methods to prevent mechanical damage during harvesting, packaging and transport. Other researchers have focused on meso- and micro-mechanics with the aim of unravelling mechanical damage mechanisms at these scales. However, it is not yet possible to relate data from the different scales. This is because there is no real understanding of what is happening at the cellular, micromechanical level during macro-mechanical testing. Without such understanding, it possible that small changes in testing protocols might have large and inexplicable effects on the measurements, making comparison of results between laboratories or even between cultivars unreliable. Furthermore, little account is taken of significant differences between the various tissues in tomato fruits, despite obvious differences in the size and arrangement of cells within them.

Secondly, in Table 1, it can be seen that loading position had a significant effect on the macro-scale mechanical properties of half-ripe tomato fruits with an even number of locules. This factor has generally been neglected in studies previous to that of Li *et al*. (2011a) even though mechanical damage usually occurs as a result of impacts that might be fruit to fruit and/or fruit to objects such as a container, effectively with a range of loading positions. The loading position is therefore an essential factor in determining fruit macro-mechanics. This view is supported by other researchers (Van linden et al., 2006; Van Zeebroeck et al., 2007).

Thirdly, the mechanics depend on the variety, mainly because of different anatomical characteristics. Matas *et al*. (2004) and Hetzroni *et al*. (2011) noted an obvious effect of variety on the elastic modulus and strain-hardening rate of exocarp tissues between two tomato fruit varieties and proposed that this resulted from different exocarp thicknesses and cuticular membrane content in subepidermal cell layers. Devaux *et al*. (2005) proposed that changes in the rupture energy of pericarp tissue between two varieties resulted from different chemical composition and structure of the cell walls.

Finally, there is the effect of ripening that causes great changes in anatomical characteristics during fruit development (Section 2.2). Bargel and Neinhuis (2004) proposed that the ripening stage of tomato fruits had a significant effect on mechanical parameters such as the elastic modulus and strength and strain at failure of exocarp and cuticle membrane because of morphological changes during ripening (Bargel & Neinhuis, 2004, 2005). Sirisomboon *et al*. (2012) proposed that firmness, energy absorption, elastic modulus and rupture force were sensitive mechanical parameters for identifying maturity stages in tomato fruits because of softening. Babarinsa and Ige (2012) showed that ripeness of (Roma) tomato fruits had highly significant effects on stress and load at bioyield (when cells start to rupture or move with respect to their neighbours) because of reduction in turgor. The fact that variety has a significant effect on mechanical damage to tomato fruits is supported by other studies (Desmet *et al*., 2002;

Geitmann & Ortega, 2009). Furthermore, although some researchers have proposed that the storage time, temperature, humidity and harvesting date have significant effects on the mechanics of tomato fruits (Hertog *et al*., 2004; Matas *et al*., 2005), the main reason for these observations may be that the ripening was gradually occurring during storage. Ripening stage may be a good surrogate for all of these factors.

4 Multi-scale mechanical relationships

Developing multi-scale relationships between or (if possible) correlations of mechanical behavior from single cells through tissues to whole fruit is very important in investigating internal damage to fruit caused by external forces during mechanical handling. Previous investigations can be summarized in three categories.

4.1 Relationships between organ (fruit) mechanics and tissue mechanics

Kabas *et al*. (2008b) developed a finite element model of cherry tomato fruits (variety 1018 *F*1) to link organ (fruit) mechanics to tissue mechanics. For modeling, a fruit was regarded as a nearly spherical homogeneous solid consisting of a single tissue, whose deformation behavior upon drop crashing was simulated based on the mechanical parameters of whole fruit. It was shown that the maximum deformation of the fruit, initial diameter 30.5 mm and height 25.62 mm, was 4.33 mm when it was dropped from 237 mm and the maximum resulting Von Misses stress internally was 0.0529 MPa. A comparison between experimental data and finite element simulation shows that the two sets of results agree well. This interesting work might be criticized for the clearly unrealistic assumption of homogeneity but it does provide some indication of the internal stresses likely in a tomato fruit caused by an external force that might well be a consequence of handling.

Gao *et al*. (2008) developed a 2D finite element model consisting of six elongated two-force rods to relate fruit mechanics to skin mechanics. The relationship between applied external load, fruit deformation and skin stress were simulated using a finite element method. Skin stress showed a linear increase with external force but a nonlinear increase with the deformation of the fruit during compression. Although it is useful to understand the stress in the protective skin (cuticle) of a tomato fruit due to application of an external force, bruising and other mechanical damage is caused by rupture or relative movement of cells in the inner tissues (Van linden *et al*., 2008), which requires more extensive multi-scale modeling.

Li *et al*. (2012a) therefore proposed that a *Fenguan906* tomato fruit should be considered as a multi-tissue system that consists of different types of tissues i.e. the exocarp, mesocarp and locular gel tissues. A multi-scale, nonlinear, finite element model was developed to relate whole fruit to multi-tissue mechanics for a three locular fruit. The deformation and progression of damage of the different tissues when a fruit is subjected to an external force of 37 N (Fig.4) were predicted. The results showed that mechanical damage would appear in the locular gel tissue prior to the mesocarp and exocarp. The maximum simulated Von Misses stresses in the exocarp, mesocarp and locular gel tissues were 615 kPa, 132 kPa and 13 kPa respectively. These exceeded the respective failure stresses (582 kPa for exocarp, 122 kPa for mesocarp and 12 kPa for locular gel) of the tissues based on previously determined values from Li *et al*., (2012b).

4.2 Relationships between tissue mechanics and cell mechanics

Ghysels *et al*. (2009) simulated (onion) tissue deformation from individual cell mechanics. A mass-spring model was used for the mechanical behaviour of the cells under application of an external force. These were used in so-called ñrepresentative volume elementsò (RVEs) to represent the micro-scale behaviour at mesh points in a finite element description of the tissue. This model allowed for elastic behaviour only but it was suggested the method might be extended to account for viscous and plastic effects. Ghysels *et al*. (2010) then presented another multi-scale model linking tissue and cell mechanics. Individual cells were considered to consist of a viscoelastic fluid enclosed in an elastic cell wall. The former was modelled using smoothed particle hydrodynamics (SPH), which is a mesh-free method typically used to address problems in fluid dynamics and which allowed for cell wall hydraulic conductivity and cell failure. The cell wall was modelled using discrete elements. Once again the meso- and micro-scopic scales were linked through RVEs (Ghysels *et al*., 2010). Van Liedekerke *et al*. (2010a, 2011) also used non-linear discrete elements and SPH to model parenchyma tissues but as aggregates of single cells. Cell walls were treated as visco-elastic-plastic, with yielding handled using two (limiting) elastic moduli for low and high strains. A discrete element method was used to model cell-cell adhesions i.e. the effect of there being middle lamellae between cells. It was shown that this

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approach could reproduce experimental ñquasi-staticò compression data from apple. In this context, quasi-static implies very little or no unloading during application of a force, which seems a reasonable restriction when investigating mechanical damage to fruit in handling. These workers suggest the modeling of tissues with great sub-cellular detail will be prohibitively expensive and suggest that the complexity might usefully be reduced by using the RVE approach of Ghysels *et al*. (2009, 2010). There seems little reason why sophisticated modeling of this type should not be applied eventually to tomato tissues, although the macro-scale with its different tissue types (section 4.2) would remain a further challenge.

4.3 Mechanical relationships between cell and its wall

Wang *et al*. (2004) used micromanipulation to compress single suspension-cultured tomato fruit cells (*Lycopersicon esculentum* vf36) in order to obtain force-deformation data. Using a model that treated a cell as a liquid-filled sphere with thin compressible walls being compressed between two flat parallel surfaces, the low-strain elastic modulus could be found. The cell wall and membrane were taken to be permeable, but the compression was so fast that water loss could be neglected in the simulations. The mean Young's modulus for 2-week-old cells was 2.3 ± 0.2 GPa at pH 5. Using this method, Wang *et al*. (2006) characterized the mechanical behaviour of single tomato fruit cells from shop-bought varieties. Single cells were isolated by gentle washing from inner pericarp tissue. The low strain elastic moduli of the cell walls were found by modeling to be 30 to 80 MPa, significantly lower than suspension-cultured cell walls. The cell

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walls yielded at about 2% wall strain. The modeling in this work was analytical and it was not possible to extend this approach to high strains with plastic behaviour, which might have allowed stresses and strains at cell wall failure to be determined. It was also not possible to consider visco-elastic effects nor non-spherical cells. Dintwa *et al*. (2011) developed a finite element model of the same system with the same assumptions and showed this gave similar results. It seemed that a finite element approach to the analysis would be of value. This was confirmed by Van Liedekerke *et al*. (2010b) who used data from Wang *et al*. (2004) and from other sources to model single tomato cells successfully.

In the work of Wang *et al*. (2006), intact single tomato fruit cells could be isolated from the pericarp by gentle washing because the cells are quite loosely attached within the tissue during this ripening stage. It is not known how to isolate single intact and turgid cells from other tissues, including unripe tomato fruits at harvesting. This means that the mechanical properties of cells in different types of tissue of unripe tomato fruits cannot yet be determined. This remains a challenging problem for compression testing by micromanipulation. If single cells could be isolated from tomato fruit tissues then there are other powerful techniques that could be brought to bear on this problem. For example, atomic force microscopy (AFM) stiffness tomography has been applied to the relatively small cells of suspension cultured *Arabidopsis thaliana* (Radotic *et al*., 2012). This method was used to determine the stiffness distribution in the various cell wall layers and its evolution with growth. This could be related to cell wall composition using Fourier

Transform infrared (FTIR) spectroscopy. It would be of great benefit to apply these methods to cells isolated undamaged from tomato fruit tissues.

It is possible that other techniques might be used to characterize the mechanical properties of cells within tissues excised from tomato fruits. For example, Hillier *et al*. (1996) used a micro-penetration method to measure the force required to push a 20 εm probe into cells within potato tuber parenchyma, obtaining information on cell wall stiffness and fracture energies. Hayot *et al*. (2012) measured wall viscoelastic properties of single cells within *Arabidopsis thaliana* leaf tissues using nano-indentation. Although the method of Hillier et al. (1996) might be used to penetrate more than one cell layer, these are essentially surface techniques most suited to studying epidermal cells. They might be applied to cells on the surface of excised tissues, although such cells might have been damaged during sample preparation or otherwise not be representative. In general, AFM has had limited use on cells in plant tissues and again those cells that have been studied have mainly been epidermal e.g. of the meristem of *Arabidopsis thaliana* plants (Milani *et al*., 2011).

4.4 Discussion of multi-scale relationships in tomato fruit mechanics

Although much excellent research has been done on tomato fruit mechanics, there are still some major problems to solve. Firstly, not much is known about multi-scale relationships between fruit and cell mechanics. Unless these relationships can be unraveled, it will not be possible to understand how internal damage occurs to a fruit subjected to an external force. It is essential that methods are found to allow whole fruit mechanics to be described on the basis of single cell mechanics, with the cells organized into meso-scale tissue structures. This problem has yet to be solved and remains an enormous challenge to researchers in food quality. Secondly, macro-, meso- and micro-mechanics data are not available for the same fruit, variety, ripening stage, harvesting time or producing region, despite the importance of these factors. Thirdly, nonlinearities in the stress-stain relationships of fruits, tissues or cells, are rarely considered in analysis of compression and other tests. This includes time-dependent behaviours such as water flows from and between cells and the reported viscoelasticity of the cell walls (Whitnet *et al*., 1999). For whole cells, these may be difficult to deconvolute, although this can be achieved with high strain-rate compression testing by micromanipulation (Wang *et al*. 2006). In any case, the most common assumption is that the biomaterial under test is linear elastic (although the geometry of the test may result in non-linear models anyway).

5 Future research directions

Likely directions for future research on multi-scale mechanics of tomato fruits can be summarized as follows:

(1) Improvements in methods to isolate single intact, turgid and representative cells from unripe tomato fruits, which are always harvested at this stage and are in this condition when damage during mechanical handling occurs. Methods have been suggested for single cell isolation from tissues similar to unripe tomato fruits but these might involve damage. For

instance, separation using pectinase to digest the middle lamellae could alter the wall composition (McAtee *et al*., 2009). Isolation of such cells would allow more extensive studies by micromanipulation (Wang *et al*., 2006) or AFM/FTIR (e.g. Radotic *et al*., 2012).

(2) Development of mathematical models to describe the elastic, plastic and viscoelastic properties and failure criteria of fruits and fruit components. These materials are composites and ideally they should be treated as such. At present most models have been developed by assuming linear elasticity, which long run will not be an adequate approach because the failure of fruit and/or tissues cannot be analyzed using such models.

(3) Using the information from (1) and (2), developing multi-scale mechanical models of tomato fruits. The aim of such modeling of tomato fruits is to provide a tool for investigating internal damage to tomato fruit cells caused by external forces during mechanical handling. It is difficult to monitor the deformation and failure of cells within tissues when a fruit is impacted or loaded in a texture analyser and modeling is one way to gain better understanding of the processes involved. Unfortunately, existing multi-scale models of tomato fruits are not in accordance with their anatomical structures and also have no capacity to relate macro-mechanics to micro-mechanics. Although some researchers have proposed such multi-scale modeling, tomato fruit mechanical behaviour cannot yet be described on the basis of single cell mechanics, with the cells organized into meso-scale tissue structures. This is an important future research direction for multi-scale mechanics of tomato fruits.

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Table 1 Multi-scale mechanics of tomato fruit

Multi-scale Anatomy		Variety	Ripening Stage	Loading Position	Mechanical Parameters				
					F_r (N)	E_r (J)	ε (%)	E (MPa)	σ (MPa)
Organ	Fruit[A]	*Momotaro*	Green	ES	5.25^{b}		3.5^{a}	5.64E-3^{c}	
			Pink		2.9^{a}		6.3^{b}	4.18 E-3^{b}	
			Red		2.57^{a}		7.7^{c}	3.78 E-3^{a}	
	Fruit[B]	*Jinguang28*	Light-red	CW	76.7±23.6	2.87±1.6	8.8±2.5		
				L	85.8±29.7	2.8±1.6	9.6±1.5		
Tissue	Exocarp[C]	*Jinguang28*	Light-red				8.6±1.4	4.6±1.4	0.4±0.1
	Mesocarp[C]						33.9±4.0	0.8±0.1	0.23±0.1
	Locular						34.6±1	0.05±0.0	0.02±0.

	gel[C]				1.8	2	01
	Exocarp[D]	3517	Maturity	17.0^{a}		52.0^{c}	5.5^{b}
		7423		10.9^{b}		116.3^{b}	7.1^{b}
	Exocarp[E]	*Roma*	Unripe		å11	153.0±18.6	Ò22
			Half-ripe		å11	173.8±12.9	Ò26
			Full-ripe		å8	315.8±41.5	Ò28
	Cuticle[E]	*Harzfeuer*	Unripe		å9	131.6±21.6	Ò12
			Half-ripe		å11	102.0±10.4	Ò13
			Full-ripe		å3	267.2±67.9	Ò8
Cell	Cell wall[F]	(shop bought)	Red		2.1±0.5	60.3±23.8	
	Single cell[G]	*vf*36		(3.6±0.1) E-3		(2.3±0.2) E3	

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Values and errors are as quoted by the authors

ES: equatorial section, CW: cross wall tissue, L: locular tissue, F_r: peak force, E_r: rupture energy, ε: maximum compressibility (failure strain), E: elastic modulus, σ: failure stress

A: Sirisomboon *et al*., 2012; B: Li *et al*., 2011a; C: Li *et al*., 2012a; D: Hetzroni *et al*., 2011; E: Bargel & Neinhuis, 2005; F: Wang *et al*., 2006; G: Blewett *et al*., 2000.

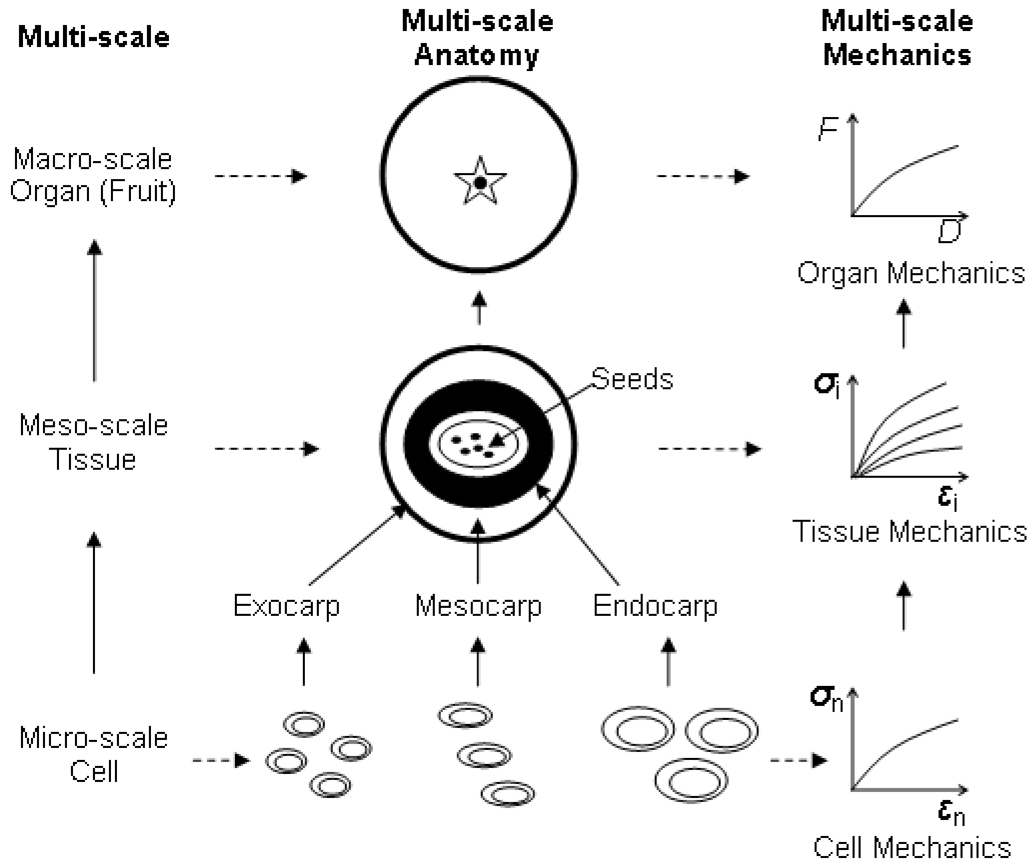


Fig. 1 Multi-scale anatomy and mechanics of fruit. *F*: force; *D*: deformation; σ_i, ε_i: stress and strain on tissue; σ_n, ε_n: stress and strain in cell wall.

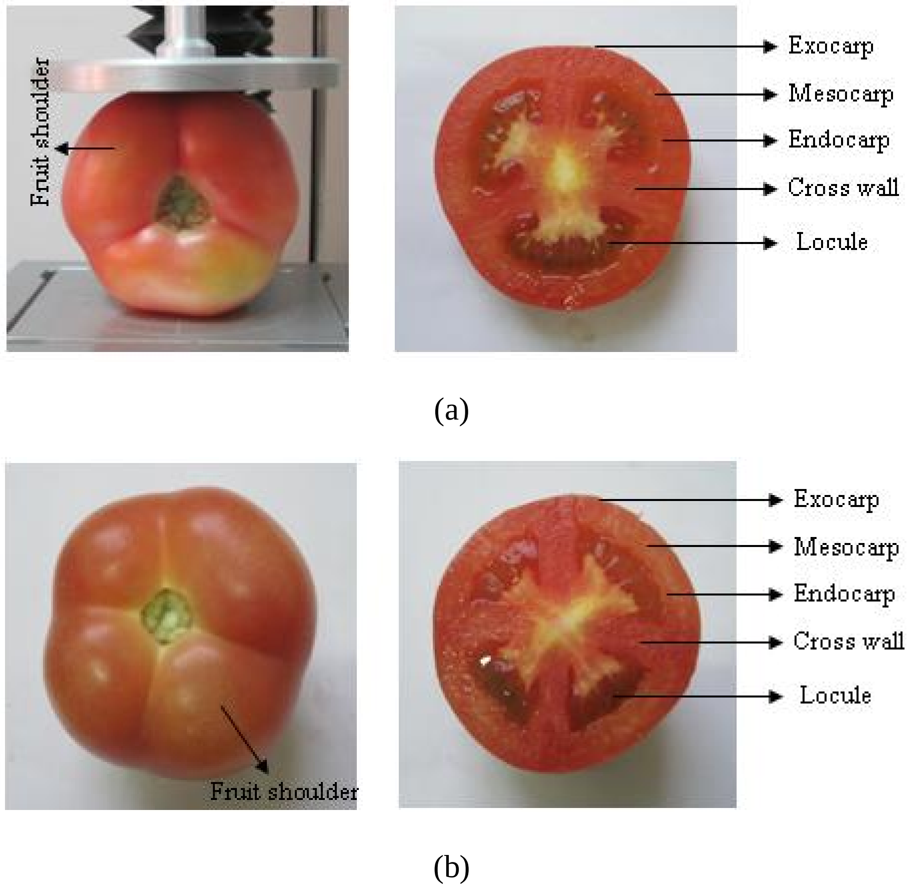
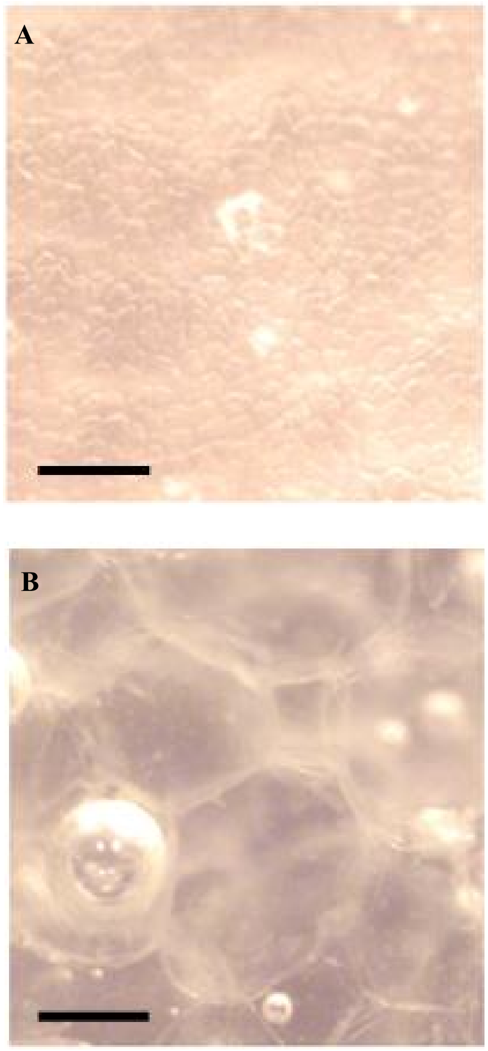


Fig.2 Three and four locular tomato fruit (Li *et al*., 2010; scale, 1:2.3). (a) Three locular tomato fruit and its equatorial section; (b) Four locular tomato fruit and its equatorial section.


A
B

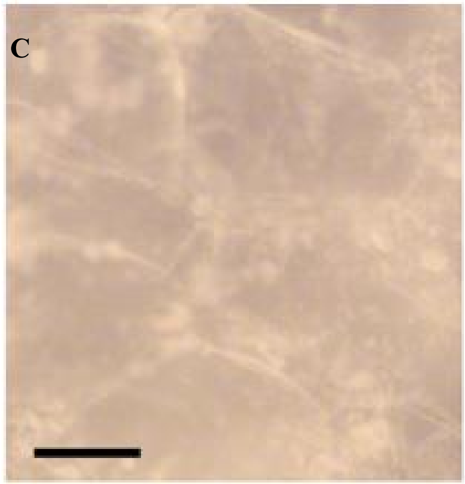


Fig. 3 Representative scanning electron micrographs of tomato fruit exocarp (A), mesocarp (B) and locular gel (C) tissues (Li *et al*., 2011a)

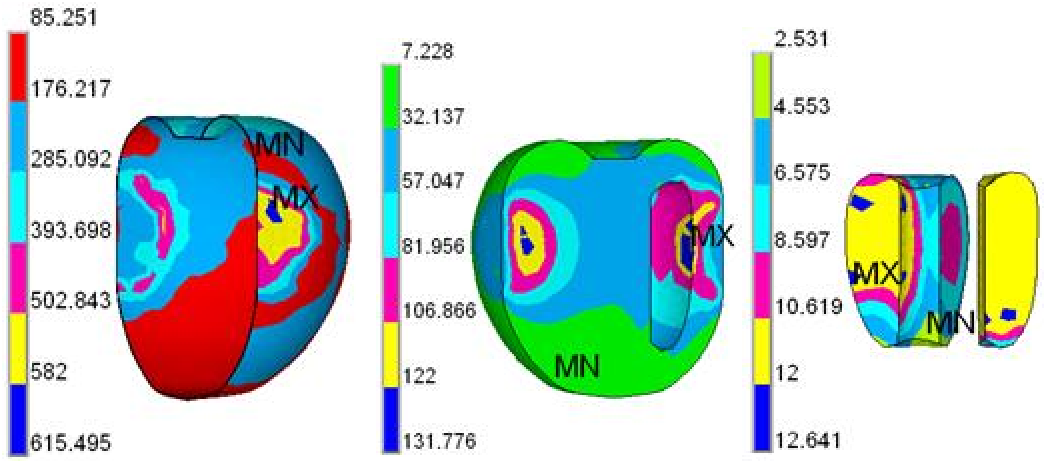


Fig. 4 Stress distribution and damage region in exocarp, mesocarp and locular gel tissues of tomato fruits caused by an external force 37 N (Li *et al.*, 2012b). Point MX indicates the position of maximum Von Mises stress of tissues and Point MN indicates the position of minimum Von Mises stress of tissues. Stress unit: kPa. The failure stress of exocarp, mesocarp and locular gel tissues are 582 kPa, 122 kPa and 12 kPa respectively.