Comprehensive Reviews in Food Science and Food Safety

Plant Cell Walls and Food Quality

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ABSTRACT: Plant cell walls constitute the key structural components of plants and many plant-based foods. They are well known for contributing to a range of "quality" characteristics, from organoleptic texture to the properties of dietary fiber. Much of the research on cell walls has focused on the physiological aspects of plant growth and development with the belief that this route holds the key to controlling quality characteristics. In addition, consideration of quality has often been determined by what is easily measurable. This review assesses critically the role of plant cell walls in relation to the ultimate determinant of quality – the consumer, but within a whole food-chain context. We conclude that effective exploitation of cell-wall research in relation to optimizing quality requires an integrated approach taking into account the multi-functional roles of plant cell walls, and the diversity of consumer-related quality dimensions.

Introduction

Plant cell walls constitute the key structural components of plants and many foods derived thereof. For decades, it has also been appreciated that they play a central role in determining the quality characteristics of many plant-based foods, particularly texture (Van Buren 1979). There is an implicit assumption that by understanding the physics, chemistry, biochemistry, and molecular biology underpinning the physiology of plant cell walls, it should be possible to manipulate plant structure and therefore cell-wall-dependent quality characteristics. The majority of cell-wall-related research has focused on understanding walls in relation to the physiology of plants. Nevertheless, a substantial amount has been directly aimed at aspects of "food quality." The purpose of this review is to explore the role of cell walls in relation to the latter. It is divided into 5 further sections—Section 2 seeks to clarify what "quality" is so as to put into context Sections 3 to 6. Section 3 briefly describes the plant cell wall in edible plant organs; Sections 4 and 5 focus on the role of cell walls in relation to a range of quality criteria; and Section 6 discusses the range of food-chain activities that can be used to control cell-wall properties and difficulties encountered.

The concept of "food quality"?

The Concise Oxford Dictionary includes in its definition of "quality" expressions such as "degree of excellence, relative nature, or kind or character." Not surprisingly, the term "food quality" is correspondingly subjective and spans a range of criteria from sensory characteristics, including flavor and texture, through to visual appearance, nutritional benefit (both actual and that perceived by the consumer), and consumer beliefs about the acceptability of production processes. In spite of this complexity, attempts are commonly made to quantify quality characteristics so as to provide an accepted means of description, to facilitate development of quality-control methodologies, and to help in improving quality characteristics. Indeed, improving food quality is commonly used as a rationale for investing in basic research. However, unless food-quality characteristics can be characterized, evaluated, and quantified, there is no benchmark against which to assess the effectiveness of that research.

Consumer perspective

In its true sense, food quality should be studied from a consumer point of view (Bech and others 2001). It is the consumer who decides what food to purchase, in addition to when, where, and how. Production of food involves many activities along the food chain (Figure 1). Sustainable production (that is, production which provides sustainable financial income) is dependent on the purchase of the finished product by the consumer. There have been a number of attempts made to understand the factors which influence consumers in making a purchase.

(1) Quality, value, and experience

The decision to purchase relates to the consumer's perception of quality and value and, according to Oliver (1997), there are 2 key aspects of quality:

(a) Quality as a concept of objective reality that is "what the product has," and

(b) Quality as a subjective reality, which encompasses the perception generated through the consideration of the objective reality that is "what the consumer gets."

In addition, product quality is usually assessed by the consumer in relation to the cost of the product, a concept dominated by price. Superior product quality is widely recognised as a major source of competitive advantage (Day and Wensley 1988). However, consumer satisfaction is thought to be determined by the relationship between quality expectation and quality experience (Oliver 1997). Hence, high-quality, good-value products will create satisfied customers who, in turn, will make repeat purchases.

(2) Product characteristics, purchase motives, and quality dimensions

The motivation of consumers to buy a food product has also been related to product characteristics, purchase motives, and quality dimensions (Grunert 1995; Peter and others 1999) (Figure 2). Product characteristics encompass the product's attributes as perceived by the consumer. Examples include the color or smell of a fruit or vegetable. Purchase motives, on the other hand, are abstract entities; for example, enjoyment of taste and other needs satisfaction, which motivate consumer behavior. Quality dimensions are product-specific descriptions and characterizations formed by consumers based on the product characteristics and their own experience, which they relate to the ability of the product to fulfill purchase motives. There are 3 categories of quality dimensions (Darby and Karni 1973):

- Search quality dimensions, where quality can be assessed at time of purchase (for example, from appearance)
- Experience quality dimensions, where quality can only be assessed after purchase (for example, texture of a fruit)
- Credence quality dimensions in which the quality characteristic can only be based on trust (for example, organic production, or healthiness). Food products are characterized more and more by this dimension.

Quality of a food product is predominantly characterized by experience (that is, after purchase) and, increasingly, credence aspects (Bech and others 2001). Therefore, to make purchase decisions, consumers have to form "quality expectations" based on sources of information known as quality cues (Steenkamp 1990). These can be divided into 2 groups:

(1) Intrinsic quality cues comprise physical characteristics of the food product; for example, when the taste of a fruit is inferred from its color (as in a banana)

(2) Extrinsic quality cues comprise all other information; for example, price, retailer, brand, advertising, and so on.

It is believed that consumer satisfaction of a product, and therefore the probability of repeated purchase, is the relationship between quality expectation and quality experience (Oliver 1980, 1993).

Bech and others (2001) consider that the experience quality dimension, including all sensory pleasures (taste in particular), is the most important dimension in relation to confirming or disconfirming expectations during consumption. However, other product qualities, some of which seem to span the 3 dimensions, are becoming more important. These include long-term quality characteristics, such as health benefits, and safe and environmentally friendly/sustainable food production methods.

Plant cell walls play a key role in several experience dimension quality characteristics. Some of these characteristics create an experience at the point of ingestion, such as sensory texture and flavor release. However, some take much longer—for example, physiologically based characteristics such as dietary-fiber-derived laxative effects. Cell walls also play key roles in some search dimension quality characteristics. Tactile characteristics of fruit and vegetables may provide a prediction of organoleptic quality characteristics. Ripe tomatoes provide a good example—if overripe, they will be soft to the touch. However, this does not hold for all fruits; overripe mealy apples may not easily be identified by handling. Of increasing interest are cell-wall-dependent credence dimension quality characteristics which include health-related benefits such as the impact of dietary fiber on cancer and heart disease, and the more-recently-acknowledged role of cell walls in the bioavailability of health-related micronutrients.

In an attempt to rationalize the way in which product specifications, quality cues (physical and perceived), quality dimensions, expectation, and experience contribute to future purchase, Grunert and others (1996) have developed the Total Food Quality Model (Figure 3). This, in conjunction with the variety of ap-

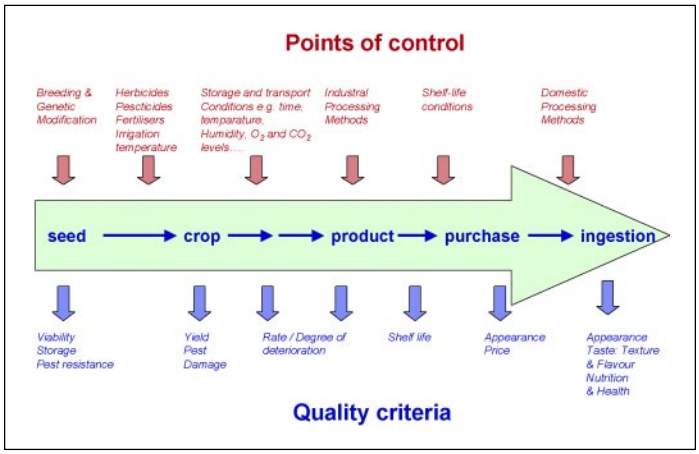

Figure 1—The food chain

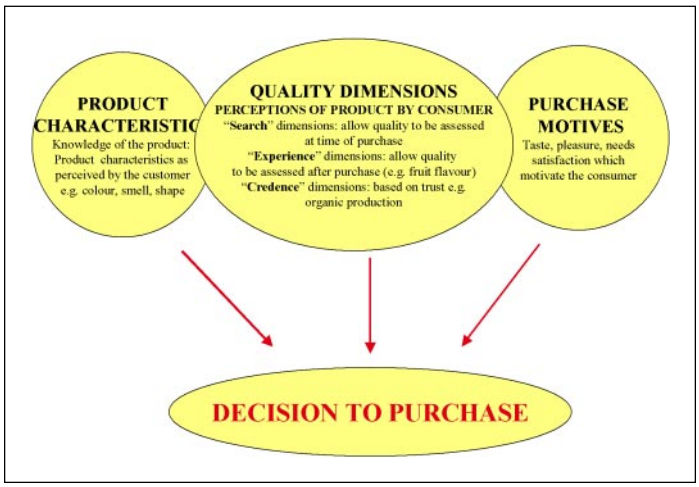

Figure 2—Quality dimensions of Darby and Karni (1973)

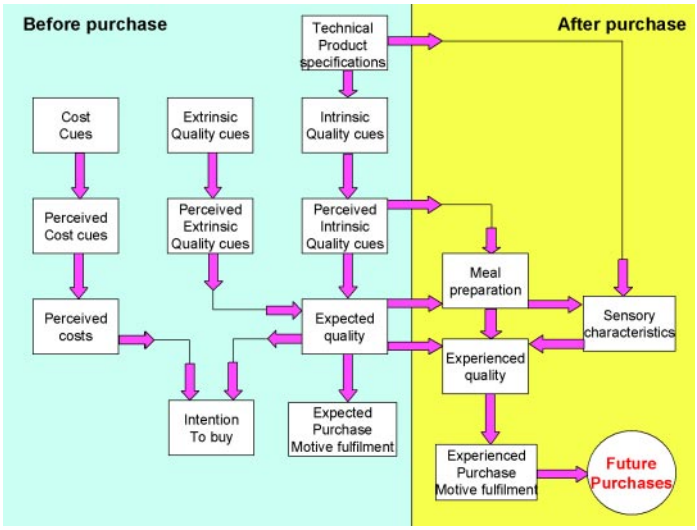

Figure 3—Total food quality model (after Grunert and others 1996)

proaches used to understand and define the different aspects of food quality, highlights the difficulty in assessing the contributions made by plant cell walls. However, it also provides a much needed framework of opportunity from which to develop research direction.

Industrial perspective

At the food industry level, final quality of food products will relate to those characteristics which meet the needs of the consumer as discussed above. However, breeders, growers, processors, and retailers will have a range of specific quality parameters that relate directly to the needs of their immediate customers within the food chain (Figure 1). The criteria may be very different to the specific quality characteristics required by the end consumer, although not always. For example, breeders and seed producers will be required to develop characteristics that relate not only to consumer quality criteria, but also to the interests of the grower. These will include uniformity of crop, resistance to pests, disease, mechanical damage and drought; requirements for chemical and agronomic controls, ease of harvest, and overall yield. Growers will want to grow crops that meet the requirements of their own immediate markets, whether they be the characteristics required of fresh fruit and vegetable produce such as sensory, storage, and nutritional properties, or processing characteristics such as gluten level in cereals or retention of texture in frozen or canned vegetables. Processors will often require year-round availability of raw materials exhibiting reliable and uniform characteristics as cheaply as possible, and seek to produce processed products which meet the requirements of the consumer, as well as the shelf life and related requirements of the retailer. Hence, "food quality" often means different things to the different players throughout the food chain.

In relation to food quality, cell walls have been considered mainly through their contribution to textural characteristics and in relation to dietary fiber. There has been relatively less consideration of their involvement in many other aspects of quality. This review concentrates mainly on the role of the plant cell wall in relation to quality characteristics as perceived by the consumer. However, consideration is also given to the quality parameters throughout the food chain which depend, in part, on the cell wall.

Description of the plant cell wall

Diversity of function

Plant cell walls are highly complex structures which perform a great diversity of functions during the life of the plant (Brett and Waldron 1996). From a plant physiological perspective, the cell wall is intricately bound up in virtually all developmental activities of the plant. In addition to providing obvious functions such as support and cell shape, cell walls are able to facilitate and regulate cell growth and division in expanding tissues, intercellular signaling and transport, protection against other organisms and environmental stresses, and storage of food reserves. As a result, the physicochemical characteristics of a cell wall and its components reflect the diversity of functional properties at different scale lengths. At the level of the individual cell, the composition of a wall involved in support (for example, that of a lignified sclerenchyma cell) differs considerably from that of a wall surrounding a storage parenchyma cell. At the level of an individual cell wall, the (bio)chemistry differs throughout the wall and relates to component structural features (for example, plasmodesmata). Hence, in describing a cell wall, and particularly in relating cell-wall structure to food quality, it is highly appropriate to consider the cell wall as part of a hierarchy of structures (Waldron and others 1997a) (Figure 4).

Cell-wall composition in relation to a hierarchy of structures

The hierarchy of structures conceptually links the molecular composition of cell-wall components through to the mechanical properties of the range of plant organs supported by cell walls, and thence to cell-wall-dependent quality characteristics (Figure 4). The hierarchy comprises 5 main levels of structure: the cell wall polymers which make up the underlying building blocks; the cell wall, consisting of these polymers; the plant cell, the morphology of which is reflected in the cell-wall shape and form; the tissue which comprises the constituent cells; and the plant organ, made up of the constituent tissues. The cell-wall-dependent characteristics of the plant organ, whether they relate to "food quality" or phenotype, will depend on the interacting properties of the different levels of structure.

Polymeric composition. The classification of the composition of wall polymers has been based, historically, on chemical structure and means of extraction (Selvendran 1985). There are 3 major categories of wall polysaccharides: pectic polysaccharides, hemicelluloses, and cellulose. They are associated with varying levels of proteins and phenolics. The following provides a brief overview of the most common polymer species found in cell walls in higher plants. More detailed information and classification can be found in other reviews (Gibeaut and Carpita 1993; Brett and Waldron 1996).

Cellulose. Cellulose provides the microfibrillar component in the cell walls of higher plants and consists of β(1-4)-linked glucose (Glc) with a degree of polymerization (DP) of between 2000 and 6000 in primary cell walls to more than 10000 in secondary walls (Delmer 1983, 1987). Cellulose comprises the single most abundant polysaccharide component of vegetables. Its glucan chains interact closely through hydrogen bonding, excluding water to produce areas of crystallinity. These impart considerable tensile strength. The naturally-occurring crystalline structure is known as Cellulose I. However, several other forms (II, III, and IV) can be produced as a result of thermal or mechanical treatments. Cellulose II is the most stable thermodynamically.

Noncellulosic polysaccharides. Noncellulosic polysaccharides have been investigated principally after extracting from cell walls, using methods that minimise polymer degradation (Redgwell and Selvendran 1986; Selvendran 1985). They have been analyzed for their chemical characterization including carbohydrate composition, linkage analysis, and average molecular weights. More

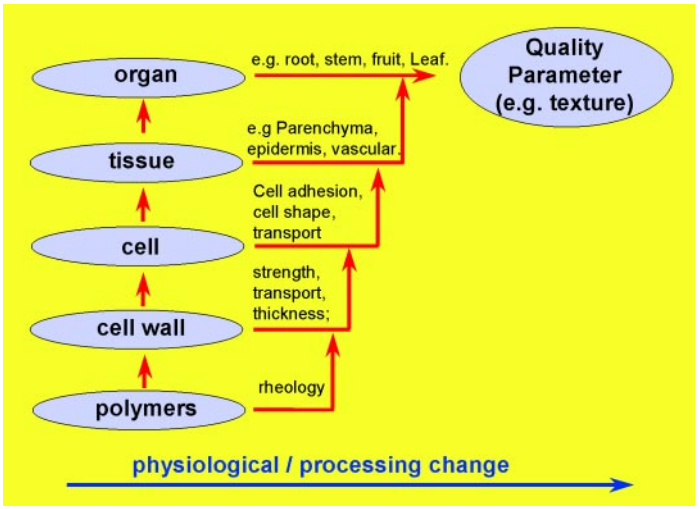

Figure 4—Hierarchy of structures

modern spectroscopic techniques now enable some analysis to be carried out *in situ*, providing information on polymer mobility and cross-linking (Wilson and others 2001).

Pectic polysaccharides. Pectic polysaccharides consist of polysaccharides rich in galacturonic acid (GalA), and often contain significant amounts of rhamnose (Rha), arabinose (Ara), and galactose (Gal). They are thought to be present throughout all primary cell walls, and probably form a gel matrix interspersing the cellulose-hemicellulose network. They are particularly concentrated in the outer region of the wall, in the middle lamella area between adjacent cells (Steele and others 1997). The 3 major pectic polysaccharides currently defined are: homogalacturonan, rhamnogalacturonan-I, and rhamnogalacturonan-II. It is thought that these polymer groups can be linked covalently to form a matrix throughout the primary wall.

Homogalacturonan (HG*).* This domain comprises long stretches of α(1-4)-linked GalA residues up to 200 (Thibault and others 1993), possibly containing occasional Rha residues) 70 to 80% of which are methyl-esterified on insertion into the cell wall. They may be de-esterified by the action of cell-wall enzymes such as pectin-methyl esterase (PME), and contiguous stretches of un-esterified GalA facilitate interpolymeric cross-linking via divalent cations, particularly calcium (Morris and others 1982; O'Neill and others 1990). GalA may also be acetylated on C-2 or C-3; recent research has revealed that it may also be substituted with xylose (Xyl) residues to create xylogalacturonan (Schols and others 1995).

Rhamnogalacturonan I (RGI). These polymer domains comprise up to 100 repeats of the disaccharide (1-2)-α-L-Rha-(1-4)-α-D-GalA. A large proportion of the Rha residues are substituted at C-4, with side chains of several sugars including (1-4)-linked β-Gal and (1-5)-linked α-Ara. These side chains may be branched and complex, and RG-I domains are often described as "hairy" regions when compared with the "smooth" regions of HGA with which they may alternate, thus producing very long molecules.

Rhamnogalacturonan II (RGII). RGII is a complex polysaccharide found in small quantities in some plant cell walls, and is probably attached to RGI.

In addition to HG and RGI, primary cell walls often contain neutral-sugar-rich molecules. The main ones are arabinans, galactans, and arabinogalactans.

Arabinans. Arabinans are highly branched molecules comprising a backbone of 1-5-linked αAra and single-residue side-chains of αAra linked by (1-3) or (1-2). Oligosaccharides of (1-5)-linked αAra may also be attached to the backbone.

Galactans. Galactans consist of (1-4)-linked βGal, although occasional 1-6 links have been found.

Arabinogalactan I. Arabinogalactan I molecules consist of (1-4)-linked βGal backbone to which short side-chains of (1-5)-linked αAra are attached to the C3 of the Gal.

Hemicelluloses. Hemicelluloses, unlike pectic polysaccharides, are usually solubilized only by treatments that disrupt the hydrogen bonds which link them strongly to cellulose microfibrils. Such treatments include increasing strengths of alkali. Hemicelluloses are found in both primary and secondary cell walls of both monocotyledonous and dicotyledonous plant tissues. They can differ greatly in different cell types, and in different species.

Xyloglucans. These are the prominent hemicelluloses in primary walls of edible vegetables and fruits of dicotyledonous plants. They are generally found in only small quantities in monocotyledonous plant cell walls. They consist of a backbone of (1-4)-linked βGlc (as in cellulose), to which side chains of (1-6) linked αXyl residues may be attached. A proportion of the xylose residues have other sugars attached including (1-2)-linked βGal and disaccharides of fucose and galactose. In endosperm cell walls of some seeds such as tamarind seeds, xyloglucans can also function as storage polysaccharides. These polymers generally lack fucose.

Xylans. Xylans comprise a backbone of (1-4)-linked β xylose (Xyl) residues, to some of which are attached (1-2)-linked α 4-O-methylglucuronic acid (GlcA), (1-2)- and (1-3)-linked αAra. In addition, the xylose residues may be acetylated on C2 or C3. Xylans are the principal hemicellulose in primary and secondary cell walls of monocotyledonous plants, where the arabinose residues often have ferulic acid attached (see below). They are, however, also found in small quantities in dicotyledonous cells.

Glucomannans. These polymers form the main hemicelluloses in secondary walls of gymnosperms, and are minor components in angiosperm walls. They consist of a (1-4)-linked backbone of βGlc and mannose (Man) residues, usually in a ratio of approximately 1:3 (1:2 in angiosperms) but with no precise pattern. Some of the mannose residues may be acetylated, and in glucomannans of gymnosperms, single Gal residues are found attached as side chains.

Mannans and galactomannans. These polymers have been found as cell-wall carbohydrate reserves in some cotyledons (for example, lupin) and some seed endosperm (for example, dates). Mannans comprise a (1-4)-linked chain of βMan residues. Galactomannans consist of mannans with (1-6)-linked αGal.

Glucuronomannans. These are found in small quantities in many cell walls, and consist of (1-2)-linked αMan with (1-2)-linked βGlcA alternating in a backbone, to which side-chains of Gal and Ara may be attached.

Proteins and glycoproteins. There is a wide range of different wall proteins. These can be classified into 2 groups: enzymes and structural. The enzymes have a range of functions, including polymer turnover, wall degradation, and wall remodeling associated with plant growth, development, maturation, and senescence. Some of the main groups are considered in relation to ripening and postharvest storage below. Considering the structural proteins, the majority are glycosylated, and the most abundant ones contain the amino acid hydroxyproline (OH-Pro), which is not generally found in intracellular proteins. These hydroxyproline-rich glycoproteins (HRGPs) comprise several groups, including extensins, arabinogalactan proteins (AGPs), proline/hydroxyproline-rich glycoproteins (P/HRGPs), and solanaceous lectins (Sommer-Knudsen and others 1998; Cassab 1998). OH-Pro can be O-glycosylated with side chains of between 1 and 75 residues, comprising arabinose and/or galactose. Such glycosylation may extend from 1 to 98% of the weight of the molecule (Fincher and others 1983; Osman and others 1995). O-glycosylation may also occur on serine or threonine. Tyrosine, also found in HRGPs, provides the possibility of both intramolecular and intermolecular cross-linking through peroxidative formation of isodityrosine (Fry 1982; Fry 1987).

Extensins and P/HRGPs are thought to be structurally-relevant HRGPs. Extensins are rich (40%) in OH-Pro, with serine and lysine. They are characterized by a Ser(Hyp)4- repeat or similar sequences (Sommer-Knudsen and others 1998) and are highly glycosylated. It has been proposed that they act as an anchorage for lignin and link pectic components. P/HRGPs commonly contain certain protein sequence motifs which probably contain OH-Pro in varying degrees, and these may be extensively glycosylated. In addition to having a possible structural role, they may also play a role in defense; some are rapidly insolubilized in the cell wall by peroxidatively-mediated cross-linking after wounding or elicitation.

In contrast, AGPs (often known as proteoglycans due to their high carbohydrate content) are generally highly soluble, and their subcellular localization is not always clear. It is believed that most are secreted extracellularly, and a number of roles have been proposed for different types, including cell signaling in development,

and adhesives on styles and stigmas.

An additional group of structural cell-wall proteins includes the glycine-rich proteins (GRP). These proteins exhibit a highly repetitive primary structure which contains up to 70% Gly in short amino acid repeat units (Cassab 1998). These proteins are thought to play a role in the development of a number of tissues, including vascular tissues, nodules, and flowers.

The interactions between structural proteins within the cell walls are largely undefined (Cassab 1998), indicating there is a requirement for further research to establish their roles both in relation to plant physiology and thence wall-related quality characteristics.

Phenolics. Phenolic moieties are frequently present in plant cell walls. They can be divided broadly into 2 main classes. The major class, known as lignin, is produced from oxidative cross-linking of phenolic alcohols. The second class consists of relatively simple phenolic esters which are attached to wall polysaccharides, and which can be used for producing covalent cross-links through peroxidative and related activity (Brett and Waldron 1996). Lignin provides compressive strength and is important in supporting tissues. It is found in relatively small quantities in most edible fruit and vegetable tissues. Simple phenolic esters such as ferulic acid may be found in the primary cell walls of a number of plants and can affect cell adhesion. A range of other phenolic moieties including biogenic amines such as tyramine can also be found in the wall as a response to wounding and pathogenic infections (Negrel and others 1996). There are numerous covalently linked simple phenolics in cell walls, the functions of which are largely unknown (Parr and others 1997).

Type I and II walls. The polymer species described above are not all found in all cell walls. There will be significant differences between tissues, within a plant organ, and also differences related to the plant's taxonomic classification. However, in comparing primary cell walls, 2 general types have been identified: Type I and II. Type I primary cell walls are found in dicotyledonous plants including fruits and vegetables, most nongraminaceous monocotyledonous plants, and gymnosperms. Here, the major polysaccharides are pectic polysaccharides and xyloglucans. Type II primary cell walls are found in the Gramineae (cereals and grasses). These have little pectin, and much arabinoxylan with (1-3)(1-4) β glucans (Gibeaut and Carpita 1993).

While there is abundant information concerning the general composition of cell walls from different plants, organs, tissues, and even cells, there is still much to be learned about the exact nature of the polymeric species and interactions between them.

Cell-wall structure. Traditionally, the cell wall has often been described as a network of cellulosic microfibrils embedded in a matrix of noncellulosic polysaccharides, protein, and often phenolics. However, this definition fails to highlight the detailed structure and underlies some of the difficulties in elucidating the relationships between cell-wall components, functionality, and thence quality. For example, sequential extraction of excised algal walls (Toole and others 2001, 2002) points to the mechanical role of the pectic polysaccharides. A number of attempts have been made to model a general wall structure which concentrate on interactions between microfibrils, hemicelluloses, pectins, and proteins (for example, Fry 1986; Gibeaut and Carpita 1993; McCann and others 1991). However, the cell wall is highly ordered, and the location of its components will relate to their functions within the wall. For example, some polymers are involved in the structure of the plasmodesmata which facilitate intercellular communication, while others may be specifically involved in cell adhesion. Many of the above components are complexed with each other to different degrees, depending on the wall type (for example, Waldron and Selvendran 1992; Fry 1987). Cross-links include covalent interactions such as those involving cinnamic acids (see above) and proteins (for example, isodityrosine) in addition to noncovalent, ionic linkages including those involving calcium (Morris and others 1982), borate (O'Neill and others 2001), and hydrogen bonding. All will contribute to the overall mechanical properties of the composite cell wall, as well as the adhesion between cells. However, elucidating their roles is complicated by their likely involvement in a range of functionalities, from wall extension to wall hydration characteristics. Exciting information about cell-wall structure has been gained from recent advances in technology, particularly those associated with microscopy. Early studies relied on light microscopy: the use of dyes and stains revealed the layered appearance of the cell wall and led to the identification of middle lamella, primary wall, and secondary wall layers. The advent of electron microscopy, both scanning and transmission, facilitated much greater resolution. The recent development of the environmental SEM (ESEM) has enabled visualization of fully hydrated, uncoated cell walls at EM resolution (Donald A, Baker F, Smith AC, Waldron KW) (Figure 5). Microscopic techniques are now being used to glean information about the molecular characteristics of the plant cell wall. For example, FTIR microscopy provides information on wall chemistry and polymer interactions (Wilson and others 2001). Atomic force microscopy can be used to provide high-resolution images of the cell surface (Morris and others 1997), and the use of probes such as antibodies and proteins are providing some information on the localization of polymer species (Willats and others 2000a,b; Orfila and others 2001). These techniques are pushing forward the frontiers of knowledge at the level of cell-wall architecture and provide an important basis from which to develop a more in-depth understanding of quality characteristics in relation to the different levels of structure. However, there still remains a paucity of knowledge particularly concerning the relationships between polymer physicochemistry, location, and function.

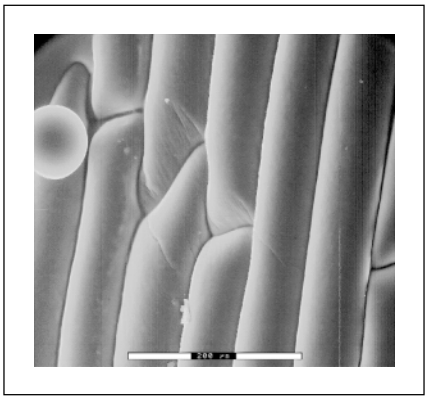

Figure 5—Environmental scanning electron micrograph of plant cell walls of onion epidermis. Bar 200 μm. Image courtesy of Donald A, Baker F, Smith AC, and Waldron KW.

Cell and tissue structure. Edible plant tissues are usually rich in parenchymatous cells which are thin-walled and nonlignified. However, these tissues usually contain other cells which serve other functions, and which will have an impact on quality through their contribution in the hierarchy of structures. The heterogeneity of tissue types is illustrated in Figure 6, 7, and 8.

Plant organs. The (edible) plant organ (fruit, leaf, seed, root, or stem) lies at the apex of the hierarchy (Figure 4). Its overall properties will depend on the integrated characteristics of the lower structural levels as modified by physiological and processing events throughout the food chain.

Role of plant cell walls in food quality

Extracted components

Extracted polymers. The roles of cell-wall architecture in determining food quality are described in the sections below. However, mention should be made of the important roles that several

groups of extracted cell-wall polymers play, usually as food thickeners, stabilizers, and emulsifiers. Such polymers are referred to as hydrocolloids.

Noncellulosic polysaccharides, particularly pectins, are usually extracted from plant material with aqueous solvents, often at high temperature and low pH (for example, boiling 2M nitric acid), after which they may be recovered by precipitation with water-miscible organic solvents such as acetone or ethanol. The sources of such polymers are often (waste) residues from other processes; for example, apple pomace which is a byproduct of juice extraction. Other polymers may be sourced directly from unprocessed plant material; for example, wall-based storage xyloglucans from tamarind seeds. Different extraction conditions and post-extraction treatments can be used to alter the chemistry of these polymers, including molecular weight and substitution patterns, and hence their physical properties. The majority of traditional extraction processes have been developed empirically.

Cellulose is also used in an extracted form for modification and use in foods. It is generally derived from cotton linters and wood pulp (Stephen 1995). The most widely used cellulose derivative in foods is sodium carboxymethylcellulose (CMC). The chemistry involved in its production may also be manipulated to control characteristics such as viscosity, pseudoplasticity, and thixotropy (Coffey and others 1995).

Some of the key cell-wall-derived hydrocolloids of relevance to food quality are shown in Table 1. These polysaccharides have been traditionally used as thickening agents. With the rapid growth in food processing over the last 20 y, additional roles have been developed; for example, in the development of ready-to-eat meals, and in confectionary dairy products, desserts, pet foods, meat products, bakery products, sauces, and food dressings (Lillford and Norton 1992). Roles in fat replacement are becoming more common (Setser and Racette 1992).

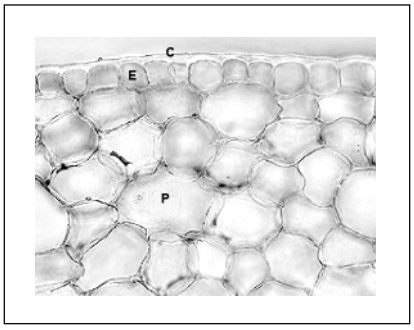

Figure 6—Light micrograph of transverse section through onion tissue. Abbreviations: C: cuticle, E: epidermis, P: parenchyma

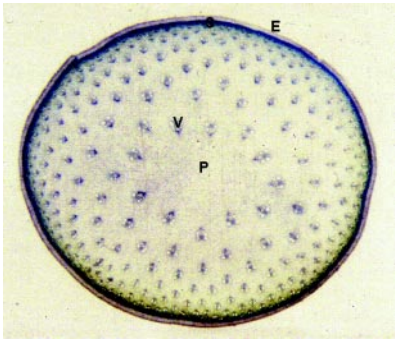

Figure 7—Light micrograph of transverse section through an Asparagus spear. Abbreviations: E: epidermis, S: sclerenchyma, V: vascular bundle, P: parenchyma

Figure 8—Transverse section though a tomato. Abbreviations: E: epidermis, S: seed, F: flesh

The bulk of the food uses to which these polymers are put have been found empirically. It is only due to recent advances in the understanding of polysaccharide physicochemistry and rheology, particularly in relation to complex food systems, that structure-function relationships are beginning to be elucidated (Stephen 1995). Such an understanding is likely to provide a useful basis upon which to develop designer molecules with tailored functionalities.

Structuring additives. Plant cell-wall preparations, particularly those which are byproducts of other food processes such as milling and vegetable/fruit processing, are increasingly being used as additives to foods. They provide a range of functionalities from putative health benefits, such as those associated with dietary fiber, through to rheological and related properties. Process-induced changes in cell-wall characteristics, including particle size, porosity, and waterholding capacity can be used to confer a range of physicochemical characteristics to food materials. These changes can be induced by a range of processes including physical, chemical, and biochemical treatments (for example, Ng and others 1999). Most of these approaches have been developed by experimentation. As a result, there is relatively little understanding of the relationships between cell-wall physical chemistry and the food-structuring properties induced. However, advances in the measurement of wall properties through studies on the structure and state (for example, Georget and others 1997, 1998a, 1998b, 1999a, 1999b, 1999c, 2003; Ng and others 1999; Kunzek and others 1999, 2002) pave the way towards an understanding of how food processes may be developed to increase the exploitation of cell-wall residues.

Organoleptic (sensory) and mechanical texture of intact fruits and vegetables

Texture is one of the most prominent quality attributes to which cell walls contribute. Much research has been carried out on plant cell walls in relation to texture (Van Buren 1979; Waldron and Brett 1996; Harker and others 1997a; Ng and others 1998; Toole and others 2000; Parker and others 2000, 2003), the bulk of it considering the mechanical properties of the tissues rather than the quality parameter which is essentially sensory.

Sensory texture. The term "texture" was originally used to describe the tactile and visual characteristics of fabrics (Guinard and Mazzucchelli 1996) and was later applied to other materials such as foods. Texture perception involves the interrogation of food in the mouth and involves the skin, muscles, and connective tissues of the face. Visual and preparatory information from handling and cutting are also important (see earlier), and hence the evaluation of texture of food begins before it is consumed (Guinard and Mazzucchelli 1996; Wilkinson and others 2000; Bech and others 2001). In spite of this complexity, a number of researchers have sought to define food texture, usually in relation to food properties and the sensations created during eating. Probably the first, by Matz (1962), defined texture as "the mingled experience deriving from the sensations of the skin in the mouth after ingestion of a food or beverage, as it relates to density, viscosity, surface tension, and other physical properties of the materials being sampled. Bourne (1982) defined the textural properties of a food as the group of physical characteristics that:

- arise from the structural elements of the food
- are sensed by the feeling of touch
- are related to the deformation, disintegration, and flow of food under force
- are measured objectively by functions of mass, time, and distance.

More recently, Szczesniak (1990) has defined food texture as "the sensory manifestation of the structure of food and the manner in which this structure reacts to the applied forces; the specific senses involved being vision, kinaesthesia, and hearing." (Kinaesthesia comprises the sensation of presence, movement, and position as resulting from nerve-ending stimulation). Because of the

Table 1—Cell-wall-derived hydrocolloids

Polysaccharide	Typical plant source	Main structural features	Typical role in food quality
Pectins	Citrus pomace apple pomace	Backbone of (1-4)-β-D GalA, (partially acetylated and methylated); and (1-2) α-L Rha to which side chains containing in Ara and/or Gal may be attached	Gelling agent either through use of calcium cross-linking in the case of low DM pectins, or sugar-induced dehydration in high DM pectin (jam production); thickener and stabilizer
Galactomannans	seeds of guar, locust bean and fenugreek	(1-4)-linked β-D mannan backbone with (1-6)-linked α-D galactose side chains	Stabilizer, increasing water-holding
Xyloglucans	tamarind seed	(1-4)-linked β-D Glc backbone with (1-2)-linked β-D Xyl side chains	Thickening agent, stabilizer
Alginates	brown seaweeds	(1-4) β-D-ManA and (1-4)-α-L-Gululose (Gul).	Gelling agent, stabilizer
Agars	red seaweeds	Sulphated galactans with various other sugars	Gelling agent
Cellulose	wood and cotton fibers	(1-4)-β-D Glc	Derivitised to CMC and used as a thickening agent.

crucial sensory aspect to texture, there is a large body of work exploring the consumer perception of texture in foods. Indeed, Guinard and Mazzucchelli (1996) state that "analytical sensory evaluation and consumer testing provided the most meaningful and reliable information about the textural qualities and acceptability of a food or beverage."

Sensory assessment. Sensory assessment is usually "hedonic" or "analytical." Hedonic testing involves untrained consumers who state their level of liking preference and acceptability of a sample. Analytical assessment involves trained panels who are able to provide an objective assessment of sensory attributes (Civille and Szczesniak 1973). Szczesniak (1963) developed an organized system for the classification of textural characteristics in 3 groups: (1) mechanical, (2) geometrical, and (3) compositional. The mechanical characteristics were divided into 5 basic parameters (hardness, cohesiveness, viscosity, elasticity, and adhesiveness), and 3 secondary parameters (brittleness, chewiness, and gumminess). Geometrical characteristics comprised 2 general groups: those related to size and shape, and those related to shape and orientation. The compositional characteristics were principally related to moisture- and fat-contents. In the context of vegetables, Szczesniak emphasized that, for a thorough textural analysis, the mechanical characteristics of each of the phases in a multiphase food should be considered and, in doing so, also emphasized that texture is a highly complex concept.

Recent studies on sensory attributes and consumer perception include those of Harker and others (2002) on apples, and Fillion and Kilcast (2002) for fruits and vegetables.

Acoustic emission. Vickers (1985, 1988) has reviewed the evaluation of crispness and auditory perception (Vickers and Bourne 1976), and concluded that the number of emitted sounds per unit biting distance and the intensity of those sounds changed with perceived crispness. Measurement of sound emission to evaluate crispness can be carried out during compression of foods either with instrumentally or manually deformed samples, or by holding a microphone against the outer ear (Vickers 1985). Analysis of data can be achieved through the use of a frequency analyzer, and vibratory stimuli can lead to the distinguishing of crisp and crunchy foods (Vickers 1984; 1985). Crisp products are characterised by sudden, clean, and total fractures. For example, fresh celery is crisp because it snaps cleanly, and crunchy because its cellular structure results in a series of successive fractures when eaten (Szczesniak 1988). Loudness, crunchiness, and crispness are judged to be very closely related.

Instrumental texture. The desire to monitor and evaluate the texture of foods during food production and processing, and to relate texture to underlying food composition, has stimulated the development of instrumental methods. Thus, a considerable amount of research has been carried out to elucidate the mechanical properties of plant-based foods in relation to composition and structure. The Scott-Blair approach divides instrumental methods of texture measurement into 3 types: empirical, imitative, and fundamental (Szczesniak 1963; Brennan and Jowitt 1977):

Empirical tests have been developed from practical experience and are often marked out as arbitrary, poorly defined, lacking an absolute standard, and effective for only a limited number of foods (Bourne 1994).

Imitative tests are often seen as a subset of empirical tests that subject the food to a process that partially mimics the consumer. Unfortunately, empirical tests cannot easily be expressed in fundamental terms and are dependent on test geometry, friction, and sample size (Peleg 1983).

Fundamental tests are more rigorously defined, usually in engineering units (Smith and others 2002; Waldron and others 1997). Many fundamental tests use low stresses that do not cause the material to break or fail and also use rectilinear motion, whereas the movement of the teeth is along an arc and much faster than speeds in the universal test machine. Interestingly, empirical tests are often more successful than their fundamental counterparts.

Instrumental compared to sensory texture. Brennan and Jowitt (1977) found that their instrumental results correlated well with sensory crispness and hardness. Sensory tests revealed that textural crispness was more sensitive, but less reproducible, than hardness to changes in moisture content. Descriptors for appearance were waxy, crumbly, sticky, breakable, and mashable; for mouthfeel they were waxy, crumbly, sticky, firm, moist, grainy, and mealy. Jowitt (1974) considered the terminology of food texture and gave more general descriptors for structural, mechanical, and mouthfeel terms.

The validity of instrumental texture measurements relates closely to their ability to predict sensory attributes of texture. Szczesniak (1987) lists 4 basic tenets of establishing links between instrumental and sensory texture: (1) quality control, (2) consumer response, (3) an understanding of sensory assessment, and (4) improved or optimized instrumental methodology. A generally held assumption is that there is a relationship between sensory texture and instrumental measurements; however, the reality is complicated by lack of precision in sensory descriptors. Sensory terms can be used interchangeably; for example, crunchy, crisp, and brittle; likewise firm, tough, and hard (Peleg 1983). There are a number of studies which have attempted to relate sensory attributes to structure, mechanical properties, and instrumental measurements.

Sherman and Deghaidy (1978) associated crispness in carrot, cucumber, and celery with both the later stage of mastication and the initial linear slope of the force-deformation curve from a flexural test. In studies on a range of foods including celery, turnips, and radish, Vickers and Christensen (1980) found that peak force in a 3-point bend test indicated tactile "firmness," and Young's modulus was correlated with sensory crispness. Crispness appeared to be closely related to sensory acoustic "loudness" and less related to "firmness." Sensory tests on cooked potato have considered appearance and mouthfeel for different cultivars after storage (Van Marle and others 1997). Harker and others (2002) used a range of instrumental tests to study the texture of apple, including acoustic emission. They correlated these data with sensory texture attributes which included crispness, firmness, crunchiness, and mealiness. However, a number of sensory textural differences between apples remained inadequately described by instrumental measurements, indicating the continual need for sensory assessment and the lack of understanding of the link(s) between sensory quality, mechanical texture, and plant structure.

Physical tests often produce single values, while consumers may change rates and manipulate the food during mastication. Further information on plant food texture may be found in recent reviews by Jackman and Stanley (1995); Harker and others (1997a); and Smith and others (2002). Objective studies on the human mouth during mastication, chewing, and swallowing enable an alternative approach to simulating these conditions with laboratory instruments (Kilcast and Eves 1993).

The role of cell walls in the failure of edible plant tissues during mastication. Tissue failure is central to the key organoleptic quality parameters, texture, and flavor release. Organ and tissue failure classically involve cell separation or cell breakage, or a combination of the 2. The release of cell contents, and therefore juice and associated flavor compounds will generally depend on cell rupture. If forces adhering cells to one another are stronger than the cell walls themselves, then failure will occur in the walls. Alternatively, if the cell walls are stronger than the forces holding cells together, then the cells will separate. Thus, uncooked vegetables and unripe fruit are generally firm; tissue fracture in these organs will involve wall rupture and associated release of cell contents. These tissues will therefore be "juicy" and mastication will increase flavor release. In addition, a high level of turgor pressure will result in such tissues being perceived as "crisp" and "brittle." Turgor pressure results from the osmotically driven influx of water into a cell as a result of the higher concentration of solutes within the protoplast which is bounded by a semipermeable (plasma) membrane. Turgor pressure is the key driver of cell expansion, which then occurs as a result of controlled slippage between cell-wall polymers. For a cell to exhibit turgor, the cell wall must exhibit elasticity over a range of tensions which counters the osmotic influx of water. Without elasticity, there can be no turgidity, only a rigid state or a flaccid state (Brett and Waldron 1996). The internal pressure of cells affects the mechanical properties of tissues as shown in their modeling as liquid-filled foams (Georget and others 2003). Lin and Pitt (1986) argued that turgid cells cause the cell wall to be stressed. Tissues containing turgid cells are crisper and are characterized by greater stiffness and lower toughness or work-of-fracture than flaccid tissues containing cells with low turgor pressure (Hiller and Jeronimidis 1996).

Failure of plant organs or tissues is complicated further by the heterogeneity of cell types that may be present, many with different mechanical and fracture properties which reflect their physiological function. For example, tissues within fleshy onion scales are relatively homogeneous (Figure 6), comprising mainly of storage parenchyma cells which are generally isodiametric. In contrast, the tissues within an asparagus spear reflect the immature stage of a rapidly growing stem with vascular and strengthening cells and tissues (Figure 7). It is in the nature of thick-walled and lignified strengthening tissues to be much stronger and tougher than the thin, nonlignified walls of parenchyma cells. Hence, the mechanical and fracture properties of asparagus stems will differ considerably from those of onion tissues.

Juiciness is a very commonly used texture parameter, often described as "succulence" in reference to young vegetables (Szczesniak and Ilker 1988). Szczesniak and Ilker (1988) suggested that cell-wall thickness and cell size influenced sensory juiciness in plant foods. More details concerning the role of cell walls in juiciness is considered below. The succulometer was designed to measure juice volume expressed from sweet corn (Bourne 1982) under pressure from a ram confining the sample in a chamber. Harker and others (1997b) measured juice content and juice released from a freshly cut surface, and found that tissues with large cells which broke open in tensile tests were juicy. They commented that instrumental measures of juiciness seem to be more directly related to sensory assessments than instrumental hardness with sensory hardness.

Events which modulate sensory texture of fruits and vegetables

There are several well-known treatments which can cause the softening of edible plant tissues. One of these, fruit ripening, is a natural and biochemically mediated process, often considered to be the initial stages of a form of senescence. Another, thermal processing, is a physicochemical process, the extent of which can be modulated by postharvest storage. In both cases, the softening occurs mainly as a result of a weakening of cell-cell adhesion.

Fruit ripening. Ripening of fruits is a complex process that generally involves tissue softening. This is important in the development of sensory properties that are acceptable to the end consumer. It is also the main factor in determining postharvest deterioration of fruit crops, and has a considerable impact on shelf life and waste production (quality parameters at earlier parts of the food chain) (Figure 1). The exact nature and extent of changes in the cell wall differ from species to species, and most research has been carried out on economically important crops which might lend themselves to improvement over a reasonable time scale. Tomato fruit has been studied most widely, and the majority of attempts to control the softening element of the ripening process by molecular genetic means have involved this fruit. Nevertheless, much research has been carried out over a wide range of fruits (Harker and others 1997a).

Ripening-related softening of fruit tissues is generally associated with, and probably due to, a decrease in the strength of cell-cell adhesion. As a result, tissue fracture increasingly occurs by cell separation as ripening progresses (Pitt 1982; Pitt and Chen 1983; Harker and others 1997a). In overripe and mealy fruits, the high level of cell separation results in poor juice release and a dry mouthfeel.

In addition, the organoleptic texture of ripening fruits may be affected by changes in turgor and, in later stages, by membrane damage and dehydration.

Interest in extending the shelf life and storage of edible fruits has stimulated research to elucidate the biochemical mechanisms that control fruit ripening. Much of this has focused on the numerous enzymes involved in cell-wall degradation during ripening (Giovannoni 2001). Early histochemical studies on fruit ripening demonstrated dissolution of pectic polysaccharides from the middle lamella of many ripening fruits. In keeping with the long-held assumption that the middle lamella is generally responsible for cell adhesion (for example, Harker and others 1997a), particular interest has been taken in enzymes which modify pectic polysaccharides which enrich that part of the cell wall. Enzymes responsible for ripening-related modification of pectic polysaccharides in

a range of fruits include endopolygalacturonase (endo-PG), pectin methyl esterase (PME), and β-galactosidase. Other wall-degrading enzymes have also been detected during ripening of various fruits including cellulases, xyloglucan endotransglycosylase (XET), and expansins. The proteins of this latter group are unusual in that they exhibit no endo or exohydralase activity. They are thought to act by disrupting hydrogen bonds between wall proteins (McQueen-Mason and Cosgrove 1994), possibly at the interface between cellulose microfibrils and matrix polysaccharides. It seems a reasonable proposition that textural changes in fruit will involve the activity of 1 or more wall-modifying enzymes. However, the exact mechanism is not yet clear. Over the past 15 y, there have been many attempts to test the significance of individual enzymes through transgenic modification, mainly in tomato. From this research, a number of conclusions can be drawn (Brummell and Harpster 2001):

- PG activity is the main enzyme responsible for the depolymerisation and associated solubilization of pectic polysaccharides. Its activity requires de-esterification of pectic polymers by PME. Suppression of PG reduces fruit softening only slightly (but shelf life is extended).
- A β-subunit protein of PG limits pectin solubilization. Suppression of its accumulation increases the rate of softening by facilitating cell separation.
- Reducing accumulation of either PG or PME increases viscosity of tomato paste, probably through reducing depolymerisation of pectins during processing.
- β-galactosidase activity, if suppressed early in ripening, significantly reduces fruit softening, indicating that the removal of pectic galactan side chains is of significance in the ripening process.
- Endo 1-4 glucanase appears to have little impact on fruit softening or the depolymerization of matrix glycans.
- XET has no clear role, but the depolymerization of xyloglucans is of importance and the mediator is yet to be identified.
- Ripening-related expansin levels correlate with fruit softening, and indirectly stimulate pectin depolymerisation.

The texture of ripe fruit depends on more than a simple understanding of cell adhesion; indeed, it is clear that there are many structural factors throughout the hierarchy (Figure 4) that contribute to the final organoleptic texture. For example, the component tissues within a fruit will often exhibit different mechanical properties, and these will be affected to varying degrees by the ripening process. This is demonstrated by commonly recognized textural differences between tomato fruit tissues before, during, and after fruit ripening (Figure 8). At the level of the cell, the shape and orientation of parenchyma (and other) cells and intercellular spaces can influence tissue-fracture properties. As a result, the perceived textural characteristics may be influenced by the angle at which a fruit tissue is bitten; for example, in apples (Khan and Vincent 1993). At the level of the cell wall, biochemically mediated changes in the cell walls during ripening may be specifically localized in distinct domains, creating considerable structural heterogeneity (Steele and others 1997). In addition, separation of parenchyma cells may be modulated by modes of attachment throughout the wall; for example, by plasmodesmata. These can contribute toward the maintenance of adhesion at pit fields by failing to break down during ripening of most fruit. As a result, they can act as points of wall rupture in tissues where most of the walls have separated, thus ensuring cell rupture and juice release in a softened tissue (Ben-Airie and others 1979; Martin-Cabrejas and others 1994) (Figure 9). Similarly, lignification of cells such as sclereids may retard separation of adjacent parenchyma cells (Martin-Cabrejas and others 1994) (Figure 10), preventing these areas from softening. The sclereids themselves contribute to the grittiness characteristic of pears. In addition, wall dissolution and associated swelling (Redgwell and others 1997) may also contribute to the fracture properties of the walls. Different internal tissue structures will also be important, as highlighted by the differences in structure and texture between an apple, peach, orange, and banana. Hence, the changes in organoleptic texture of fruits during ripening is dependent on a range of factors throughout the hierarchy of structures and the relative contribution of these changes as ripening progresses.

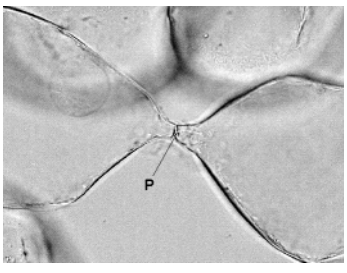

Figure 9—Parenchyma undergoing separation in ripe pears, but remaining attached at a pit field (P)

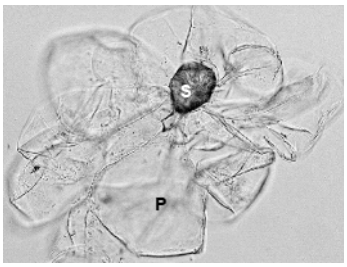

Figure 10—Parenchyma (P) in ripe pears attached to a lignified sclerieid (S)

Thermal processing of fruits and vegetables. Many changes occur in edible fruits and vegetables during thermal processing, and these can impact on one or more parts of the structural hierarchy. Thermal treatments cause an initial loss of instrumental firmness due to the disruption of the plasmalemma. This allows the free diffusion of water and low-molecular weight moieties, and results in a loss of turgor (Greve and others 1994). The latter may result in the development of a rubbery character. However, the most significant softening occurs subsequently as a result of an increase in the ease of cell separation in many nonlignified tissues (Van Buren 1979). This has been of considerable interest for decades, and has been generally attributed to the β-eliminative degradation of pectic polysaccharides (BeMiller and Kumari 1972; Keijbets and Pilnik 1974) which have long been considered to play a major role in cell adhesion. β-elimination of pectins involves a hydroxyl-ion-catalyzed breakage of glycosidic linkages under nonacid conditions, and is typical of thermal processing (BeMiller and Kumari 1972). Such depolymerization is strongly influenced by pH, and is enhanced considerably under increasingly alkaline conditions (Neukom and Deuel 1958). In addition, it can be affected by other ions and is enhanced by, for example, Ca, Mg, K ions, citrate, malate, and phytate organic acids (Keijbets and Pilnik 1974). In contrast, the softening of thermally-treated acidic fruit tissues has also been attributed to acid hydrolysis of glycosidic bonds in cell-wall polysaccharides, although this has been refuted recently by Krall and McFeeters (1998).

These characteristics have helped to provide some understanding of a number of routes by which thermal softening can be affected. For example, modulating pH and the levels of monovalent and divalent cations in cooking media can influence softening rate (Van Buren and others 1990). Furthermore, controlling the levels of intracellular cations through fertilizer application also has an impact on the characteristics of postharvest thermal processing (for example, Peck and Van Buren 1975; Sams 1999). However, these approaches have been developed empirically by processors for specific applications and there is a poor understanding of the mechanisms involved.

In addition to causing cell separation in many edible tissues,

thermal treatment of plant tissues is often accompanied by the swelling of the cell walls (Warren and Woodman 1974; LeCain and others 1997) (Figure 11). The underlying reasons for this are not clear. It may be due to the thermal degradation of polymers that stabilize the wall laterally, facilitating disruption, and may also be affected by changes in the ionic composition of the cell wall. Interestingly, the ability of calcium to cross-link pectic polysaccharides and thereby reduce their solubilization provides a dual role for this ion as a promoter of pectin degradation through eliminative degradation and as an agent that enhances texture through cross-linking.

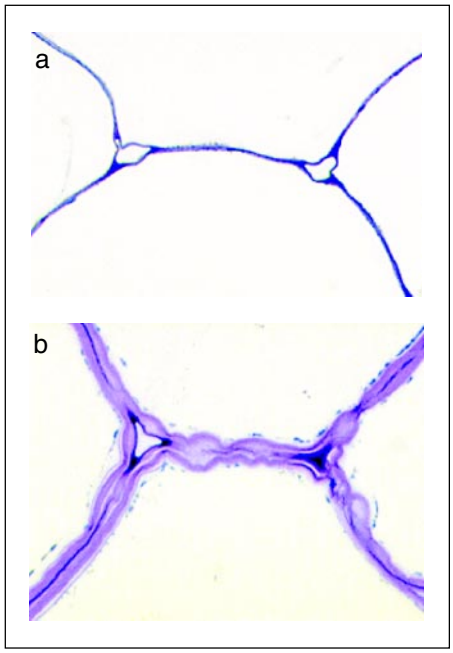

Figure 11—Transverse light micrographs of onion parenchyma cell walls: (a) fresh tissue (b) cooked tissue

Precooking effect. Certain edible plant tissues, if thermally treated at 50 to 60 °C, typically for 30 min or more, are much less prone to softening during subsequent high-temperature processing such as canning. This has been attributed to the thermal-stimulation of wall-bound pectin methyl esterase (PME), which de-methyl-esterifies the pectic polysaccharides involved in cell adhesion (Van Buren 1979). The reduction in methyl ester groups reduces the rate and extent of β-eliminative degradation at high temperatures, and provides a greater opportunity for the pectic polymers to be ionically cross-linked by divalent cations such as calcium. Similar effects can be induced by chemically de-esterifying cell-wall pectic polysaccharides in cold, dilute alkali (Van Buren and Pitifer 1992).

In some vegetables, such as carrots, the effect of such precooking can be considerable (Ng and Waldron 1997a). In some others, potatoes for example, it is often less and it is generally variety dependent. However, the changes in cell-wall chemistry are similar (Ng and Waldron 1997b). It is likely that the precooking effect on thermal stability of cell adhesion relies not only on the PME-derived de-esterification of pectic polysaccharides, but is also dependent on the availability of divalent cations to produce extra ionic cross-links (Ng and Waldron 1997b) and the impact of intracellular organic acids which can chelate them. Indeed, the precooking effect on carrots can be reversed by soaking the precooked tissue in CDTA (Ng and Waldron 1997b). In addition to studies of precooking on intact vegetable tissues (Greve and others 1994), there have been several studies on solubilized polymers (Sajjaanantakul and others 1989). There have also been attempts to relate the kinetics of PME activity to the firming process (Tijskens and others 1997 a,b). However, industrial exploitation of precooking has generally been developed empirically, and is carried out in conjunction with the addition of calcium salts to control texture. Precise control is currently difficult because little is known about the exact PME enzymes involved, their location, the identity of functionally relevant pectic polymers that they modify, and the effect that modification has in relation to polymer physicochemistry. Such knowledge could provide a valuable contribution to exploiting breeding and genetic approaches to enhancing quality.

Fruits that are thermally processed, by canning for example, will also be subjected to the effects of ripening as well as those of the processing. In such situations, it is more difficult to maintain and control textural quality, especially when an increase in temperature can stimulate the activity of ripening-related wall-degrading enzymes. Inhibition of such enzymes by genetic means can be beneficial in this respect (Errington and others 1998) (see below).

Role of cinnamic acids in thermal stability of texture. There are a number of edible plant tissues in which the nonlignified parenchyma tissues fails to soften during thermal treatments. These include Chinese water chestnut (Parker and Waldron 1995; Parr and others 1997), chufa (Parker and others 2000), and mature sugar beet and beetroot (Ng and others 1998; Waldron and others 1997b). In Chinese water chestnut (CWC), which is the corm of a sedge, the edible tissues comprise thin-walled, starch-rich storage parenchyma among which thin vascular bundles are dispersed. After extensive cooking or canning treatments, CWC retains its firm and crisp texture as demonstrated by both tensile strength and toughness (Waldron and others 1997a). CWC maintains its textural characteristics because its cells fail to separate, and thus the mechanical properties of the cell wall and plant structure are largely retained. Hence, tissue fracture occurs only by cell-wall rupture. A number of studies have been carried out to elucidate the nature of the polymers which confer these characteristics. These have indicated that in CWC, arabinoxylans, which are cross-linked by ferulic acid (Parr and others 1997), are responsible for thermal stability of texture. Chufa, which is closely related to CWC (Parker and others 2000), demonstrates similar properties. Sugar beet and beetroot, both dicotyledonous plants, can exhibit similar characteristics as a result of the ferulate-cross-linking of pectic polysaccharides (Waldron and others 1997a), and this can be enhanced considerably by increasing the cross-linking by peroxidation (Ng and others 1998). In all these examples, the ferulic acid cross-links comprise a family of 6 dehydrodimers. In CWC, 40% of the FA is in dehydrodimer form. Nevertheless, the level of ferulic acid in the cell wall is relatively low compared with other wall components, being less than 2% (dwt), and this is probably why it was overlooked in earlier studies (Loh and Breene 1981). There are currently studies underway to investigate the molecular-genetic control of such cross-linking. Recent investigations have suggested that the 8,8′ diferulic acid (aryltetralyn form) plays a central role in the thermal stability of CWC (Parker and others 2003), indicating that there may be considerable precision in the biochemistry of cell adhesion. There may be other, as yet unidentified, cross-linking moieties that also have functional significance.

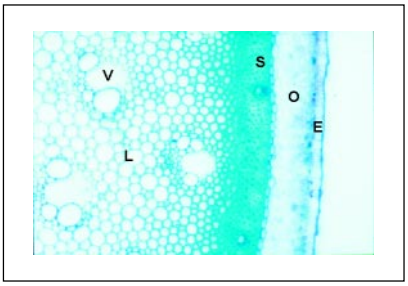

Figure 12—Transverse section of mature, inedible, asparagus spear. Abbreviations: E:epidermis, O:outer cortex, S:sclerenchyma, L:lignified parenchyma, V:vascular tissue

Postharvest toughening of vegetables. Rapidly growing edible vegetable tissues such as those in immature stems and leaf organs often undergo postharvest extension and toughening. This is usually attributed to the continued development and maturation of tissues involved in mechanical support in the parent plant. Examples include stem tissues of cauliflower and asparagus (Figure 12). The continued development of vascular

and support tissues involves natural wall thickening (secondary wall development) with associated lignification. The latter makes an important contribution to the mechanical strength of support tissues. In addition, permeation of the cross-linking phenolics into the walls of adjacent nonlignified cells (for example, parenchyma) creates intercellular cross-links that are resistant to thermal treatments; thus the extent of tissue softening during thermal processing is reduced (Femenia and others 1999a,b). In asparagus, it is well known that postharvest toughening is accompanied by an increase in lignification and the formation of interpolymeric complexing (Waldron and Selvendran 1992a). However, it has recently been demonstrated that there is also a large increase in feruloylated polysaccharides which become cross-linked with diferulic acid (Rodriguez-Arcos and others 2002). This is probably a wound response, stimulated by the harvesting process, since the levels of ferulic acid are much lower in all parts of the stem during normal growth. It is possible, therefore, that wound responses may also play a part in postharvest toughening of vegetable tissues. Much research relevant to the control of postharvest toughening has focused on environmental control so as to slow the process; for example, modified and controlled atmosphere packaging and refrigeration (Burton 1981). While researchers have investigated changes that occur during such control processes (Waldron and Selvendran 1992), there is relatively little research into alternative routes using modern biotechnology.

Hard-to-cook defect in legume seeds. The hard-to-cook (HTC) defect arises during storage of legume seeds in conditions of high temperature and high humidity (HTHH) typical of tropical countries. The defect reflects a lack of cell separation in cotyledon tissues during cooking and, consequently, cooking time is increased (Mattson 1946). Normal, freshly harvested bean cotyledons will cook in about 20 to 30 min. However, HTC beans may take several hours to soften sufficiently for ingestion. In addition to the inconvenience of having to cook the beans for a longer time, related impacts include a necessary increase in the use of wood fuel and water, both of which may be scarce in arid regions. Hence, the HTC defect crosses a number of "quality" criteria and has both nutritional and economic effects (Hohlberg and Stanley 1987). There are several review articles on this subject (Aguilera and Stanley 1985; Reyes-Moreno and Parades-Lopez 1993; Liu 1995).

There are a number of hypotheses to explain the HTC defect. The earliest postulated mechanism involves a storage-induced decrease in intracellular phytic acid (phytin) which is a chelator of calcium (Mattson 1946; Mattson and others 1950). In this mechanism, storage at HHHT is postulated to promote the degradation of phytin by the enzyme phytase, thereby releasing chelated calcium. During imbibition of water and cooking, the free calcium is able to displace the monovalent cations bound by the pectin, resulting in pectin insolubilization and a strengthening of cell adhesion. The mechanism is supported by observations that cooking times of non-HTC beans were increased considerably after imbibition of Ca^{2+} or Mg^{2+} solutions, whereas cooking times of HTC beans were decreased by soaking in chelating agents such as EDTA. Despite many studies, no correlation between the level of phytic acid content and cookability has been demonstrated (Liu 1995), so this model may be insufficient to explain fully the HTC defect. Other postulated mechanisms include "lignification-like" reactions, possibly by nonenzymic mechanisms; roles for tannins (Stanley 1992); and possibly cinnamic acid derivatives (Garcia and others 1998) which might cross-link pectic polysaccharides. The situation is complicated further by storage-related changes in the extent of electrolyte leakage during imbibition of beans (Liu and others 1992), and the decrease in the ability of intracellular starch to gelatinise (Aguilera and Steinsapir 1985)—an effect which may be due to protein coagulation around the granules (Liu 1995). Some researchers have postulated multiple mechanisms of HTC development, the most comprehensive description of which has been written by Liu (1995). However, the HTC defect remains an unsolved phenomenon that has a considerable socioeconomic impact in many developing countries.

Another cooking difficulty of beans, which is often confused with the HTC defect but which is significantly different, is the "hard shell" effect (Shehata 1992). In this situation, stored beans are unable to imbibe water due to the impermeability of the testa which surrounds the cotyledons. Some forms of hard shell increase during storage, while others may decrease. Relatively little is known about the role of cell walls in the testa which cause these changes.

Role of cereal cell walls in product quality

Cereals consist of edible grains such as wheat, barley, oats, maize, and rice, and are globally the most common sources of food. They are processed in very many ways, and the cell walls often have a significant impact on processing characteristics and thence on product quality.

Baked products. Cereals are used extensively in the formulation of baked products commonly after milling into flour which may be refined further. Milling breaks down the higher levels of the structural hierarchy (Figure 4), particularly grain bran and underlying tissue structures (see below). As a result, the influence of cell walls on processing and product quality relates more to the impact of solubilized polysaccharides (such as soluble arabinoxylans) and particulates including insoluble particles of bran (where included). The processing of baked products is complex and has been developed over millennia, mostly through the incremental development of empirically derived methods. There has been a wealth of research to elucidate the physics of baking, particularly of wheat and maize products. The importance of cereal cell-wall components in product quality has been highlighted by the effects of cell-wall degrading enzymes. For example, the degradation of endosperm-derived water-soluble and insoluble wheat arabinoxylans with exogenous endoxylanases has a significant impact on dough viscosity and bread volume (Hilhorst and others 1999; Courtin and others 2001), batter viscosity (Redgwell and others 2001), and the rheology of spaghetti doughs (Ingelbrecht, and others 2000). As a consequence, commercial preparations of such enzymes are frequently used in these processes. This is accompanied by interest in controlling the activity of endogenous enzymes such as xylanases and the levels of xylanase inhibitors in cereal flours (Cleemput and others 1995). In addition to arabinoxylans, β-glucans (1-3,1-4) have also been implicated in crumb characteristics (Wang and others 1998). The presence of ferulic acid side chains on cereal arabinoxylans has also provided routes for modifying quality; for example, through exogenously added peroxidase and laccase enzymes (Labat 2000; Hilhorst and others 1999). Indeed, the properties of water-soluble arabinoxylans are known to be modified by the presence of diferulic acid cross-links (Saulnier and others 2000).

Milling. The quality of baked products will relate, in part, to the milling characteristics of the grain. Milling behavior will depend on the hierarchy of structures in the grain and the milling techniques employed. In (dry) cereal grains, structurally significant components comprise not only cell-wall components, but also dehydrated intracellular components including starch and protein bodies, and the way in which all materials interact is also important (Piot and others 2001). For example, soft wheat contains starch to which the protein friabilin remains attached, while hard wheat apparently does not (Darlington and others 2000). Behavior during milling will depend on these characteristics in addition to several other criteria, including the degree of kernel hydration, and the type of milling technique such as grinding, rolling, or

hammering (Campbell and others 2001). Different milling streams can be produced which will contain different ratios of grain tissues and particle sizes, and these will exhibit different baking properties. Indeed, different quality flours for bread, pasta, cakes, and biscuits may be derived from one type of grain (Villanueva and others 2001). The particle size of bran can have a considerable impact on dough rheological properties as well as final bread quality (Zhang and others 1997).

Popping. Popping is a process used traditionally for maize, sorghum, finger millet, and some pseudocereals (Parker and others 1999; Park and Maga 2002). It occurs when the grain is heated, producing an internal pressure build-up followed by a sudden pressure release. The process relies heavily on specific aspects of grain tissue structure. The strength of the pericarp layers around the maize kernel (Figure 13) is one of the crucial factors in making good, high-volume popcorn. It acts as a pressure vessel, and must be robust and undamaged in order to resist the build-up of steam pressure of about 9 atmospheres within the heated kernel. If the pericarp did not act as a pressure vessel, the pressure within the heated kernel would be released gently and gradually rather than building up for an instantaneous explosion. When the pericarp can no longer resist the pressure within the kernel, it splits and peels back as the molten white starch foam flows out and quickly cools. Kernels with damaged pericarp may pop partially or not at all.

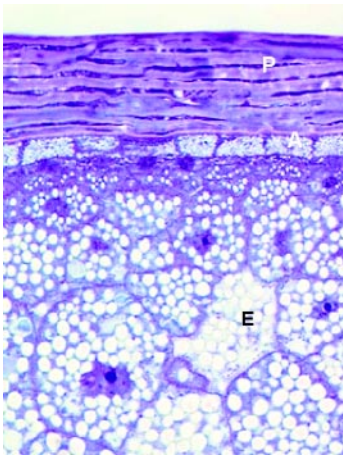

Figure 13—Transverse section through popcorn kernel showing tough outer pericarp. Abbreviations: P: pericarp, A: aleurone, E: endosperm parenchyma

Brewing. Many cereals are used worldwide for brewing alcoholic beverages, and grain-derived plant cell-wall polymers can have a considerable impact on final product quality as well as on the processing characteristics. In brewing beer from barley, for example, undegraded β-glucans solubilized from endosperm cell walls can block filtration systems during the brewing process, and may also contribute to the development of haze in the final product (Sadosky and others 2002). A considerable biotechnological effort has been made to address these issues, particularly using polymer-degrading enzymes (Faulds and others 2002).

Release of cell contents

Flavor release. The organoleptic quality of fruits and vegetables is influenced not only by texture, but also by taste and aroma. The taste of an ingested plant tissue will be dependent on the extent to which flavors and volatiles within the food are released into the mouth, enabling them to come into contact with saliva and then sensory cells. The most relevant cell-wall-related influence relates to the fracture or separation of plant cells, and therefore to texture (see earlier). Cell rupture releases cell contents into the saliva, as is the case in crisp, juicy apples. In some foods, cell rupture will also be instrumental in flavor creation. In fresh onions, for example, wall fracture results in organelle disruption, which facilitates the action of alliinase on the sulphur-containing flavor precursors alkyl cysteine sulphoxides. Where tissue fracture involves cell separation, as in thermally softened vegetables or overripe, mealy fruits, a degree of encapsulation will occur. This is why mealy apples are generally perceived to have a dry mouthfeel. In such circumstances, the opportunity for the juice (cell contents) to reach the sensory receptors responsible for taste will depend on the rate of diffusion across the intact cell wall into the surrounding saliva in addition to the ability of the saliva to transport them to the receptors.

Flavor is the combination of taste and odor influenced by sensations of pain, heat, and cold, and by tactile sensation. Aroma, taste, texture, and mouthfeel account for the major stimuli that make up flavor (Taylor 1996). Chemicals from the food come into contact with sensors in the nose and mouth and interact with mucous membranes. Plant cell walls in tissues and organs affect the chewing process and interact with the mouth lining. Studies of chewing using electromyography can be combined with the volunteer's direct recording of time-intensity signals, with swallowing recorded indirectly with a throat microphone or directly with a swallow button on the volunteer's console. The time-intensity device can be used to record any sensory or quality attribute, including flavor intensity. Again, indirect measurement of volatile flavor can be carried out. Most analyses of volatile flavors have been carried out on whole foods by extracting all aroma compounds by distillation or extraction. However, physical changes occur in the mouth with regard to both texture and flavor. The surface area of food may increase initially, and then decrease during bolus formation. Exhaled-breath sampling during eating using mass spectrometry techniques is an objective approach to quantify aroma release, often in combination with the generation of time-intensity profiles by the subject. Interestingly, Taylor's group has shown that for strawberries (Ingham and others 1995) and tomatoes (Linforth and others 1994), the aroma profiles during eating are significantly different from conventional headspace or total volatile measurement.

It is evident that aspects of plant structure throughout the hierarchy (Figure 4) can impact considerably on flavor released through wall rupture as described in this section. The role of plasmodesmata in creating localized areas of wall rupture and the impact of lignification in tissues adjacent to parenchyma cells may provide potential targets for manipulation in the future.

Commercial extraction of cell contents. The quality of commercially extracted cell contents such as vegetable and fruit juices, oils, and flavors can be significantly affected by plant cell-wall components. Fruit juices, for example, can be affected by pectic polymers which are often solubilized during pressing. The pectins may gel during dehydration of the fruit juice, preventing effective concentration prior to transport. This has been addressed for many decades by the addition of commercially available cell-wall degrading enzymes such as pectinases from microbial sources. Indeed, the rapid growth of the enzyme biotechnology industry has facilitated the improved extraction of juices and oils (Demir and others 2001) and the development of many novel products, for example sweet pulpy fruit juices in which the whole fruit is subjected to wall-degrading enzymes (Missang and others 2001; Will and others 2000). Native wall-degrading enzymes can sometimes cause problems in some fruit processes, and will be influenced by the state of ripeness. In tomato juice extraction, for example, native endoPG may uncontrollably reduce viscosity. This can be partly addressed by thermal treatments to inactivate the enzymes, although the coincident heat-induced eliminative degradation of pectic polymers may also be deleterious (Hurtado and others 2002). A biotechnological approach involving the genetic downregulation of the enzymic activities has proved successful in relation to controlling product viscosity (Errington and others 1998).

Nutrition.

Dietary fiber (DF). The historical interest in dietary fiber has

arisen from the hypothesis that the consumption of diets low in fiber is related to a large number of gastrointestinal and metabolic diseases in the developed world. Dietary fiber was defined originally as "that portion of food which is derived from the cellular walls of plant which is digested very poorly by human beings" (Trowell 1972); that is, plant cell walls. This definition has since been extended to include polysaccharides and lignin in the diet that are not digested, thereby including some polymers in food additives. Such materials will traverse the stomach and small intestine, and eventually pass into the colon.

DF may be measured in a variety of ways, and is usually defined as dietary nonstarch polysaccharide (NSP) and lignin. Some methods quantify DF gravimetrically after removing starch and lipid, and then take into account protein and ash content. More recent approaches have focused on measuring the carbohydrate composition of simple, starch-free cell-wall preparations (Englyst and Cummings 1988). The quantification of DF has been complicated by the realization that some foods contain starch, which is resistant to digestion.

The quantification of DF does not provide much indication of its physicochemical properties other than the amount of cell wall that will be available for fermentation in the colon (see below). The physicochemical properties of DF are dependent on a number of factors, including the plant and tissue of origin and the nature and extent of processing. For example, milling can alter DF particle size, and this can have a direct impact on water-holding capacity and fecal bulking of certain DFs, cereal bran, for example (Malkki and Virtanen 2001). Indeed, the role of DF as "roughage" to alleviate constipation is well known. Thermal treatments of vegetable and fruit tissues will increase soluble fiber and alter particle size as a result of cell separation. Soluble DF from some sources, for example, oat grains, may have viscosity-enhancing properties which can reduce the rate of gastric emptying. This can modulate absorption rates of nutrients such as glucose which is important in controlling certain types of diabetes. In addition, some DF preparations can bind bile salts, reducing their reabsorption in the small intestine. This may have implications in cholesterol metabolism and heart disease (Dongowski and others 1998).

Once in the colon, DF provides a substrate for fermentation by the anaerobic bacterial flora. The 5 predominant genera in the colon are Bacteroides, Eubacteria, Bifidobacteria, Peptostreptococci, and Fusobacteria. The rate and extent of fermentation of DF will be dependent on factors such as surface area, solubility, and porosity, as well as the structural characteristics of the cell walls. Fermentation results in the production of short-chain fatty acids such as acetic acid, butyric acid, and propionic acid. These are absorbed by the colon and exploited as an energy source, and have been implicated in the maintenance of health of the colon.

Nutrient bioavailibility and bioaccessibility during gastrointestinal transit. The plant cell wall has a significant impact on the rate and extent of digestion of nutrients within the diet. Of particular significance is the encapsulation effect of the cell wall on the availability of intracellular components (Faisant and others 1995). While this may be modulated by process-related changes in wall structure and porosity, there is increasing evidence that significant quantities of nutrients may be undigested and then carried through to the colon. Indeed, there has been a suggestion that these unavailable nutrients should be included in the definition of DF (Ha and others 2000). Digestion of bulk nutrients such as proteins and starch may be adversely affected (Melito and Tova 1995). In addition, digestion of phytochemicals such as β-carotene and lycopene may be reduced. For example, crystals of β-carotene are poorly digested from carrot tissues if the cell walls are not ruptured. This is due to the inaccessibility of the crystals to bile salts, fats, and lipases (Figure 14). Lycopene bioavailibility may also be reduced by cell-wall encapsulation (Shi and Maguer 2000), and recent studies have demonstrated that this also applies to fats in some oil-rich seeds such as almond (Ren and others).

Although the scope of this review is focused on human foods, it is useful to note that cell walls also have a significant impact on the nutrition of animals (Chesson and others 1982; Wilson and Mertens 1995). In ruminants, for example, the rate and extent of wall degradation in the rumen can affect nutritional value of plant-based animal feeds. Nutritional value may be modified by the pretreatment of feeds either chemically or with wall-degrading enzymes. In addition, the effect of cell walls and their solubilized polysaccharides on gastrointestinal rheology and, in particular, fecal rheology, may have considerable economic impact on both animal and poultry production.

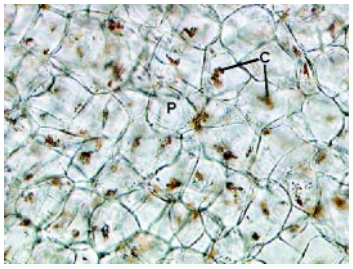

Figure 14—Encapsulation of β-carotene in carrot cells. Abbreviations: P: parenchyma, C: β-carotene

Bioactive polysaccharides. Most work on bioactive cell-wall polysaccharides have concentrated on polymers from fungal cell walls (Hearn and Sietsma 1994; Duan and others 1994; Vetvicka and others 1997; Misaki and Kakuta 1997). However, plant cell-wall polysaccharides have been implicated in the modulation of the human immune system (Mueller and Anderer 1990 a,b; Waldron and Selvendran 1992b), mainly as a result of research into the active components of herbal drugs. Such polysaccharides are generally of high molecular weight (10^6 Daltons) and have often been associated with small amounts of protein. Bioactivities include antitumor, antiviral, antibacterial, anticomplementary, anti-inflammatory, anticoagulatory, and phagocytotic activities. The mechanism of action of most bioactive polysaccharides is not known. However, there has been considerable research into the mode of action of certain antitumor polysaccharides, including pectic polysaccharides. Development of in vivo bioassays involving murine tumors have facilitated the detection, fractionation, and purification of antitumor polysaccharides in materials from fungi, yeasts, lichens, algae, and higher plants (Waldron and Selvendran 1992b).

Antitumor pectic polysaccharides from higher plants. Pectic polysaccharides with RG I-like structures from the leaves of *Cassia angustifolia* and the roots of *Angelica acutiloba* have been shown to demonstrate antitumor activity (Muller and others 1989; Yamada and others 1990). The presence of RG I pectic polymers in higher plants has led to the suggestion that there may be antitumor pectic polymers in plant-based foods (Waldron and Selvendran 1992). Such polymers are likely to be solubilized as a result of thermal processing and fruit ripening. This will increase the likelihood of absorption by gastrointestinal lymphoid tissues during gastrointestinal transit, and may explain why many herbal remedies involve hot-water infusions of those plants. However, the levels of soluble RG I-like polysaccharides present in normal diets are probably much lower than those which might have an effect by oral administration.

The modes of action of antitumor pectic polysaccharides are poorly understood. One plausible mechanism (Mueller and Anderer 1990a,b) has suggested that RG I pectic polysaccharides can enhance the ability of natural killer (NK) cells and lymphokine-activated killer (LAK) cells to bind to tumor cells and then destroy them. This mechanism involves the binding of rhamnose and galacturonic acid residues to receptors on the surface of killer

cells and tumor cells respectively, stabilizing adhesion after initial antigen recognition.

Role of cell walls in determining additional quality parameters along the food chain.

Many of the cell-wall-dependent quality characteristics of plant-based foods at different stages of the food chain relate to the role of cell walls in plant development. For example, the level of pest and pathogen damage that occurs during growth, development, and postharvest storage will be affected by the cell wall. The cell wall has a direct role in combating pathogenic invasion by acting as a physical barrier. This is of particular importance in the resistance of dormant organs such as stored seeds, roots, tubers, and bulbs, to pathogenic invasion. In addition, wall components released after degradation by enzymes from pathogens can elicit wound response mechanisms in the plant (Brett and Waldron 1996). The wall itself may then be involved in that response; for example, by enhanced cross-linking of native wall components and newly inserted molecules such as biogenic amines (Waldron and others 1997a). Hence, the cell wall can influence the marketable yield of crops and edible organs, particularly the visual appearance which may be significantly altered by evidence of previous responses to infection (for example, aberrations in organ color and visible textural characteristics). Changes in cell walls during wound responses may also affect subsequent organoleptic quality, as in the case of asparagus. The protective roles of the plant cell wall are becoming more important in organic crops where the use of pesticides and other chemicals is much reduced. Organic products are important in fulfilling purchase motives based on environmental concerns.

Cell adhesion as a focus for quality improvement

The sections above have highlighted the crucial importance of cell adhesion in the maintenance of texture and related quality attributes such as flavor in plant-based foods during both physiologically induced senescence/ripening or thermal processing. Studies on cell adhesion have generally focused on the role of pectic polysaccharides, since they are abundant in the middle lamella region. There are now several clear lines of evidence which indicate that cell adhesion may not be dependent on the entire middle lamella layer, but on components that are located specifically at the edges of cell faces and which therefore comprise only a small proportion of middle lamella polymers.

Development of dark-staining regions during cell division

One of the earliest indications that control of cell adhesion may be localized within the wall comes from SEM studies in the mid 1980s (Kolloffel and Linssen 1984). These investigations focused on visualizing cell-wall formation during cell division. Cell adhesion comes into being at the later stages of cell division when new daughter-cells are formed. A specific region of the parent cell wall is degraded, thereby enabling connection of the newly formed cell plate (which separates the daughter-cells) to the middle lamella surrounding the parent cell (Kolloffel and Linssen 1984; Knox 1992). The cell plate later becomes the middle lamella between the daughter cells. Subsequently, within the tricellular junction between the two daughter cells and the adjacent cell, intercellular space formation initiates and spreads along the middle lamella. The extent of the space appears to be highly regulated. Kolloffel and Linssen (1984) demonstrated that, in pea cotyledons, cell separation is terminated at electron-dense intrawall structures which are thus located at the corners of predetermined intracellular spaces. If separation is not terminated in this way, it would continue until the cells separate completely. Kollofel and Linssen (1984) speculated that these electron-dense regions represent sections of continuous arcs along the edges of intercellular spaces. However, the work did not preclude the rest of the middle lamella from being involved in cell adhesion, and it did not provide any information on the chemical or biochemical composition or nature of the arcs.

Location of calcium-cross-linked homogalacturonans

Immunocytochemical localization of low-ester pectic polysaccharide. The role of calcium cross-linking in cell adhesion of many edible plant tissues is well established (see earlier). Investigations into the localization of such polymers were pioneered by the development of monoclonal antibody (Mab) technology. Using the antipectin Mabs JIM5 and JIM7, sections of carrot tissues (Knox and others 1990), suspension-cultured carrot cells (Liners and Van Cutsem 1992), and ripe cherry tomato (Roy and others 1994) were immunolabeled. The electron-dense regions of the cell wall highlighted by Kolloffel and Linssen (1984) were found to be rich in low-esterified HG sequences. In contrast, the highly esterified pectins did not exhibit such localization. This characteristic has been investigated in a 3-dimensional manner by SEM (Parker and others 2001) and by using FITC-tagged JIM5 antibodies (Waldron, Faulds and Rigby, unpublished data (Figure 15). This image shows a single, intact, potato parenchyma cell which has been fluorescently immunolabeled with JIM5 antibody. These bind preferentially to the edges of the cell faces consistent with the role of these locations in cell adhesion. During the past 5 y, more highlycharacterized Mabs have been raised to calcium-binding homogalacturonan. Of particular note is the anti-HG Mab (LM7) which is specific to a nonblockwise pattern of methyl esterification. This antibody has been found to bind specifically at the corners of all parenchyma intercellular spaces examined to date (Willats and others 2001).

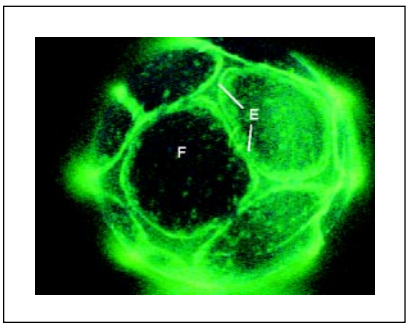

Figure 15—Fluorescence pattern at cell surface after labelling with JIM5 Mabs. Abbreviations: E:edge of face, F:face

Localization of calcium. Techniques such as secondary ion mass spectrometry (SIMS) have demonstrated that calcium may also be located in the middle lamella, particularly at the corners of intercellular spaces (Roy and others 1995). This is consistent with the distribution of unesterified pectic polysaccharides which can be cross-linked by calcium.

Esterified phenolics

Early studies on CWC involving the sequential extraction of intact tissue slices demonstrated that extraction in hot, dilute alkali resulted in cell separation. Under the appropriate extraction conditions, only a proportion of the phenolics were released from the cell wall. Subsequent analysis by fluorescence microscopy revealed that the phenolic moieties that remained were located predominantly at the perimeters of the cell faces (Figure 16). This provides further considerable evidence that the edge of the cell face is important in cell adhesion. In addition, analysis of the phenolic remaining in the cell wall indicated that they were particularly enriched in 8,8′-DiFA in the aryltetralyn form (Waldron and others 1997a), suggesting that there may be some specificity in the role of this dehydrodimer as later highlighted by Parker and others (2003).

Middle lamella as a separate entity

There have been numerous studies of fractured, edible tissue in

which the ratio of cell breakage to cell fracture has been investigated. This has often been done by SEM analysis of the fractured surface. However, little attention appears to have been paid to the actual structures remaining on the surfaces of separated cells. In most cases, many of the components of the middle lamella zone will have been solubilized, leaving a relatively smooth surface. However, if tissues such as potato are thermally or chemically treated so that softening is only partial and the cells are only just beginning to separate, useful information can be obtained about the way in which wall architecture is disrupted during cell separation. Parker and others (2001) have done this with partially softened potato tissues and have observed that the middle lamella is a separate entity that is attached to the cell walls only at the edges of the cell faces. These results, in conjunction with other studies involving Mabs, do not preclude the involvement of the middle lamella pectic polysaccharides across the whole cell surface from contributing to cell adhesion. However, it is clear that the chemistry of adhesion of the middle lamella to the primary wall surface differs considerably with location. In particular, bonds that attach the edge of the cell face and those which cross-link the polymers within the middle lamella appear to be more stable to thermal and chemical treatments compared to bonds that attach (if at all) the face of the middle lamella to the outer surface of the primary walls.

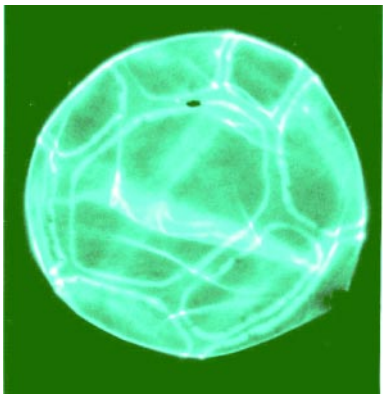

Figure 16—Autofluorescence of single Chinese water chestnut cell

Mathematical modeling

Turgid cells, particularly isodiametric ones such as CWC parenchyma, will tend to become spherical. As a result, cell separation will be initiated at the edge of each face. This issue has been explored mathematically by Jarvis (1998). His model is consistent with the view that turgor-generated stress within the cell wall will concentrate at the corner of tricellular junctions and intercellular spaces, in the very location that electron-dense material (Kollofel and Linssen 1984), low-ester HG (Parker and others 2001; Willats and others 2001), calcium (Liberman and others 1999) and ferulate cross-links of CWC (Waldron and others 1997a) are located.

Controlling quality by controlling cell walls

Considerable effort is being made to elucidate the molecular biology which underpins the structure and function of the cell wall (Carpita and others 2001). For several decades, numerous research groups have sought to identify those genes which control plant structure, architecture, and dynamics. There are many genes relevant to cell-wall architecture ranging from those which play a part in the control of biosynthesis through to those which are involved in the control of post-insertion modification. In *Arabidopsis*, for example, it has been suggested that more than 2000 genes participate in wall biogenesis during plant development. An insight into the genes involved in wall metabolism continues to be gained through use of forward and reverse genetic approaches (Carpita and others 2001). The potential to modify and modulate cell-wall-dependent quality characteristics provides an economic rationale for genetic research, as exemplified by attempts to increase the shelf life of ripening fruits.

One widely used technique to identify genes relevant to quality characteristics involves the mapping of quality trait loci (QTL) on chromosomes. For example, in wheat, QTL mapping has been used to relate certain chromosome loci, and in some cases specific genes, to quality characteristics of final products such as dough rheology and bread properties. In barley, it has been used in understanding malting quality, and in maize it has been used to investigate the genetics related to lignification and cell-wall digestibility in forage crops (Mechin and others 2001). Even if individual genes cannot be identified, techniques are available to map the loci affecting the quality characteristic of interest with tightly linked markers, thereby enabling their presence to be monitored and to facilitate selection. More recent technological developments are enabling the identification of patterns of genetic expression (genomics) in relation to quality characteristics, via patterns of protein content (proteomics) and metabolic profiles. However, the success rate of genetic approaches to controlling cell-wall-dependent quality characteristics may be attenuated due to the key factors outlined below.

Precision of the description of quality

The complexity associated with defining quality characteristics is highlighted by the range of quality dimensions described earlier. Most cell-wall-related research has focused on experience quality dimensions. There has been relatively little in relation to search and credence quality dimensions. Most cell-wall-dependent experience quality dimension characteristics, particularly those of a sensory nature such as texture and juiciness, are ill defined, and generally described in a subjective manner. Furthermore, there will be a variance in sensory perception between individuals which can be affected not only by differences in the neural interpretation of sensory information, but also, for example, by different mastication patterns that may be affected by differences in skeletal (jaw) dimensions and dentition (Heath and Lucas 1986). Sensory-based quality characteristics are generally dependent on a number of criteria which span the hierarchy of structures (Figure 4); for example, tissue type, composition and dimension, and so on). This reflects the contribution of numerous plant physiological characteristics (involving cell walls) to a sensorial quality parameter. This lack of precision often makes it difficult to define "quality" traits suitable for targeting, and those that are used are often selected in relation to ease of measurement rather than precise relevance. Future research will need to emphasize the more precise description of perceived quality characteristics in relation to the physiological functions of plant cell walls.

Genetic modification, however, has provided a basis for enhancing non cell-wall-related quality characteristics that are dependant on one or a few clearly identified genes. For example, the production of insect-resistant corn and herbicide-resistant soya (Tucker 2003) are resulting in benefits to the quality of produce in relation to the production end of the food chain (Figure 1). Likewise, the potential to increase nutritional status of crops has been exemplified by the development of Golden Rice through modification and formation of pathways needed in β-carotene synthesis. The latter acts as a precursor to vitamin A in the human diet (Ye and others 2000).

Multiple influences

Quality characteristics of an end product are not dependent solely on gene expression, but also on other events that occur throughout the food chain such as agronomy and processing, and the resulting response of the plant. The end quality characteristics of interest to the consumer will depend on the integration of food chain activities and inputs (Figure 17). These may often differ from crop to crop, cultivar to cultivar, and location to location (Sams 1999). Growing conditions may be affected by local climate, geography, and farming practices; processing may differ

from manufacturer to manufacturer. This has been recognized for several decades, and total food chain control is fundamental to the production of uniform, high-quality produce by both food processors and the large retailers, as exemplified by the production of high-quality frozen vegetable produce.

Interactive elements

The cell wall is central to a number of quality characteristics throughout the food chain (see earlier). Altering a cell-wall property so as to change a targeted quality character is also likely to have a significant impact on other plant characteristics that also depend in some way on that wall property. For example, changing phenylpropanoid metabolism to modify the stability of cell adhesion may also have an impact on the solubility of the dietary fiber component and its physiological impact. It is also likely to modify flavor profiles due to changes in the nature and levels of intracellular metabolites. It may also alter the release of flavors and nutrients during ingestion. Further back along the food chain, such changes may affect disease resistance, cell-extension characteristics, or compressive strength of the plant tissues, thereby influencing many other quality characteristics in Figure 2. Of course, the modification of other interrelated quality characteristics may be beneficial.

Acceptance of technology

The acceptance of the technology is a major issue and reflects the increasing importance of the credence quality dimension. Regardless of the quality of a product in relation to the experience quality dimension, consumers will be less likely to purchase it if they do not agree with the technology used to produce it.

Conclusions

All these factors are consistent with the experience that the control of cell-wall-dependent quality characteristics is complex and requires integration of activities and extensive interdisciplinary testing. What is clear is that it is essential that the activities of scientists are integrated (in part) with the other aspects of the "Research—Knowledge—Technology—Quality" chain so as to provide focus and technology transfer (Waldron 2003). It is interesting that much research emphasis is being placed on the experience quality dimensions of food. Many future socio-economic projections indicate that the world is moving rapidly into a position where issues of sustainability may well dominate consumer interest through the credence dimension.

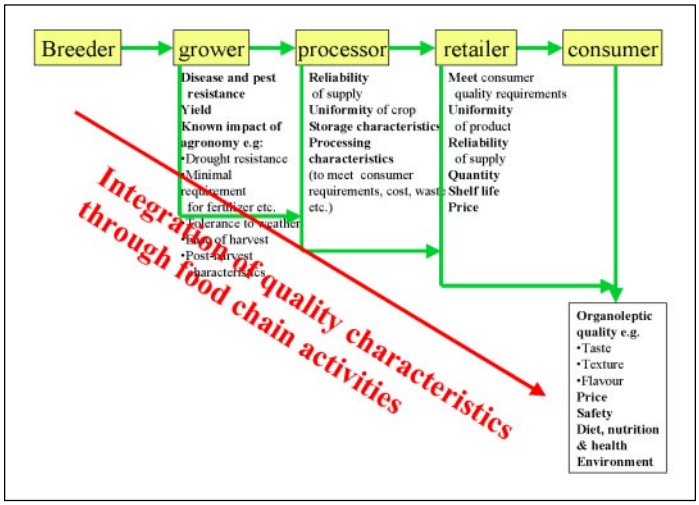

Figure 17—Consumer quality as a result of integration of food chain activities.

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