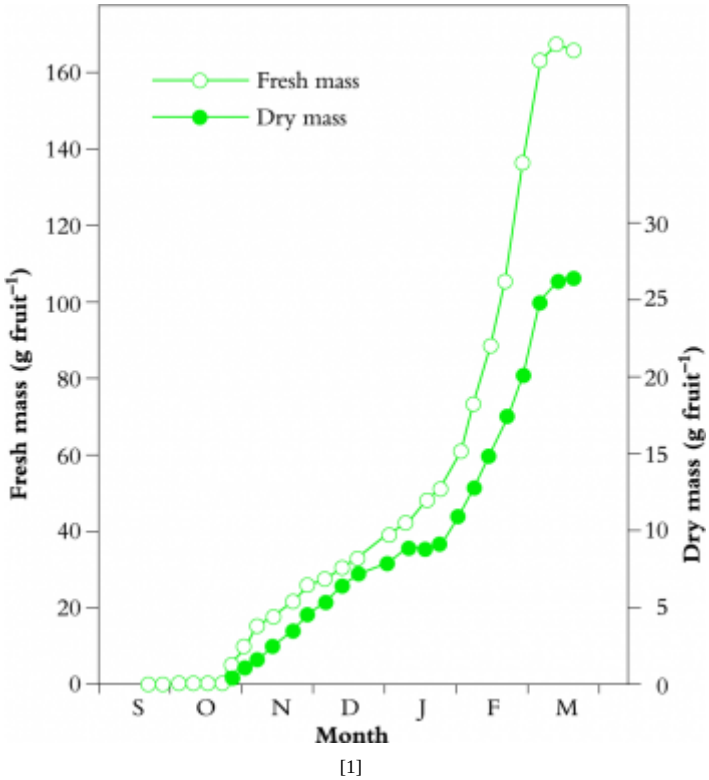
11.2?Dynamics of fruit growth

11.2.1?Time-course



[1]

Figure 11.2 Peach growth is biphasic, showing a double sigmoidal pattern in terms of both fresh mass and dry mass. Pericarp cell division is especially active during early stages of phase 1, while enlargement of an existing population of cells is largely responsible for growth during phase 2.

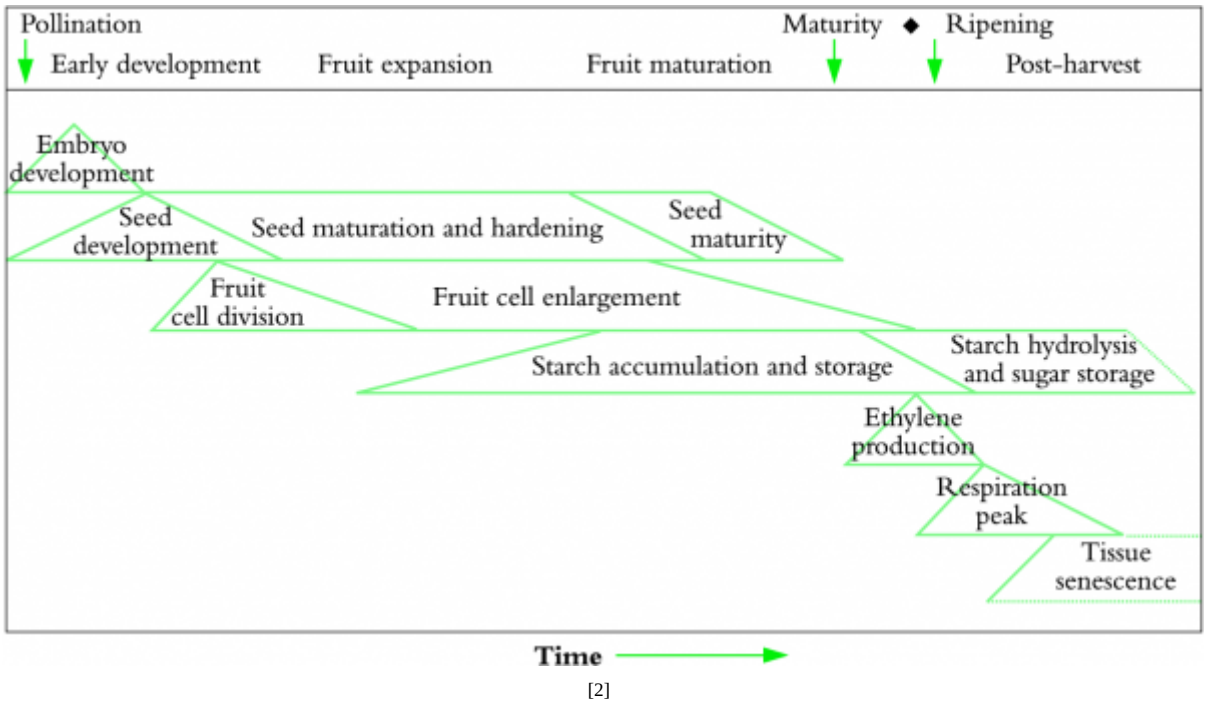
(Based on Chalmers and van den Ende 1975)

Fruit can increase in mass or volume by 100-fold or more from fertilisation to maturity, and such changes commonly follow a sigmoid curve (Figure 11.2 for peach; see Harris *et al.* 1968 for grape). Interpretation of such growth curves is complex because a single variable (mass, length, volume) is commonly applied to an object which contains several organs and different tissue types, each

developing at their own rate and in accordance with their own program. Moreover, at a cellular level, comparative levels of division and expansion change with ontogeny, while shifts in airspace percentage also play a part in volume increases. Added to this, changes in storage products (oil, starch and sugar) and structural carbohydrate (endocarp thickening) influence dry matter content. Representative cases are covered later.

11.2.2?Cell division and enlargement

Despite complexities of fruit growth and development, there are some overall consistencies in patterns of cell division and enlargement, as well as tissue differentiation and fruit enlargement (Figure 11.3). During the ?rst one to four weeks, flesh volume increases rapidly and embryo volume remains small. Growth at this time is mainly the result of cell division. In many commercial fruits (e.g. apple, kiwifruit, tomato and peach), cell division may cease a few weeks after anthesis, and fruit growth slows down, reflected as an inflection in the growth curve, and signalling an end to the ?rst sigmoid phase.



[2]

Figure 11.3 A great number of complex process are intergrated in space and time during seed developmnet and fruit growth and shown here schematically. In broad terms, embryo differentiation and seed development are already well advanced as pericarp enlargement gets underway, and seed maturation usually precedes onset of ripening; consequently fruits ingested prematurely still represent vehicles for seed dispersal. A phase of carbohydrate accumulation during fruit maturation gives way to starch hydrolosis and sugar storage during maturation, accompanied by a peak in ethylene output and respiratory activity as fruits ripen.

(Original diagram courtesy I.B. Ferguson)

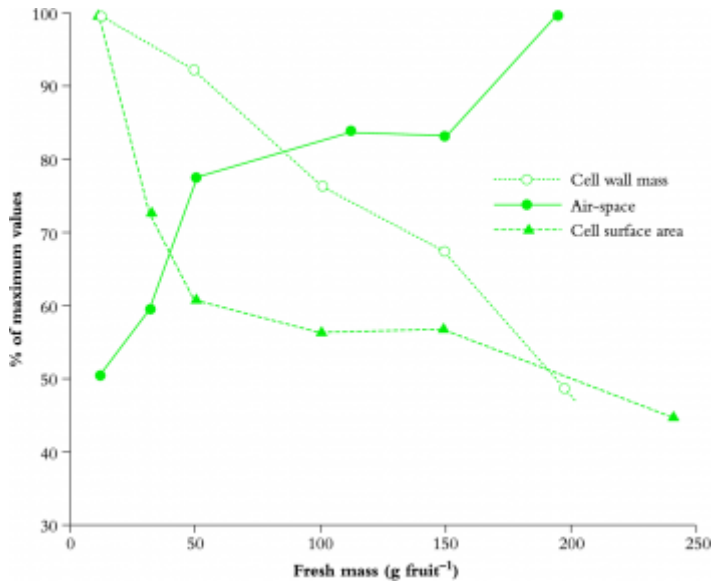
During early growth, the fertilised embryo and endosperm develop and seeds start to form (Figure 11.3). A second phase begins where the pericarp resumes growth and continues to enlarge until slowing for a second time as fruit mature. This second phase in fruit growth is mainly accomplished by cell expansion in longitudinal, radial and tangential planes. Longitudinal growth, where cells enlarge

parallel to the long axis of the fruit, will often be a big factor for development of elongate fruits such as cucumber and marrow. Radial growth increases diameter as in some pumpkins. Increases in cell volume during fruit growth can be considerable. Mature watermelons end up with some of the largest parenchyma cells in the Plant Kingdom, about 0.7 mm in diameter (Bollard 1970).

In contrast to this general pattern where cell division ceases after a few weeks, pericarp cells of avocado fruit continue to divide over the whole growth period so that cells in mature fruit are still relatively small (Schroeder 1953).

Cell enlargement is not a uniform process. Cells in various regions of a fruit often enlarge at different rates and in different planes, so that many mature fruit show strong gradients in cell size from their surface to the centre. In apple fruit, cells closest to the core are smallest, with cell size increasing towards the fruit surface. Conversely in many berries, such as cucumber, kiwifruit and grape (Harris *et al*. 1968), the smallest cells are found in outer regions of the pericarp, with size increasing progressively towards inner regions.

11.2.3?Cell differentiation



[3]

Figure 11.4 Physical characteristics of apples change during growth and development with a notable increase in gas space to a maximum of around 0.1 mL gas mL^{-1} tissue at maturity, and corresponding decrease in cell wall mass to around 15 mg g^{-1} fresh mass. Cell surface area shows an early rapid decrease from around 340 cm^2 mL^{-1} tissue.

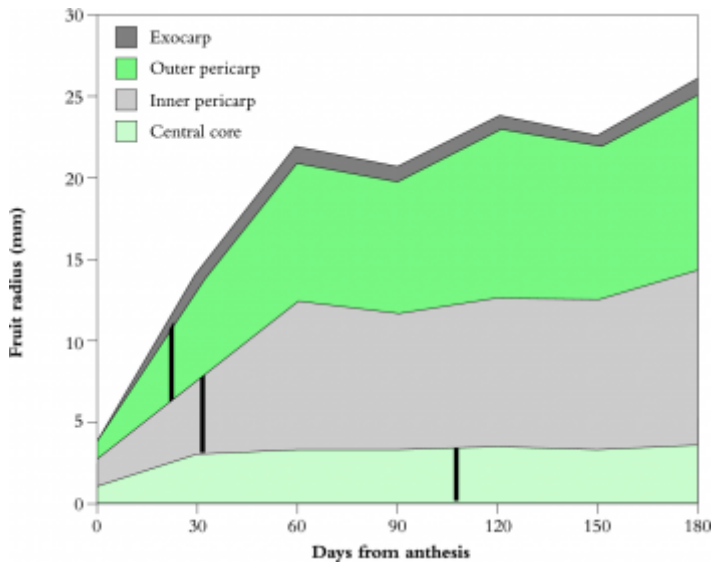
(Based on Harker and Ferguson 1988)

Patterns of cell growth and differentiation in cell layers can influence the quality of mature fruit. For example, pepino fruit with a compact exocarp composed of tightly packed cells are less likely to bruise during postharvest handling than cultivars having large intercellular airspaces. As cell size increases during development, other accompanying characteristics also change, such as cell wall thickness, differentiation of speci?c cell types (e.g. sclereids) and formation of cell inclusions (oil, raphides). In feijoa and pear, development of sclereids in the mesocarp provides the characteristic gritty texture. As another example, juiciness of orange depends on prior differentiation of juice sacs in the endocarp (see

Bain 1958 for anatomical development of citrus fruits).

Extent and distribution of airspaces are particularly important, affecting both fruit texture and physiological properties. For instance, in apples, airspace relative to fruit volume can double during development, while cell wall thickness and relative cell surface area both decline (Figure 11.4). Such changes affect gas exchange and diffusion of solutes through pericarp tissues due to increased tortuosity.

11.2.4?Kiwifruit development: a case study



[4]

Figure 11.5 Radial growth in kiwifruit is due mainly to enlargement of outer and inner pericarp. Vertical lines indicate cessation of cell division in each tissue.

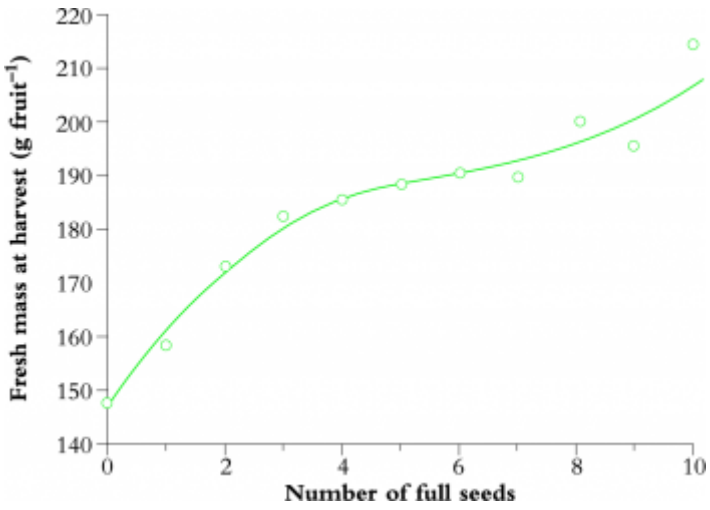
(Unpublished data courtesy K. Gould and I.B. Ferguson)

Development of kiwifruit fruit is particularly complex. All tissues of the mature fruit (exocarp, outer and inner pericarp and central core) are already discernible in the ovary before anthesis and pollination. Each layer grows to a different extent and at different rates, so that the relative contribution of each to the total fruit volume varies with time (Figure 11.5). Cell division ceases ?rst in the exocarp and last in the innermost regions of the central core. The outer pericarp is ?rst seen as a homogeneous population of cells but by 14 d after pollination two cell types become visible, namely small isodiametric parenchyma cells full of starch grains, and much larger heavily vacuolate ovoid cells in which the frequency of starch grains per unit volume is low. The larger cells grow more rapidly than the smaller cells, and both cell types grow more rapidly in the inner regions towards the central core.

Anatomy affects our perceptions of kiwifruit quality. Hairs are developed as multicellular projections of the skin, giving a characteristic bristly appearance and rough feel. Tough skin relative to soft flesh is another important character imparted by development of primary cell wall thickenings in the hypodermal collenchyma. Ripe fruit colour is due to tannin deposits in those same cells. In addition, some small parenchyma cells in the outer pericarp deposit calcium oxalate crystals (raphides), surrounded by polysaccharide mucilage, and this tissue can cause throat irritation in many people.

11.2.5?Seed development and fruit growth

Fertilisation is generally crucial for fruit set and pericarp development (Figure 11.1). As fertilised ovules develop into seeds, this influence on pericarp growth continues where production of hormones by the endosperm and developing embryo promotes pericarp growth. The importance of seeds as sources of hormones for initiation and stimulation of fruit growth is implied by fruit response to exogenous hormones in parthenocarpic systems (development of fruit without seeds).



[5]

Figure 11.6 Fruit size in Braeburn apples depends closely on number of viable seeds per fruit (up to a normal maximum of 10 per fruit) emphasising the strong influence that seed development has on fruit growth.

(Based on Broome 1995)

Applying auxin and gibberellins to unfertilised embryos is one way of achieving parthenocarpy; another is to use auxin transport inhibitors such as chloroflurenol to prevent loss of auxin from embryos so that a threshold level for pericarp response is exceeded. Studies of parthenocarpy in tomatoes and cucumbers indicate that high auxin levels enhance embryo cell division, and this cell division phase seems to be more critical than subsequent cell expansion in determining ?nal fruit size.

Such results imply a cooperative mode of action where gibberellins combine with auxins to initiate cell division. Seed cytokinins and cell division are similarly related (Gillaspy *et al*. 1993) because tomato seeds accumulate cytokinins which subsequently influence cell division in surrounding pericarp tissue (Bohner and Bangerth 1988).

Such interdependence between seed development and fruit growth shows up in ?nal size, and apple seed numbers frequently correlate with fruit growth (Figure 11.6) or with shape and size of fruit. As a case in point, inadequate pollination of kiwifruit (Figure 11.1) results in distortion, and a curvilinear relationship emerges between seed number and fruit weight (Hopping 1986). A similar response is obtained when young seeds are surgically removed from immature strawberry fruits, causing a corresponding distortion in flesh development.

Despite ample evidence that natural control of fruit shape is primarily exerted by plant hormones originating from seeds and stimulating growth to varying degrees, this is not true for all fruit. In banana, fertile seeds actually suppress development of the fleshy pulp. In this anomalous case, fertilisation failure *allows* an ovary to grow.

In marrow, tomato and kiwifruit, ovary shape dictates spatial distribution of seeds. They in turn influence pericarp growth, so that fruit size and shape then become a function of initial ovary shape plus subsequent fertilisation and seed development.

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