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Fruit set and development: Pre-requisites and enhancement in temperate fruit crops

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Abstract

Fruit set is the transformation of ovary to a rapidly growing young fruit which is initiated after successful pollination and fertilization. The various prerequisites for good fruit set are the development of flower buds, certain temperature range for good pollination, pollen tube growth, fertilization and relatively high level of photosynthates for developing fruit. Three general categories of limited fruit set recognised may be attributed to limited pollination, limited nutrients and precocious abscission of flowers (Verma and Jindal, 1985). Pollination is an essential process for fruit set, fruit growth, fruit quality, and seed set of temperate fruits mostly apple cultivars. The first step of successful pollination is the transfer of pollen to the stigmatic surface (typically vectored by bees) followed by an adhesion of pollen grains to the papilla cells of the stigmatic surface (Dresselhaus and Franklin-Tong, 2013). Once pollen reaches the base of the style, one sperm nucleus fuses with the egg cell to produce the embryo (resulting in seed set), and the other fuses with the two polar nuclei to produce the endosperm. Pollen source and temperature have a tremendous influence on the rate of pollen tube growth. Almost all apple cultivars are reported to be either self-incompatible or semi-compatible and require cross-pollination to set fruit in marketable quantities (Garratt *et al*., 2014). For commercial production, at least two cross-compatible cultivars with synchronous flowering are recommended (Banday and Sharma, 2010). There is significant decline in fruit set with increasing distance between pollinizer and main cultivars, and pollinizers should be planted at proper ratio i.e. 11%, 15%, 25% and 33% for effective pollination (Pandith, 2014). Pollen source is considered to be one of the most influential factors affecting the fruit set. Pollen density on the stigmatic surface is positively correlated with pollen tube growth and fruit growth rate (Zhang *et al*., 2010). Fruit set improvement can be increased by growth regulators like auxins, cytokinins and gibberellins. This effect can be obtained by natural hormones extracted from the plant itself or by exogenous application of synthetic substances. Other substances like thidiazuron, CPPU (Petri *et al.*, 2010), Prohexadione calcium (P-Ca) (Greene, 2008), and some micronutrients, especially the boron (Lee *et al.,* 2009) increases fruit set especially in apple. Apple seeds, during their development in the fruit, produce a sequence of different types of hormones, the appearance and disappearance of which is linked with successive stages in the development of the endosperm and embryo. Fruits with no seeds or with only a low seed content are not normally able to survive this competition (Bramlage *et al*., 1990).

Keywords: Fruit set, pollination, growth regulators, seed content

Introduction

Fruit set is the transformation of ovary to a rapidly growing young fruit which is initiated after successful pollination and fertilization. The various prerequisites for good fruit set are the development of flower buds, certain temperature range for good pollination, pollen tube growth, fertilization and relatively high level of photosynthates for developing fruits. In spite of adequate flowering, low fruit yields in orchards have been experienced because of low initial fruit set and subsequently higher fruit-let abscission. In an orchard, all the trees do not bear fruits equally or regularly and sometimes fail to flower and bear fruit under similar conditions where another fruit tree bears heavily. Initial fruit set is one of the serious problems of orcharding and its causes need to be understood properly for effective control and obtaining of an economically acceptable production level. In most plants, fruit set does not occur with all flowers, even though every flower or floret is pollinated and plant is in good health. The extend of natural shedding varies with species. Large fruited types such as apple may shed 95% or more of their flowers and young fruit, while as small fruited species like blueberry might shed only 20-30% of them (Westwood, 1967) [67]. Factors affecting fruit set may be broadly categorized into two categories: internal factors and external factors. Internal factors include Pollination (Pollinating agents & Pollinizers), Sex distribution, Defective sex organs, Stigmatic receptivity, Incompatibility, Non-viable pollen. External factors include: temperature, humidity, rain, chemical & pesticides, wind, light and nutrition.

Factors affecting fruit set

1. Pollination

Pollination is an essential process for fruit set, fruit growth, fruit quality, and seed set of most of the temperate fruit cultivars. The first step of successful apple pollination is the transfer of pollen to the stigmatic surface (typically vectored by bees) followed by an adhesion of pollen grains to the papilla cells of the stigmatic surface (Dresselhaus and Franklin-Tong, 2013) [15]. The deposited pollen hydrates and germinates and then pollen tubes penetrate the stigma and grow down the style. Pollen recognition occurs both on the stigmatic surface and within the style (Dresselhaus and Franklin- Tong, 2013) [15]. Once pollen reaches the base of the style, one sperm nucleus enters the egg cell to produce the embryo (resulting in seed set), and the other fuses with the two polar nuclei to produce the endosperm. The factors influencing pollination and fertilisation are similar for all temperate deciduous tree fruits. The pollinating cultivars (pollinizors) must produce sufficient quantities of viable and compatible pollen and flower at approximately the same time as the main commercial cultivar. There also must be adequate pollen vectors, usually insects such as bees, in the orchard at flowering time and the pollen must be sufficiently attractive to these vectors. Almost all apple cultivars are reported to be either self-incompatible or semi-compatible and require cross-pollination to set fruit in marketable quantities (Garratt *et al*., 2014) [18]. For commercial production, at least two cross-compatible cultivars with synchronous flowering are recommended (Banday and Sharma, 2010) [5]. There is significant decline in fruit set with increasing distance between pollinizer and main cultivars, and pollinizers should be planted at proper ratio i.e. 11%, 15%, 25% and 33% for effective pollination (Pandith, 2014) [41]. Pollen source is considered to be one of the most influential factors affecting the fruit set. Pollen density on the stigmatic surface is positively correlated with pollen tube growth and fruit growth rate (Zhang *et al*., 2010) [71].

Features of a good pollen source variety

- Has viable pollen that germinates well
- Is cross-compatible with the main variety
- Bloom period overlaps that of the main variety
- Blooms at a young age
- Blooms annually
- Is not excessively susceptible to diseases
- Is winter hardy
- Produces pollen at relatively low temperatures
- Bear good, attractive, marketable fruits

Recommended varieties and pollinizers for apple in Jammu and Kashmir

Season	Main	Pollinizers
Early Season	Irish Peach, Benoni, Early Shanburry, Mollie's Delicious, and Early Red One.	Tydeman's Early Worcester, Summer Queen.
Mid Season	Gala Mast, Cooper IV, Oregon Spur, Vance Delicious, Well spur, Red chief, Imperial Gala, Red Fuji, Red Spur, Firdous, Shireen and Top Red.	Sparten, Red Gold, Ginger Gold, McIntosh and Lord Lambourne.
Late Season	Royal Delicious, Ambri, Rich-a-Red, Lal Ambri, Red Delicious and Akbar.	Golden Spur, Granny Smith, More Spur Gold, Sunhari, Golden Delicious

Compatible Pollinizers for pear

S. No.	Cultivars	Pollinizers
1.	Bartlett	Fertility, d'Anjou, Bosc, Comice, Clapps Favourite and Conference.
2.	Bosc	Bartlett, Comice, d' Anjou, Seckel.
3.	Comice	Bartlett, Bosc, d' Anjou Seckel.
4.	d' Anjou	Bartlett, Comice Bosc, Seckel.
8.	Seckel	Comice, Bosc
9	Conference	William, Beurre Bosc, Anjou and Docteur Jules Guyot

Compatible Pollinizers for peach

S. No.	Cultivars	Fruitfulness	Pollinizer
1.	Almost all common varieties of peaches	Self-fruitful	
2.	J.H. Hale, Earlihale, Hal-Berta, Candoka and July Elberta of peaches.	Self unfruitful	Mostly all other varieties of peaches will pollinate these self unfruitful varieties

Pollinizers for sweet cherry

S. No.	Cultivars	Pollinizers
A.	**Sweet cherry**	
1.	Bing	Sam, Van, Montmorency, Rainer, Stella, Compact Stella, Garden Bing
2.	Lambert	Sam, Van, Montmorency, Rainer, Stella, Compact Stella, Garden Bing
3.	Rainer	Sam, Van, Bing, Royal Ann, lambert, Montmorency, Stella, Compact Stella, Garden Bing
4.	Royal Ann	Sam, Van, Montmorency, Rainer, Stella, Compact Stella, Garden Bing
5.	Stella, Compact Stella, Garden Bing, Vandalay, Black Gold, White Gold, Glacier.	Self- Fruitful
B.	**Sour Cherries:**	
	Montmorency, North Star, Montmore, Meteor, English Morello, Early Richmond, Hansen Bush Cherry and Nanking.	• Self-fruitful

Compatible pollinizers for plums

S. No.	Cultivars	Pollinizers
1.	Burbank	Satsuma, Shiro, Santa Rosa.
2.	Santa Rosa (partially self fruitfull)	Satsuma, Shiro, Burbank.
3.	Satsuma	Shiro, Santa Rosa, Burbank.
4.	Damson, Green Gage (Reine Claude), Stanley	Self-fertile

Pollinizers for almond varieties

Cultivars	Pollinizers compatible
Makhdoom	Shalimar and Waris
Shalimar	Makhdoom and Waris
Waris	Makhdoom And Shalimar
Parbat	Makhdoom
Most of the cultivars except Non-Pariel	IXL and Ne- Plus Ultra
Peerless and Price	Non-Pariel

Pollinizers for Kiwifruit

S. No.	Pollinizers for Kiwifruit
1.	Tomuri, Matua
2.	Aresti, Chico male
3.	Hermaphordite cultivars Blake

Recommended number of hives in different fruit crops.

Fruit crop.	Number
1. Almonds.	5-8 hives/ha.
2. Apple.	3-5 hives/ha.
3. Apricot.	2-3 hives/ha.
4. Cherries.	2-3 hives/ha.
5. Pear.	3-4 hives/ha.
6. Peaches, plums and nectarines.	2-3 hives/ha.

Temporary aids to pollination

Used when low temperature kill or delay the bloom on pollinizer variety or weather condition reduce honey bee activity. These methods include:

- Flowering branches of other cultivars ('bouquets') can be placed in containers with the cut end in water. The bouquets should consist of large branches and some dehiscing as well as unopened blossoms. Large concentrations of bees should also be maintained in the orchards at the time when bouquets are placed.
- Pollen can be purchased from commercial companies and used in inserts placed at the entrance of honey bee (Aphis melifera). Bees exiting the hive unwillingly pick up pollen and carry it to the flowers visited.
- Pollen can also be 'dusted' on trees by dropping it into the draught created by an air-blast sprayer.
- Flowers can be pollinated by hand, but the labour cost is high, even though only one or two flowers in several cluster need to be treated.

2. Plant Growth Regulators

According to Looney (1996) [29], and Taiz and Zeiger (2004) [59], growth regulator substances containing auxins, cytokinins and gibberellins may influence the final fruit size by increasing the division and cell elongation (Table 1). Plant growth and productivity increase, as well as resistance to stress periods, can be obtained by bioregulators application (Jorquera and Yuri, 2006) [24]. Among the plant hormones, auxins, cytokinins and gibberellins may be effective in increasing fruit set (Mariotti *et al*., 2011) [33]. This effect can be obtained by natural hormones extracted from the plant itself or by exogenous application of synthetic substances. To improve fruit set in apple trees are cited the substances like thidiazuron (Petri, 2010; Amarante *et al*., 2003; Table 2) [43, 3], CPPU (Argenta, 1991) [4], P-Ca (Greene, 2008) [20], and some micronutrients, especially the boron (Nyomora *et al*., 2000) [39]. The vigorous growth of branches reduces productivity by increasing of gibberellins in tissues and reducing light penetration in the canopy (Prive *et al*., 2004) [44]. Vigorous growth may negatively affect productivity, fruit quality and disease control. Application of certain growth regulators at specific stages of development can reduce tree vigor (Miller, 1988) [35]. A class of inhibitors of gibberellins biosynthesis, the cyclohexane trione has the ability to control the vegetative growth (Rademacher *et al*., 1992) [46]. This class includes the Prohexadione calcium (P-Ca), which is particularly effective and has the potential to increase the productivity of apple trees and reduce the need for pruning (Rademacher, 1992) [46]. Although the apple tree needs 5 to 10% of flowers fertilized to obtain high production (Dennis, 1996) [14], in adverse pollination conditions or when the flowering intensity is small, it may be necessary the growth regulators application to improve fruit set.

Table 1: PGR's in Fruit Set

Fruit Crop	Growth regulators	Response
Apple	Paclobutrazol 1000ppm	Improve fruit set
	GA3+NAA	Increase initiation and final set
	Daminozide @ 2000ppm	Increase flower buds
	Ethephon	Decrease fruit set Increase size of fruit
Grapes	GA3	Increase fruit set causes berry enlargement
	CCC@ 2000 mg/l	Increased fruit set Inhibited shoot growth
Mango	Paclobutrazol	Improve fruit set and retention
	CPPU (10 ppm) 14 days after bloom	Increase fruit retention, yield and quality
Citrus	GA_3	Increase fruit retention
	2,4-D@10ppm	Increase fruit retention
	Paclobutrazol @ 2.5g/L	Increase fruit set
Pear	GA3@50ppm	Increase fruit set and retention, Parthenocarpy
	Chlormiquat@ 500ppm	Role in flowering & fruit set
Peach	CCC 1000 ppm	Improved fruit set in Le Conte
	Alar @ 500ppm	Increase fruit set and fruit size

Table 2: Effect of Pro-hexadione calcium and Thidiazuron on fruit set in Royal Gala/M9 (Rootstock)

Treatment	Fruit set %	Number of Fruits/tree	Yield(kg/tree)
Control	50.75	332.83	32.75
TDZ (10mg/L)	70.95	361.33	38.97
P-Ca (55mg/L)	62.38	430.50	48.40
TDZ + P-Ca	96.88	606.50	62.6

3. Stigmatic receptivity

It is the ability of the stigma to support pollen germination and it limits the effective pollination period (it is defined as the number of days during which the pollination is effective in producing a fruit and is determined by the longevity of ovules minus the time lag between pollination and fertilization) in fruit crops. Cessation of stigmatic receptivity has been associated with degeneration of stigma and rupture of papillar integrity in kiwi fruits (Sanzol and Herrero, 2001) [53]. In 'Agua de Aranjuez', pear stigmatic receptivity is a limiting factor for flower receptivity. The highest initial fruit set was recorded for flowers pollinated at anthesis and 2 days after anthesis. After 4 to 6 days, fruit set was significantly reduced. Thus, stigmatic receptivity could be an important factor limiting pear flower receptivity (Sanzol *et al*., 2003; Figure 2) [54]. Fruit set in kiwifruit after hand pollination was high, averaging 80% during the first 4 days following anthesis. However, when flowers were pollinated 5 days after anthesis, fruit set was decreased to 36% followed by 7 days after anthesis where fruit set was practically nil (Figure 1). Thus, the effective pollination period (EPP) was limited to the first 4 days and the stigmatic receptive averaged 84% and sharply reduced to nil after 7 days (Gonazel *et al*., 1995; Figure 1) [19].

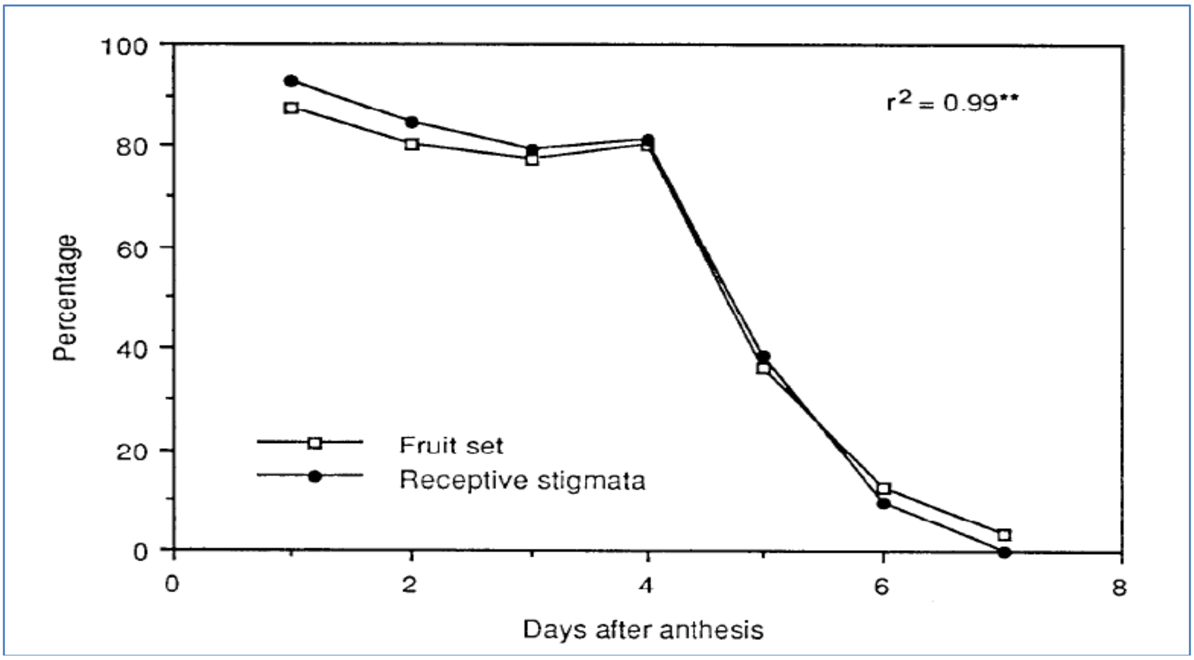


Fig 1: Stigma receptivity and fruit set in "Hayward" cv. of kiwi fruit

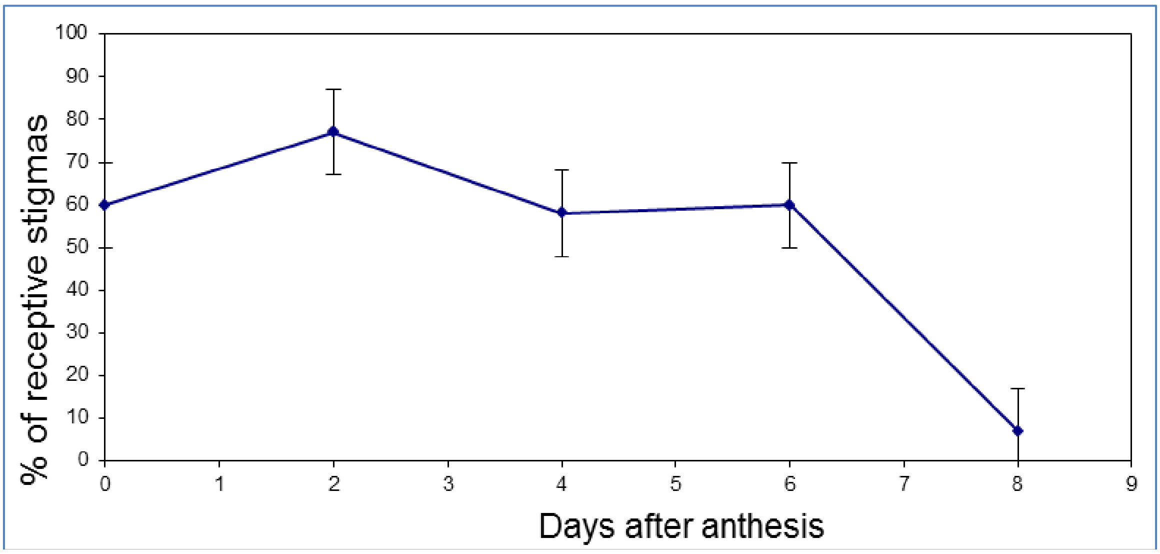


Fig 2: Percentage of receptive stigmas of flower pollinated 0, 2, 4, 6, 8 and 10 days after anthesis in pear (cv. Agua de Aranjeuz)

4. Incompatibility

Incompatibility is defined as failure of viable pollen to grow down the style of flower of the same variety (self in compatibility) or of the different varieties (cross incompatibility). Many cross-pollinating species exhibit self-incompatibility, so that fertilization by their own pollen is disfavored or prevented through physical or biochemical factors. There are different degrees of self-incompatibility, and many self-incompatible species will produce a few fruit even when self-pollinated. Thus, a single apple tree may have a bushel or so of fruit, since apples are not completely self-incompatible, but the same tree may produce several bushels if cross-pollinated. Horticulturists have coined the terms "self-fruitful" and "self-unfruitful" to describe cultivars that can set commercial crops or cannot set commercial crops (respectively) when self-pollinated. Thus, self-fruitful and self-unfruitful are economic or horticultural terms, whereas self-incompatible or cross-incompatible are botanical terms. Self in compatibility is more common in fruit crops like apple, pear, sweet cherry, almond, avocado, fig, mango, citrus, olive, etc. than cross incompatibility (apple, pear, sweet cheery, European plums and almond). The sexual incompatibility is a genetic mechanism to ensure outcrossing of plants, thus it brings together germ cells of potentially greater genetic diversity. Incompatibility is a genetically controlled character manifested by the presence of multiple alleles at a single locus. In fruit production, incompatibility may create a platform to create variation leaving no scope for inbreeding. In mango, self un fruit fullness is reported in cvs. Dashehari, Chausa and Langra (Ram *et al.*, 1976) [47]. Most pear (*Pyrus communis* L.) cultivars are impaired to set fruit under self-pollination because self-fertilization is prevented by game tophytic self in compatibility system (Sanzol, 2007) [52]. In loquat varieties, improved golden yellow, pale yellow, golden yellow and the pollen tube penetrated the stylar canal up to 1/4 to 1/3rd of its length and did not go further below, even after 72 h of pollination. As such, this suggests incompatibility in loquat (Singh and Rajput, 1964) [56]. In pear cv. ‘Agua de Aranjuez’, 80% of the pollen tube reaches the base of the style and fertilized 70% ovules after cross-pollination, whereas only 10% pollen tube reaches the ovule and fertilized only 5% of the ovule which indicates a high degree of incompatibility in pear (Sanzol, 2007) [52].

5. Non viable pollen

It is due to non-functional pollen or the ovule. Non-viability or impotence of pollen results in unfruitfulness. Unfruitfulness in the case of muscadine grape is due to defective pollen. In grapes, sterile pollen results from degeneration processes in the generative nucleus or arrested development prior to mitosis in microspore nucleus. Triploid apples are examples of varieties whose pollen has poor viability. Late flowering in apricot genotypes showed lower pollen viability than early flowering genotypes (Ruiz and Egea, 2008) [50]. Under field conditions at moderate temperatures, high humidity, and high light intensity, pollen has a short life and normally is viable for only a few hours, however, at low humidity, low light, and sub-freezing temperatures, pollen may remain viable for several years.

External factors

1. Temperature

Among the environmental factors, temperature has a great importance. It affects flowering and fruit set in several ways. Also temperature is important in bee flight. Bees will not fly well in rain, strong wind or at temperatures below 10^0C. It is a common knowledge that a period of cool, yet frostless, weather is conducive to better blossoming, fertilization and fruit set. However, the abscission of flower bud, fruit, etc. is a function of temperature.

High temperature: Above 32°C, desiccation of the stigmatic surface and more rapid deterioration of embryo sac occurs (Jindal *et al.*, 1993) [23]. Rodrigo and Herrero used a polythene cage induced a mean increase in the maximum temperature of 7.6°C (warm treatment) and results revealed that in the control treatment, most of the flowers (92%) had morphologically well-developed pistil, while in warm treatment, 33% of the flowers presented pistils that are not completely developed and 13% of the flowers shows short styles and unswelled ovaries (Rodrigo and Herrero, 2002; Figure 3) [49] As temperature increases, ovule senescence become faster in ‘Italian’ than in ‘Brooks’ cultivar of plum. At 15°C, only one ovule per flower remains viable by 8 DAFB for Italian, whereas for ‘brooks’ cultivar, higher temperature results to a decrease in ovule longevity (Moreno *et al.*, 1992) [37].

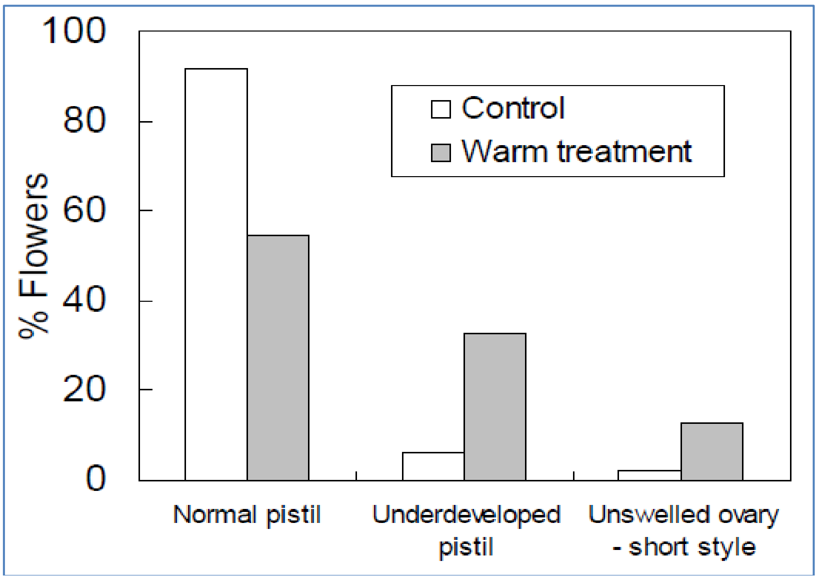


Fig 3: Effect of temperature on flower development of apricot (cv. Monique)

Low temperature: In plum, cherry, apple, pear, etc., the temperature of 4.4°C or lower, completely check the blooming, fertilization and fruit set (Jindal *et al*., 1993) [23]. Fruit set and production of fruit in peach var. Granda were absent or very low in green house grown trees in orchards. Nava *et al*. (2009) [38] found that a rise of the diurnal air temperature in the interior of the greenhouse promoted a significant reduction in the production of pollen grains. De Long in his studies on pollen tube growth rate of crab apple cv's found that pollen tube growth increased with increasing temperature until 24^{0}C (Table 3) but pollen tube growth rate didn't increased further between 24^{0}C & 30^{0}C. The study also indicated that maternal genotype also influences the pollen tube growth rate with highest being in cripps pink followed by fuji at 24^{0}C

Table 3: Apple pollen tube growth rates as regulated by environment

	Mean apple pollen tube length (mm)		
Temp (^{0}C)	**Cripps Pink**	**Golden Del.**	**Fuji**
12	0.0	0.0	0.0
18	0.9	0.0	0.47
24	1.0	0.3	0.57
30	0.2	0.1	0.24

2. Humidity

Low atmospheric humidity causes drying of stigmatic secretions. Wet and humid weather favours anthracnose and poor fruit set in mango. The poor germination of pollen in almonds is attributed to damp weather during fruit set.

3. Rain

It directly affects fruit setting by disturbing the process of pollination and germination of pollen grains and staminal fertilization. In almond washing treatment decreased the number of germinated pollen grains on the stigma mainly when the flowers were immersed before pollination and it seems to affect adhesion in forthcoming pollinations (Ortega *et al*., 2007) [40]. Rains at the time of blooming period causes unfruitfulness by washing pollen grains, inhibit pollinators and cause spread of diseases and pests. Every fruit species need a specific time period without rains at the time of blooming for successful pollinations.

4. Light

Light affects fruitfulness indirectly by its effect on photosynthesis. Light is a pre-requisite for photosynthesis and low light intensity or its duration reduces the carbohydrates reserves in the trees. In addition to this, poor light conditions promote fruit abscission.

5. Nutritive condition of plant

Nutrition of plant controls the percentage of defective pistils. Defective pistils are formed especially on exhausted or weakened plants caused by overbearing, drought and poor nutrition. Nutrition also determines the percentage of flower carried for setting, maturity and also pollen viability. Fertilization in flowering plants begins when the pollen lands on a stigma. This process continues during the pollen germination and the tube grows through intercellular spaces within the pistil, and fertilizes when the pollen tube reaches the ovary, thereby initiating the fruit setting process. Boron also appears to be a requirement for pollen tube extension, and may contribute to the formation of sugar–borate complexes which promote absorption, translocation, the metabolism of sugars in pollen, and also participate in the synthesis of pectic material, which is utilized in the formation of the cell walls of actively growing pollen tubes. The requirement of boron for proper pollen germination and tube growth has been demonstrated in both in vitro and in vivo experiments (Nyomora *et al*., 2000; Jayaprakash and Saria, 2001; Wang *et al*., 2003) [39, 22, 64]. Nyomora *et al*. (2000) [39] reported that the application of boron to almond trees resulted in enhanced pollen germination and pollen tube growth. In a study involving the 'Conference' pear (*P. communis*), Wojcik and Wojcik (2003) [70] reported that pre-bloom and post-harvest boron sprays were successful in enhancing the yields of pear trees. Nitrogen application after terminal bud formation led to the development of flower with enhanced embryo sac longevity. Pollen tube growth in pear was significantly stimulated by increasing concentration (25 – 200 mg/L of boric acid) and the values are significantly higher at 200 mg/L concentration of boric acid (Lee *et al*., 2009 ; Table 4) [26]. In walnut cv. Local selection, the highest fruit set (32.50), fruit retention (41.35) and nut yield (4.02 kg/tree) was recorded under foliar application of H_3Bo_3 + Paras (0.1 % + 0.6 ml/L) (Tomar and Singh, 2007) [60].

Table 4: Effect of foliar application of Boron on pollen tube growth in Pear

Applied boron (mg L^{-1})	Housui		Wonwhang	
	Germination (%)	Pollen tube length (μm)	Germination (%)	Pollen tube length (μm)
0	42.9	106	59.3	100
100	78.6	161	76.8	167
200	86.3	192	89.5	195

6. Wind

Wind also affects the fruitfulness indirectly by its effect on the pollinating agents, that is, it controls pollination either by promoting wind pollination or by checking insect pollination. It is desirable in wind pollinated fruit trees like hazelnut and walnut, but if its speed is too high, it is harmful because it results in low fruit set on exposed sides and heavy crop on other sides. Excessively, speedy winds cause ovary abortion (Gardner, 1952) [17] and also make the stigma dry.

7. Chemicals and pesticides

The use of pesticides can kill bees, therefore reducing pollination. Some pesticides can also be toxic to delicate flowers causing abortion and loss of fruit. Pesticides spray effects on receptive stigmatic surface, showed varying degree of injury and range from minor surface wrinkling to degeneration of stigma papillae. Controlled pollination for 1 h, after pesticides sprays, results in an inhibition of pollen germination and tube growth (Wetzstein, 1990) [68]. Commercial fungicides containing captan, dinocarp, sulphur and triforine sprayed on undehisced anthers of several apple cultivars reduced the viability of pollen, impaired pollen release, kill pollen when sprayed onto dehisced anthers (Ruth *et al.*, 1978) [51]. Pollen germination and tube growth were drastically suppressed by the spray and almost no fruit set was observed on the treated inflorescence and there was a highly significant difference between fruit set on exposed and protected cluster (Legge and Williams, 1975) [27].

Fruit Development

Fruit goes through a complex developmental sequence over a growing season. Understanding the processes involved, what supports fruit growth and what limits it, helps to support good crop management. Physiologically and biochemically fruit development can be divided into four phases:

- **Phase-I: Fruit Set** It includes ovary development in the flower, a decision to abort or proceed with further development. Growing pollen produces gibberlic acid and application of gibberlins induce parthenocarpic fruit, therefore it is believed that gibberlin is triggering signal. Thereafter there is as increased wave of auxin production by the style and then the ovary. Continued fruit development usually relies on continued presence of developing seed. Seed abortion or removal causes fruit abortion, which can be reversed by auxin application.
- **Phase-II:** This phase involves a period of most rapid cell division. This phase is controlled by developing seed. The number of fertilized ovules in a fruit is correlated with both the initial cell division and the final size of the fruit.
- **Phase-III:** It is the period of most rapid growth when cell division more or less cease, and growth is almost exclusively by cell enlargement. Early in the cell enlargement phase, vacuoles are formed in the cells and these increase in size as the cells enlarge ultimately occupying most of the space in the centre of the cell. In this phase, food reserves are accumulated and most fruits attain their final shape and size before the onset of ripening.
- **Phase-IV:** Ripening phase. It involves softening, increased juciness and sweetness and colour changes in the fruit.

Fruit Growth Pattern

Fruits undergo different developmental stages. A rapid increase of fruit volume after fruit set is usually followed by a period of slower growth. Towards the end of fruit ripening, fruit volume and weight increase again at a faster rate (Lasko and Goffinet, 2013) [25]. This sigmoid growth pattern can be explained as follows: The first stage is a period of rapid cell division with a fast increase in the total number of cells. The “lag” phase which follows is represented by internal structural changes such as the hardening of the stone (i.e. the fruit endocarp) in cherries, plums and peaches, or the ripening of embryos in pome fruits. At the next stage, a cell elongation phase associated with a rapid incorporation of water, fruits appear to grow faster (Aichner *et al*, 2001) [2]. The final fruit size potential, and generally the actual size at harvest, depends primarily on the number of cells in the fruit. And since cell numbers are set in only the first few weeks after bloom, that is a critical time for the whole season. Fruit with low cell numbers from excess competition after bloom, due to late or inadequate thinning, can never catch up later to become large fruit. Thus we can say fruit grows mainly by:

- Cell Division sets potential for ultimate size of fruit
- Cell Expansion achieves mature size

Duration of cell division in flesh of fruits

Fruit	Duration After Bloom
Apple	4-5 Weeks
Pear	7-9 Weeks
Peach	4 Weeks
Plum	4 Weeks
Sour Cherry	10 Days
Avacado and Strawberry	Until Harvest

Fruit growth curve

Apple has a typical S-shaped curve. The growth curve of pear is similar to apple except that it doesn’t show the slow growth period at the end (because pears are picked green-mature). Peach and other stone fruits (also fig, currant, pistachio, and seeded grapes) show double sigmoid curve because of a period of slow growth during pit hardening (Figure 4). During pit hardening both flesh and kernel tissues grow at reduced rates, while the stony endocarp increases rapidly in dry weight. The growth of the seed in length indicates that growth stops at the beginning of pit hardening. Yet growth as measured by dry weight shows that it continues to grow until harvest.

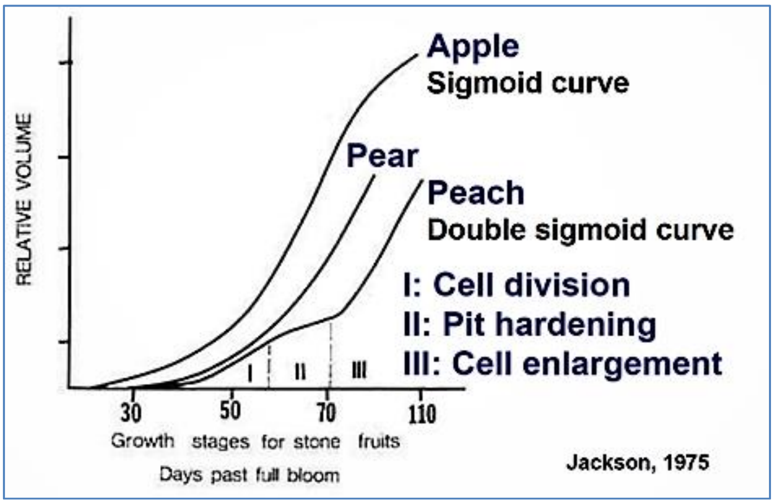


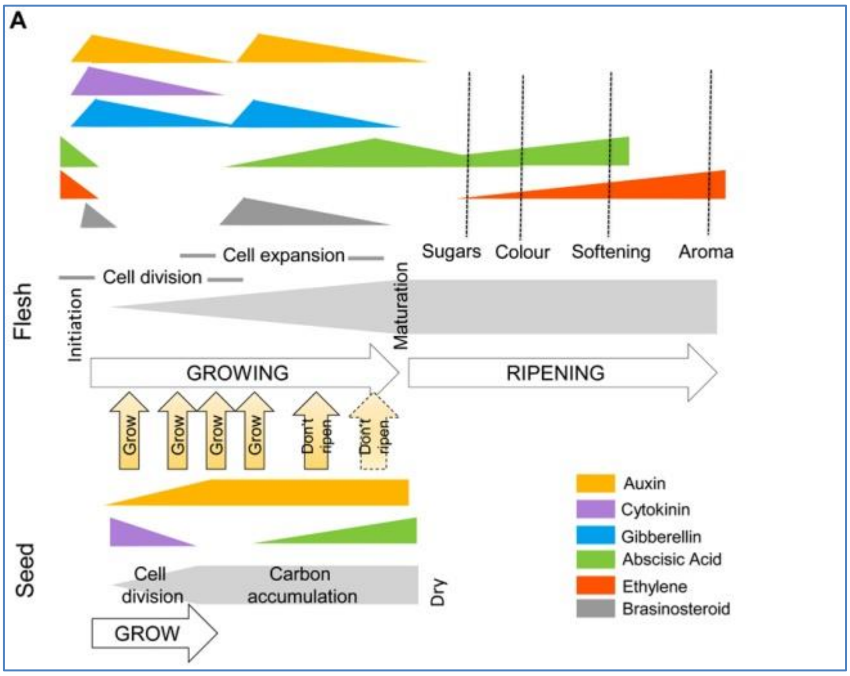
Fig 4: Fruit Growth Curves

Harmonal changes during the fruit development

Apple seeds, during their development in the fruit, produce a sequence of different types of hormones, the appearance and disappearance of which is linked with successive stages in the development of the endopserm and embryo (Figure 5). The first stage of seed development, characterized by the development of a free nuclear endosperm but very little growth of the embryo, is particularly associated with the presence of cytokinins (Zwat *et al*., 1963). Cytokinen levels increase after pollination (Matsuo *et al*., 2012) [34] and are generally considered to play a critical role in the stimulation of cell division during fruit development (Wismer *et al*., 1995; Srivastava and Handa, 2005) [69, 58]. This stage is terminated 4 to 5 weeks after full bloom by the development of the cellular primary endosperm and the appearance in the seed of two indole auxins (Luckwill, 1957) [32] identified as 3-indoleacetylaspartic acid and ethyl-3- indole acetate (Raussendorf – Bargen, 1962) [48].

The second developmental stage is associated with the rapid growth of the embryo, the digestion of the nucellus and primary endosperm and the formation of a secondary endosperm which forms a tight sheath around the fully grown embryo. Luckwill (1969) [30] confirmed the presence during this stage of gibberellins A4 and A7, which first appear 4 to 5 weeks after full bloom and quickly build up to a peak concentration at 9 weeks after bloom, at the time when the embryo has almost reached its final size. Cell expansion is regulated by auxin, gibberlin, and brassinosteroid (Pattison and Catala, 2012) [42]. Cell enlargement depends both on cell wall loosening and increase turgor pressure (Cosgrove, 2005) [10]. While auxin mostly controls cell division during fruit set, it is thought to play an important role during the growth phase by influencing cell enlargement together with gibberllins (Csukasi *et al*., 2011) [12]

One of the main functions of the relatively high concentration of hormones found in developing seeds may be the mobilization of essential metabolites-particularly carbohydrates and soluble nitrogen-against the competing demands of the growing shoots. It is certainly true that fruits with no seeds or with only a low seed content are not normally able to survive this competition, though they can be made to develop if competing vegetative growth is suppressed (Abbott, 1960) [1]. There is also rather strong circumstantial evidence that gibberellins translocated from the seeds to the bourse may inhibit flower initiation in the bourse bud, thus giving rise to the phenomenon of biennial blossoming (Luckwill, 1969) [30].



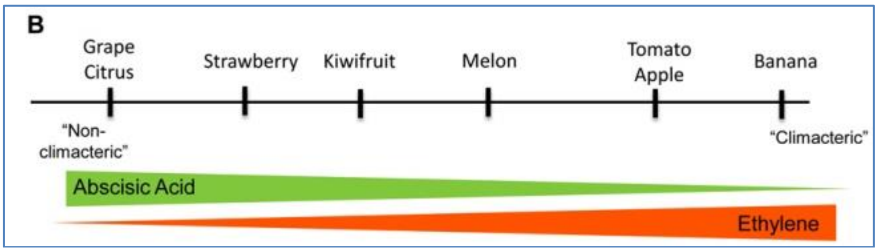


Fig 5: Harmonal changes occurring during fruit development

Factors affecting fruit growth and development

A. Pre-bloom factors and fruit size

1. Spur position and size

The apical (king flower) flower in the bud of apple (*Malus doestica*) develops first, followed by the lateral flower which develop in sequence, beginning at the base of the spur. Some fruits like plum and cherry, bear on both shoots and spurs and it is to be expected that slightly different nutritive conditions are obtained in the different tissues and a distinctly heavier June drop occurs in shoot borne fruits (Gardner, 1952) [17]. Also spur diameter has been seen related to blossom size. Larger spurs tend to be more vigourous and also tend to flower earlier than smaller ones, thus producing larger fruits. Also terminal spurs tend to be larger with considerable longer bourse shoot. Fruit of terminal spur remained significantly larger than those on lateral spurs from blossom through until harvest (Denne, 1963) [13].

2. Age of bearing wood

Two-year spurs and one-year terminals generally produce larger fruit at commercial harvest than did one-year laterals and spurs older than three years (Volz *et al*., 2015 ; Table 5) [63]. In apple, old spurs are less likely to initiate flowers than the young ones.

Table 5: Effect of age of bearing wood on the fresh fruit weight.

Cultivar	Position	Fruit weight (g)
Breaburn	2 yr spur	194
	1 yr lateral	169
	>3 yr spur	148
Granny smith	2 yr spur	177
	1 yr lateral	129
	1 yr terminal	164
	>3 yr spur	147
Fuji	2 yr spur	290
	1 yr lateral	185
	1 yr terminal	280
Royal gala	2 yr spur	153
	1 yr lateral	144
	1 yr terminal	176

3. Pre blossom temperature

Lower temperature produces smaller fruit. It is a common knowledge that a period of cool, yet frostless, weather is conducive to better blossoming, fertilization and fruit set. However, the abscission of flower bud, fruit, etc. is a function of temperature. Early fruit growth (up to 40 DAFB) was significantly affected by the growing temperature environment. Warrington (1999; Figure 6) [65] in apple reported 8 fold increase in fruit mean diameter expansion rate (10 to 40 DAFB) between the 9/3 and 25/ 15^{0}C temperature regimes. Westwood *et al*., (1967)[67] has shown that small fruit usually contain fewer ad smaller cells than larger fruits, and Bergh (1990) [6] demonstrated that higher fruit growth rates under warm early season temperature conditions were associated with increased rate of cell division in the cortical region of fruit.

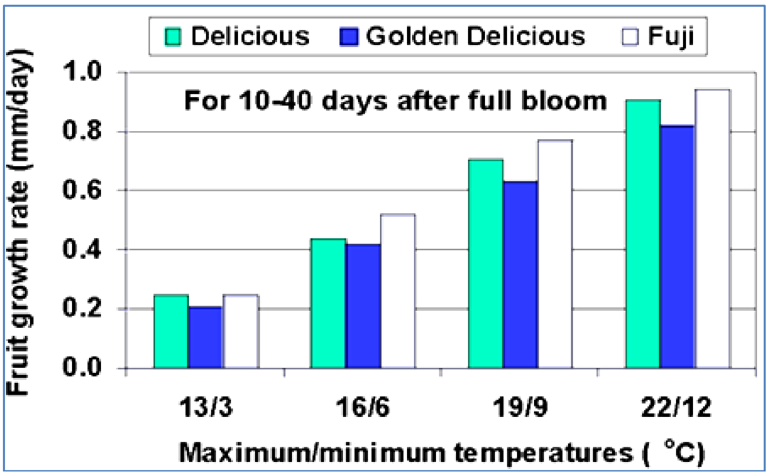


Fig 6: Fruit growth of apple cultivars as influenced by temperature

B. Post-bloom factors and fruit size

1. Crop Load

This year's crop load can influence next year's in two ways. Heavy crops lead to a hormone imbalance that causes biennial bearing (Crassweller *et al*., 2005; Sara *et al*, 2016) [11, 55]. Pear is biennial for the same reason as apple. Seeds release a hormone, gibberellin that moves into buds and prevents them from forming flowers, so they remain vegetative. With a heavy crop there is more of this hormone moving into buds, so fewer of them develop flowers. The other way a heavy crop reduces fruit set is by depletion of stored carbohydrates and nutrients. This weakens the tree and leaves less resources available for early fruit growth (Embree *et al*., 2007; Hampson and Kemp, 2003) [16, 21]. Since there is only a very small leaf canopy present at bloom, early flower and fruit growth depend on stored nutrients until the leaf canopy develops. Sara *et al* (2016, Table 6) [55] reported superior fruit quality of "Honeycrisp" apple under lowest crop load treatment (4.7 and 7.5 fruit/cm^2 TCSA) indicated by increased firmness, dry matter, soluble solids content, and TA.

Table 6: Effect of crop load on Return Bloom in "Honey Crisp" cultivar of Apple

Target No. of Fruits Per Tree	No. of Fruits /Cm^2 TCSA	Fruit Weight	Return Bloom (Blossom Clusters / TCSA Cm^2
30-40	4.7	196.3	38.14
50-60	7.5	151.8	15.68
75-85	11.3	143.7	4.81
90-100	12.5	147.7	6.79
125-135	16.0	130.8	4.28

2. Light

Light controls supply of CHO's, thus increases fruit size. The initial growth of the shoots and flowers at bud break in the spring is supported by carbohydrate reserves in the roots and branches. Gradually, as leaves are produced, there is a transition from solely depending on reserves to obtaining greater support from current photosynthesis of the leaves. According to Lasko and Goffinet (2013) [25] in the first few critical weeks after bloom the carbohydrate support for fruit growth comes from the spur leaves and small "spur like" leaves on the short lateral shoots on last years stems, not from the new extension shoot leaves. This was very clearly seen when they shaded whole trees for 6 days when the fruit averaged about 16 mm diameter and then measured how much growth occurred in fruit versus extension shoots (Figure 7). Even down to 12% of full sunlight, shoots continued to grow at the same rate while fruits were reduced to essentially zero. This heavy shade to 12% of full sun led to complete defruiting of the trees while having no effect on shoot growth.

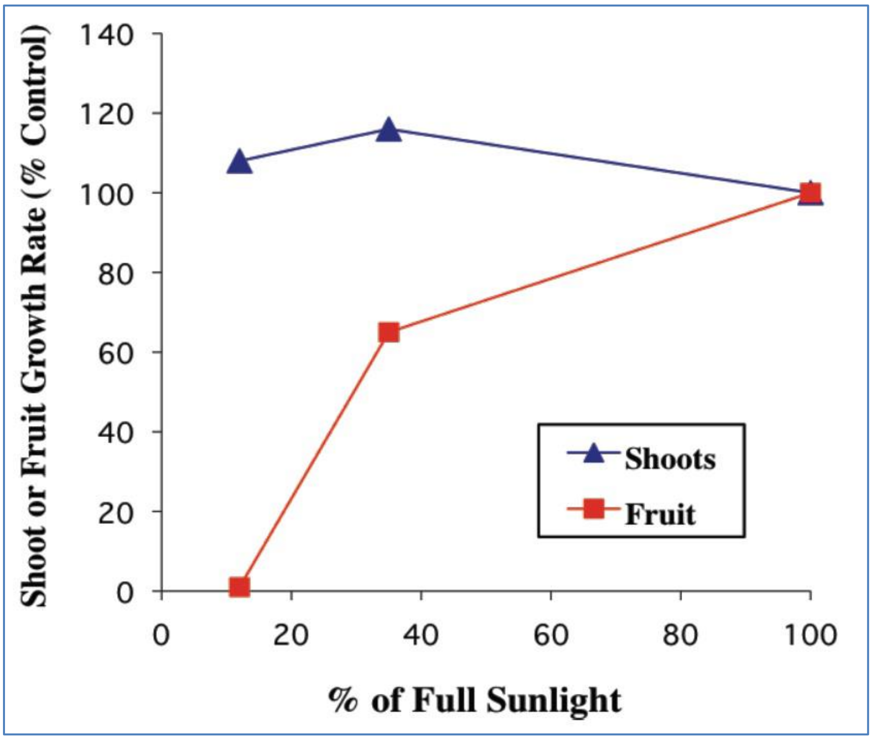


Fig 7: The effect of 6 days of varying light on the growth rate of extension shoots versus apple fruit at about 3 weeks after bloom (fruit diameter about 16 mm) [Lasko and Goffinet 2013].

3. Number of leaves per fruit

For normal fruit development a balanced leaf number (area): fruit ratio is necessary. The optimum leaf area/fruit ratio, however, varies from cultivar to cultivar mainly because of the variability in photosynthetic efficiency and the requirement of photo assimilates for fruit development (Singh *et al*., 2008) [57]. The primary spur leaves (those that come out before bloom) initially are important to support the fruit, but their importance gradually declines due to their small leaf area. Next, the leaves on the lateral ("bourse") shoots in the spur develop after bloom and support the fruit unless they are extremely vigorous. Finally, the leaves on the extension shoots with more than about 12 leaves begin to support the fruit (Figure 8).

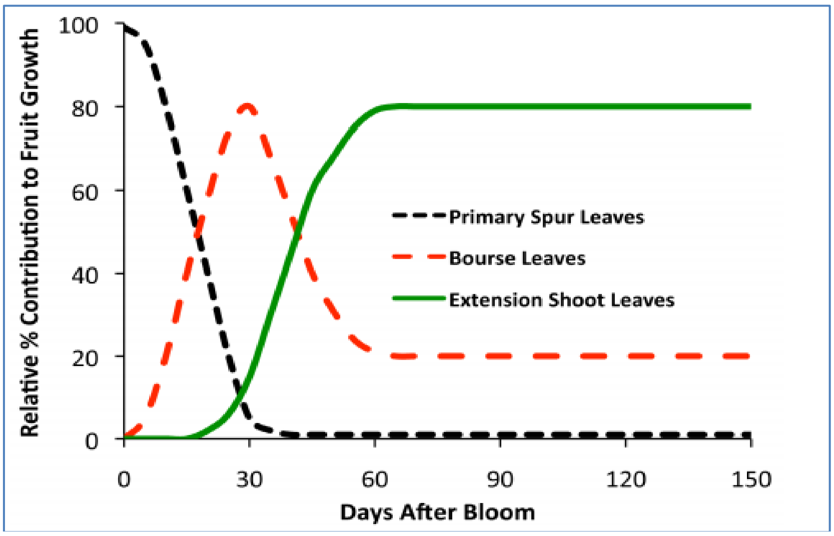


Fig 8: Seasonal pattern in which leaves contribute fruit growth.

Gradually as shoots stop growing, all their leaves can support fruit growth. For the last 2/3 of the season both bourse leaves and shoot leaves support the fruit (Lasko and Goffinet, 2013) [25]. For normal fruit development a balanced leaf number (area): fruit ratio is necessary. The optimum leaf number/fruit ratio has already been determined for many temperate, tropical and subtropical fruit crops such as apples (Tukey, 1956) [61], peaches (Weinberger and Cullinan, 1932) [66], apricots (Lilleland anld Brown, 1936) [28], grapes (Mohanakumaran *et al*., 1964; Purohit *et al*., 1979) [36, 45] and citrus.

C. Seed Number

Seed number as well as distribution effect the fruit size. Each developing seed sends hormonal signal (auxin) which stimulate pericarp and receptacle development (Luckwill, 1969) [30]. Both fruit size and calcium concentration increases with seed number (Boselli *et al*, 1995) [7]. Seeds are tissues with high intensity of harmone synthesis (auxin & gibberlin). These harmone in turn determine the sink strength of fruits and also enhance fruit growth. Seed enhance translocation of Ca into the fruit (Bramlage *et al*., 1990; Table 7) [8]. Seeds may be linked to Ca accumulation *via* auxin synthesis. Calcium transport is acropetal and is closely related to basipetal auxin transport. The greater seed number may result in greater auxin transport from the fruit and in turn enhance Ca transport in the fruit. Thus, Low seed number is probably a factor contributing to Ca deficiency in apple fruit (Bramlage *et al*., 1983) [9]. Auxin signals from young fruit also stimulate xylem vessel differentiation in the pedicel and also control fruit abscission (Bramlage *et al*., 1990, Figure 9) [8].

Table 7: Relationship of seed number per fruit in mature ‘McIntosh’ apples to the occurrence of senescent breakdown after storage in 0^0C air for 5 months plus 1 week at 24^0C

Seeds Per Fruit	Fruit Dia. (mm)	Ca (ppm)	Fruits that develop senescent breakdown (%)
0-1	67	174	23
2-3	70	208	18
4-5	71	215	13
6-7	72	223	11
8-9	74	228	8

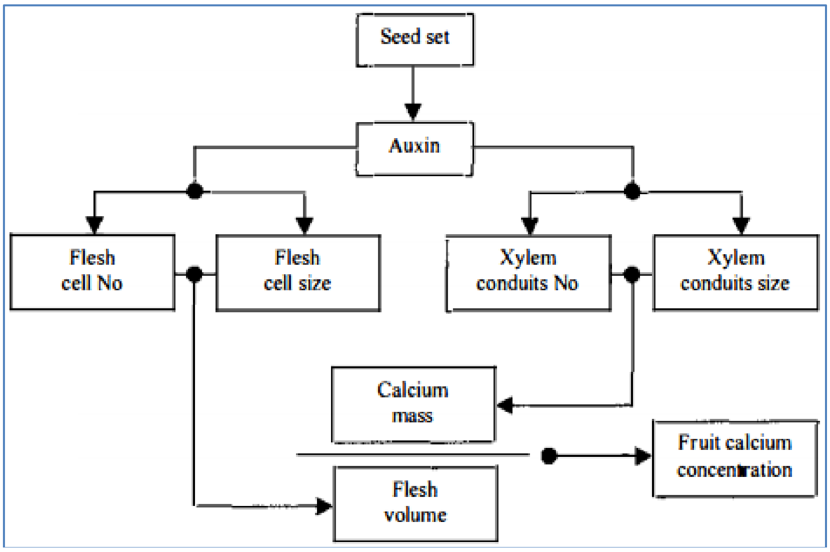


Fig 9: Relationship between seed set and calcium uptake increasing volume of flesh

Conclusion

- Pollination is also one of the factors limiting crop productivity. Problems related to pollination need attention in the early stages for better production and quality. The preferable solution to this problem is to promote planting of appropiate ratio of pollinizer varieties, and honey bees for pollination.
- The fruit grows initially by cell division for about a week, then by both cell division and cell expansion for 3-4 more weeks, then predominantly by cell expansion. Final potential fruit size depends primarily on cell numbers, which are produced shortly after bloom. So, for good fruit size thinning effectively and early is critical.
- Seed number and distribution also affects the fruit size as these sends a harmonal signal (auxin and GA_3) that stimulate pericarp and receptacle development. Fruits with no seeds or with only a low seed content are not normal to survive the competition. Auxins produced by the seeds increase the fruit cell number as well as size which in turn causes increase in fruit volume. Auxin production by seeds also increases xylem conduit number and size thereby resulting in high fruit calcium concentration.
- Carbohydrate reserves support flower development but are apparently not supporting the fruit growth after bloom. Post-bloom fruit growth is supported by the current photosynthesis of the leaves. Leaves are the source of photosynthate thus maintenace of optimum leaf: fruit ratio is essential to ensure good size fruits.

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