

## Climatic Adaptation in Fruit Crops

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### Abstract

Fruits have varying amounts of climatic adaptation. Most grow only in either the tropical, subtropical, or temperate zones. For example, fruits such as mango and pineapple grow best in a tropical climate without frosts, citrus grows best in a subtropical climate without hard winter freezes, and apricot grows best in a temperate, Mediterranean climate of uniformly cool winters and dry summers. However, strawberry has adaptation from the equator to the Arctic Circle and some apple genotypes will grow in low chill, subtropical climates while others will grow in high chill, temperate climates. Clearly, some fruits have more specific adaptation limitations than others as seen by their specialized areas of production. Fruit breeding is human directed evolution for desired tree and fruit characteristics. Climatic adaptation precedes breeding for commercial fruit qualities. Without climatic adaptation, the breeder may not be able to make hybrids and cannot adequately fruit and evaluate them. Once the breeder finds climatic adaptation for tree growth and fruiting, selection for more specific climatic requirements is possible, and primary attention can then be given to fruit characteristics necessary for making the crop economically viable. Adaptation factors for tree growth, flower bud formation, flowering, and fruit growth and maturation are photoperiod, light intensity, chilling and heat units, soil type, and temperature and water tolerance. These topics are discussed with examples of fruit species that respond to each, and the presence of genetic variability in that fruit species for climatic adaptation. Future prospects in breeding for adaptation are presented.

### INTRODUCTION

The cultivar is the cornerstone of any successful fruit crop. The grower gives most attention to the marketable unit in fruit or nut cultivars, and tree adaptation is taken for granted. However, before or with the development of fruit traits, climatic adaptation is the requirement that must be met by the breeder and confirmed by the crop evaluator for the cultivar to be grown successfully by the grower. Fruits are continually being altered through genetic selection for adaptation to new environments such as photoperiod, light intensity, chilling and heat units, soil type, and cold, heat, and water tolerance. Resistance to environmental stress (Quamme and Stushnoff, 1983) and adaptation in fruit crops (Stushnoff and Quamme, 1983) has been previously reviewed. These chapters deal with environmental stress to temperature and water, salt tolerance, and air pollution; and with adaptation to specific climates and soil environments, respectively. Light regimes (Jackson, 2000), bud dormancy (Erez, 2000), irrigation (Bravdo, 2000), fertilization (Klein and Weinbaum, 2000), flowering, fruit set, and development (Dennis, 2000), root growth and graft unions (Gur, 2000), and growth physiology (Faust, 2000) of temperate zone fruits in subtropical climates have also been reviewed. Climatic adaptation of individual fruit crops is also reviewed in *The Handbook of Environmental Physiology of Fruit Crops: Vol. I, Temperate Crops* and *Vol. II, Sub-Tropical and Tropical Crops* (Schaffer and Anderson, 1994). Genetic variability for climatic adaptation is covered in *Fruit Breeding: Vol. I. Tree and Tropical Fruits, Vol. II. Vine and Small Fruits, and Vol. III. Nuts* (Janick and Moore, 1996).

Fruit breeders have successfully selected useful variants for fruit characters, plant structure, and climatic adaptation. Climatic adaptation is probably more complex than

morphological traits, because little is understood on the mechanisms involved and how to quantify climatic adaptation. Much of the variability in adaptation is not immediately evident and the breeder may not find, even in the center of origin, the needed variability sought. Variability for adaptation is often found in special microclimates radiating out from the center of origin as different forms evolved, in the same way that Darwin visualized species evolving to fill ecological niches. Many of the adaptive traits that evolved were exploited in prehistory, with man's genotype selection from the wild. Other adaptations to climatic traits have since evolved either from selection in seedling populations and/or by modern plant breeders making crosses for adaptation. The strawberry is a good example of a fruit crop in which breeders have found high genetic variability for climate adaptation, and as breeders have exploited climatic variability, this crop is grown throughout the world from the equator to near polar circles. Peach and plum are adapted to mild subtropical to moderately high temperate climates (Byrne et al., 2000). Filbert, date, and apricot are examples of fruits in which breeders have found little variability for climatic adaptation and these fruits require very specific climates for successful commercial production.

Climate also has an effect on length of seedling juvenility and the non-bearing vegetative adult phase of fruit crops. Generally, any part of the climate that promotes growth reduces the juvenility time in seedling crops (Zimmerman, 1972; Hackett, 1985). These include are long photoperiod, long growing season, high light intensity and water supply (rainfall), warm temperature, and carbon dioxide. However, the length of the non-bearing vegetative period following propagation from mature plants is often reduced by stress. Following juvenility, there are climatic factors for adaptation that influence the ability for commercialization of fruit crops and these are discussed below. The authors are most familiar with stone fruit and their adaptation in the low to mid-chilling range of southeast USA coastal plain to the subtropical regions of the world, and thus many of the ideas discussed will drawn from observations in these crops.

## ADAPTATION FACTORS

### Light

**1. Photoperiod.** Photoperiod response is widespread in fruit crops and affects flowering in many fruits and growth cessation in deciduous fruits prior to endodormancy. The classic example of a photoperiod sensitive species is the strawberry. Three types of photoperiod responses in strawberry have been recognized in the literature: (1) long day (everbearing), in which plants initiate flower buds in summer and flower sporadically in summer; (2) short day (including June bearers) in which plants initiate flower buds in autumn, winter (if temperatures are not too low), and spring and begin flowering when their endodormancy is met or if low enough chilling during winter when temperatures are favorable for growth; and (3) day-neutral in which plants do not become dormant as the daylength shortens and flowering is continuous from early spring until growth is stopped by low temperatures in winter (Durner et al., 1984). There is now little commercial production of long day plants, high production of short day plants, and moderate but increasing production (California) of the long fruiting season day-neutral plants.

Temperature  $\times$  photoperiod interactions are very evident in strawberry. For example, most short day strawberry cultivars will flower continuously, regardless of daylength, if temperatures are below about 16°C (Heide, 1977). In fact, the three classic types of photoperiodic responses in strawberry show intermediates being classed as strong or weak short day, strong or weak day-neutral, and so forth. Further complicating the temperature  $\times$  photoperiod interactions are the genotype differences in endodormancy chilling requirements of the short day and long day cultivars, thus making classification of some cultivars difficult and perhaps different in special climates. We suggest that the three classes are artificial and a continuum exists throughout the spectrum of short day, long day, and day neutral as observed in phenotypes.

Most deciduous fruit trees initiate flower buds under short or shortening day lengths. In addition, some deciduous fruit crops (stone fruits) initiate flower buds throughout the growing season with flower buds occurring along shoots produced all year long. Other fruits (autumn bearing raspberries) initiate flower buds in long days of summer, and still others like blueberry (Hall et al., 1963) initiate flower buds only in late summer through autumn. In low chill environments of central Florida, highbush blueberry and peach flowers and leaves so early (February) that flower buds are also initiated on new shoot growth in spring (April) when day length is short, cease initiation in summer (June–September), and resume initiation in late autumn (October and November).

Photoperiod is clearly important in most deciduous fruit crops to cause cessation of growth in autumn, the first step preceding leaf abscission, initiation of cold hardiness, and endodormancy. Low-chill peaches adapted to central Florida, propagated in Tennessee nurseries, do not cease growing until November and in some years are damaged by late autumn freezes while the high chill peaches are rarely damaged because they cease terminal growth 2 to 3 months earlier. High chill peaches propagated in greenhouses at the University of Florida stop terminal growth by late August or early September and set a terminal bud, but the low chill genotypes keep growing until late November when day lengths are short enough and cool nights are low enough to result in cessation of growth (Mowrey and Sherman, 1986). We hypothesize that in breeding for low chilling requirement, we have also selected toward day neutral in respect to cessation in terminal growth. Breaking this relationship genetically should cause low-chill peach terminals to stop growing in late summer and thus reduce pruning. Low-chill peaches make excessive growth due to ca. 9 months growing season of which more than half is after fruit harvest and without fruit competition. Blueberries that are adapted to Florida must continue to grow and set flower buds into late summer and autumn if they are to have enough vigor and fruitfulness (Lyrene, 2002). Flower buds that are formed in the spring usually die over the hot, humid summers of Florida. ‘Hayward’ kiwifruit (Ferguson, 1984) and the ‘Evergreen’ peach (Rodriguez-A et al., 1994) are examples of adaptation that do not respond to reduced photoperiod by stopping terminal growth prior to endodormancy and continue terminal growth until a freeze kills the terminal bud. However, lateral flower and leaf buds of both fruits have a chill unit requirement for endodormancy.

**2. Light Intensity.** Summer pruning of many fruit crops is done to promote large diameter fruiting wood in the lower and interior of the tree to increase not only the number of flower buds, but also their quality (large diameter fruiting shoots promote strong flower buds and larger fruit size). Tree crops with dense foliage have most of their fruit in the top or on the outside of the tree, because shading inhibits the flowering processes of induction, initiation and development. However, there is much genetic diversity in most tree fruits for density of branches, leaf size and internode length to select desirable tree structure to enhance adaptation to the light intensity in which the crop is grown.

High intensity of sunlight during ripening is required for many fruits to develop high fruit sugar levels. This is evident during ripening when 1 to 2 days of cloudy weather occurs and fruit do not recover the sweetness in taste until after 1 to 2 days of sunshine. Rainfall is often blamed for decreasing sugar levels during peach ripening, but this is not as evident because overhead irrigation during full sun does not decrease sugar levels as much as clouds. There is an interaction of sunny days  $\times$  temperature for other fruits. For example, apples grown in the Pacific northwest US develop high skin color and sugars under high light intensity and cool nights. We have observed that the low chill apples ‘Anna’ and ‘Dorsett Golden’ develop high red skin when grown on Pacific slopes in mountains of Central America (less clouds than the Atlantic slope), but not where they ripen during the higher night temperatures and afternoon, cloudy rainy season of Florida. In native walnuts of Spain the erect canopy is noted to occur in western and northwestern forests where light intensity is high only in the top of the trees, whereas the round-shape canopy is better adapted to the sparse forest of the east Mediterranean where the limiting

factor is rainfall and high light intensity occurs lower on the sides of the tree. When both eastern and western forms are planted in the same area they take on the shape for that area (Tomas, 2000).

At lower latitudes the sun is at near 90 degrees to the earth for longer periods in the year (high light intensity) especially during the early and late growing seasons, thereby decreasing the influence of N-S row orientation. Furthermore, the incidence of UV radiation is high, especially in the high altitudes of the lower latitudes, and may result in a higher degree of sunburn in some fruits than when they are grown at higher latitudes.

## Temperature

**1. Cold Hardiness.** Freeze damage accounts for greater losses of fruits and vegetables than any other environmental hazard (Rieger, 1989). Tree fruits of the subtropics and temperate zone have evolved various amounts of tolerance to low temperatures. Avocado and citrus will withstand only a few degrees below freezing, while apple and cherry are among the hardier. The consequences of cold damage can range from relatively mild, the reduction or loss of a single crop, to death of the entire plant. The type of cold hardiness needed can vary markedly as do the hazards. In extreme northern climates, fall and mid-winter hardiness may be the most critical issue. In more moderate climates, subject to fluctuating temperatures, the ability to resist de-hardening during mid-winter warm periods and the ability to re-harden quickly after such periods can be crucial to avoid injury. However, in many climates, the danger of spring frost and the associated crop loss is an annual threat to most fruit crops. One of the major obstacles to the development of improved cold hardiness is the difficulty of evaluating it in perennial species. Although, lab-based artificial freezing tests have largely replaced “test” winters for evaluating hardiness, progress in breeding programs is laborious and expensive. Palonen and Buszard (1997) provide an overview on techniques and progress in cold hardiness research in fruit crops. Ultimately, the development of genetic markers is highly desirable for long life-cycle fruit crops.

Many temperate fruit species lack sufficient cold hardiness even for survival in far northern latitudes. In such cases, interspecific-hybridization with related, but non-commercial species that evolved in the local or similar climate have proven the most productive avenue. Considerable progress has been made in this way in several pome and stone fruits (Quamme and Stushnoff, 1983). There appears to be a close relationship between the ability to deep supercool and geographic distribution, i.e. hardier species typically do not supercool (George et al., 1974). Many species are thought to be restricted in their range because of a limited capacity to deep-supercool. This may be the case for many fruit crops that appear to rely on supercooling as a protection mechanism, yet are limited in their ability to supercool. Hence, their geographical distribution tends to be restricted to areas with little risk of winter minimums of  $-38^{\circ}\text{C}$ , the homogenous nucleation point for water and also the maximum protection that can be provided by the supercooling mechanism.

In most current production areas the survival of the plant is less of a concern than is the survival of flowers and, hence, the crop. The most common cause of injury is spring frost during bloom. Flowers of most tropical fruit trees are often damaged at temperatures several degrees above freezing whereas many subtropical and temperate zone species are not damaged at a few degrees below freezing. Perhaps the coldest hardy flower is the male catkin of filberts. Rodrigo (2000) provides an overview of flower hardiness and spring frost injury research and notes that there is often more variability in frost tolerance among cultivars within a species than there is across species. Hence, improvements through breeding should be attainable.

Avoidance of injury may be an alternative avenue for improvement of adaptation. Avoidance is often accomplished by increasing either chilling requirement or post-chill heat requirement in order to delay bloom. In some fruit species, variability in both characteristics may be available. However, this mechanism has limitations in some crops

as the further one delays bloom in spring, the greater likelihood of poor fruit set as temperatures during bloom tend to increase. Moreover, this approach may not be practical for industries relying on early production as the later bloom is delayed, the greater the difficulty in meeting marketing windows. Early development of leaves has been associated with the survival of flower buds on peach in the southeastern US under radiation frost conditions. Here, mild winter and spring temperatures provide maximum separation of bloom time in cultivars differing in chilling requirement and allow expression of different heat accumulation thresholds in peach leaf vs. flower buds in some cultivars. High flower bud density and extended bloom period has been associated with ability to survive spring frost in some peach cultivars (Byrne, 1986). Some crops lend themselves to unique avoidance mechanisms, such as the primocane fruiting in *Rubus*. A novel approach is to utilize modern genetic engineering techniques to clone and insert genes for fruit quality into cold-hardy cultivars which lack commercially acceptable fruit quality, but which, nevertheless, possess wood and bud hardiness for use in a given climate (Callahan et al., 1991).

**2. Vernalization.** Most fruit crops do not require cool winter temperatures to initiate flower buds as does winter wheat. However, olive (Hartman and Whisler, 1975) and feijoa (Sharpe et al., 1993), both evergreens, require vernalization for flower initiation. Olive trees grow quite well at Gainesville, Florida, but do not flower except sparsely following the coldest winters. Attempts to grow olive in the highlands of Central America have failed due to lack of flowering. Yet, planting olives far enough north latitude in the southeastern US (ca. 100 miles inland from the Gulf of Mexico) to initiate flowering usually guarantees that olive will be winter killed by an arctic air blast, especially when the temperature is below  $-12^{\circ}\text{C}$  (Sakai and Larcher, 1957). Similarly, the feijoa grows quite well south to Miami, Florida, but does not flower or flowers sparsely south of Orlando, Florida. There appears to be genetic variability in both olive and feijoa for amount of cold required to initiate flowering as some cultivars are noted to flower more regularly in areas with mild winters.

**3. Winter Dormancy—Endodormancy and Chill Units (cu).** Winter dormancy is important to keep plants from cold injury during winter. As tree fruits evolved from the tropics to high latitudes they also evolved mechanisms for adaptation to low winter temperatures. Tree fruit species that evolved as evergreen are mostly represented in the tropical and subtropical climate fruit crops whereas species adapted to coldest areas are mostly deciduous, which permits tree adaptation in cold climates without evolving cold hardy leaves. Deciduous fruit trees experience cool winter temperatures during endodormancy that are necessary to satisfy a biological clock (termed winter chilling requirement) in flower and leaf buds so that they may begin flowering and leafing after spring frost risk is low the following spring. Generally the root system is not recognized as a primary site for endodormancy control in spite of a report of low temperatures in apple roots helping to break dormancy of the top (Young and Werner, 1984). The amount of winter chilling in endodormancy of perennial deciduous fruits is especially important with the trend toward global warming (Hennessy and Clayton-Green, 1995). Fortunately, the winter chilling requirement of a fruit crop is highly variable so that it responds to selection pressure in both directions. In general, plants of the subtropics and plants of the high latitudes have low to medium chilling requirements, whereas plants of mid latitude have the highest chilling requirements. Obviously plants of subtropical adaptation must have low chill genotypes, but plants of high latitude only accumulate chilling in late autumn and early spring, as winters are mostly too cold for enzyme systems to be physiologically active to record the winter chilling. Plants use chilling requirements to keep them dormant during the warm periods of winter. If a genotype gets too much chilling (due to planting in a colder climate than it is adapted or due to an unusually cold winter at an adapted location) then it is subject to bloom early and may get damaged by spring frost. If a genotype gets too little chilling, flowering and fruiting are delayed, the plant may not set fruit, or sparse and delayed leafing is erratic.

Given that most plants or ancestors of plants originated in the tropics (including

modern fruit crops), and that most mutations are recessive, it is likely that genes for adaptation to cold climates were an accumulation of recessive genes for chilling requirement. Thus, genetic variability for low chilling requirement is likely to be quantitative and dominant as indicated by data from Lesley (1944) and Oppenheimer and Slor (1968). In fact, in seedlings from crosses of moderately high chilling and low chilling stone fruit and pome fruit, we have observed (unpublished data) the midpoint-chilling requirement of progeny to be usually closer to the low chill parent. This may explain why it is easier to breed low chill genotypes from high chill genotypes than to breed high chill genotypes from low chill genotypes. Sour cherries and prune plums (4x and 6x, respectively) originated in high chill locations and do not have low chill in their polyploid ancestors, thus it will be necessary to go back to their diploid ancestry to find low chill forms and recreate the complex polyploids in order to breed low chill genotypes.

Winter chilling can be assessed in many crops, beginning in autumn after leaf fall, as hours below 7°C in some climates (Weinberger, 1950), but is often measured in chill units (cu's) over a range of temperatures, with partial cu's occurring below and above the optimum temperature (Richardson et al., 1974). A cu is the maximum amount of chilling that can be accumulated in one hour at the optimum temperature. High temperatures during endodormancy can negate some accumulated chilling (Couvillon and Erez, 1985; Young, 1992). In choosing peach cultivars to be grown at a location, the chilling that occurs at a location must be known. The relationship between cu's per winter and mean temperature of the coldest month (or average of the 2 coldest months) at a location is linear, thus the average monthly temperature is a good measure of the relative coldness of the winter (Sharpe, 1969; Sharpe et al., 1990; Weinberger, 1956). Cu's are most easily estimated in tree crops that have little variability for heat units (see heat unit discussion below) as occurs in commercial peach, where genotypes of same age and vigor do not reverse order of bloom at different locations and years. There is also genetic variability for the optimum temperature at which chilling occurs. In general, it is thought that low chill deciduous peach genotypes have a higher optimum temperature at which they accumulate a full cu than occurs in plants with high chill units (Gurdian and Biggs, 1964). Cu's for an unknown peach cultivar can be assigned based on time of bloom in relation to bloom time in standard varieties (Sharpe et al., 1990). The lowest cu cultivar blooms first. For example, a 35-year average at Gainesville shows that ca. 10 days occurs between each 100cu group of their "standard cultivars" (Sherman and Lyrene, 1988). In contrast to peach, low chill blueberries break leaf endodormancy best following chilling at 0 to 2°C than after 5 to 7°C (Lyrene, 2002).

Endodormancy generally increases as the latitude and or altitude is increased. Deciduous plants that are native to areas above ca. 40° latitude generally go down in chill requirements as one moves to higher latitudes because plant enzyme systems generally do not record chilling below freezing. These plants usually accumulate cu's in autumn (plant cu requirement is high enough to prevent cu requirement and resulting bud activity during "Indian Summer"), before the large majority of hours in winter are below freezing. These high latitude adapted plants usually have a high heat requirement to initiate spring growth to avoid late spring freezes. Thus, plants of the sand cherry (*Prunus besseyi* Bailey), native to the upper Midwestern US, flower and leaf well in north Florida at ca. 500 to 600 cu's.

Endodormancy in deciduous fruit crops has been bypassed in some cases. In the case of mixed buds that occurs in apple, trees will grow as an evergreen in subtropical (without frost to defoliate) and tropical climates and flower and fruit on terminals sporadically throughout the year. In the case of peaches, plums, apples, and grapes that are stressed to stop growth following harvest, defoliated, and then watered, dormancy may be bypassed (George et al., 1988; Janick, 1974). Flowering and foliation follows watering, and 2 crops per year are possible if the fruit development period is short enough, dry periods are available to stop growth before restarting it again, and in the absence of winter frost (Sherman and Lyrene, 1984).

**4. Heat Units (hu's).** Hu's are important in the active growth processes of most plants including breaking of endodormancy (flowering and leafing), bud drop in some stone

fruit, pollen germination, fruit set, fruit development period, fruit shape, and blind node formation in peach (Sherman and Rodriguez, 1994). The amount of warmth necessary for flowering in spring and for fruit growth and ripening is measured in units such as degree hours or degree days. Regardless of the means by which heat is measured, an understanding is desirable of how relative amounts of heat affect various plant growth phases. Hu's (thermal time) for flowering in peach have been shown to start accumulating (base temp.) ca. 2 to 4°C (Munoz et al., 1986; Richardson et al., 1975), and may occur at lower temperatures, but accumulate at an increasing pace as temperatures rise. Likewise it has been observed that peach flowers force rapidly in the field when minimum night temperatures stay above 10°C. Experience has also shown in Florida that ca. 25 days under orchard conditions are necessary after chilling is met before enough hu's occur to force flowering in adapted cultivars. Researchers have used 10 to 14 days in a heated greenhouse to satisfy the hu requirement to determine when 50% bud break occurs, at which time chilling is thought to be met.

*Dormancy to Bloom.* Hu's are necessary in deciduous plants to break endodormancy for flowering and leafing after the winter chilling requirement (measured in cu's) is met. Some crops have high, some low, and some are highly variable in hu's. Late flowering due to high hu's is separated from late flowering due to inadequate chilling by checking relative flowering at locations of varying chilling regimes. High heat requirement crops like persimmon, muscadine grape, walnut and pecan will be the last crops to bloom, regardless of location, because they evolved in low altitudes where spring frost was problematic. Other fruit crops evolved at high altitudes and with a short fruiting season. These crops, such as apricot, have a low heat requirement for bloom and may also have a low base temperature to initiate spring growth. They evolved at high latitudes where spring frosts are not a great danger, but the fruiting season is restricted by a harsh summer climate. Thus, apricots are a good example of early blooming and are often lost to spring frost in many production areas. There is also variability for heat units within some fruit crops. For example, the most variable character of the Chilean walnuts seems to be their flowering date (Tomas, 2000). Thus, the later flowering genotypes are better adapted to the mountains where they are more likely to escape spring frosts. Japanese plum (Topp, 1987), almonds (Tabuenca et al., 1972), apple (Hauagge and Cummins, 2000) and pear (Sherman and Janick, 1964) genotypes growing in climates where they are saturated with cu's during winter when it is too cold to accumulate hu's, begin to accumulate hu's together upon warming of spring, bloom 4 weeks between the first to the last cultivars. Because plum, almond, apple, and pear genotypes differ in both cu's and hu's required for ending endodormancy, the bloom dates among some cultivars often reverse order in different climates and years where chilling and hu's are satisfied at different times. Thus, bloom dates are not as reliable in indicating chilling requirements as in commercial peach which displays little variability in hu's.

Peaches have a higher heat requirement for bloom than apricots, almonds and Japanese plums in that peach blooms later in all locations where chilling is adequate. Apricots as a group are thought to require the least amount of hu's because they bloom first in all locations where chilling is adequate. Peach has less heat requirement for bloom than pecans, persimmons and grapes because peach flowers before these crops regardless of location. Peach may be the model crop for estimating chill accumulation. There is little variability in commercial peach cultivars for heat units for bloom as evidenced by the short bloom period of all cultivars in locations where the chilling requirement of all cultivars is met before any hu's occur. Thus, all cultivars began accumulating hu's together and the flowering period for all cultivars may be only 3 to 5 days. The difference in flowering time of peach cultivars in the southeastern United States is due to genotype differences in cu's. For example, an early flowering cultivar has its chilling requirement met and accumulates its hu's before a later flowering cultivar can accumulate its higher chilling requirement and the same amount of hu's. The lower the latitude that peach is grown, the longer season over which cultivars bloom. Thus, it will be difficult to breed a late flowering peach to escape spring frosts, except by selecting for higher chill

requirement. There does seem to be variability for higher heat requirement in some close peach relatives such as *Prunus davidiana* (Carr.) Franch. and *P. kansuensis* Rehd.

*Fruit Set.* Hu's have a major control in fruit set, but little is understood on amounts of heat required. Pollen germination in peach occurs best when orchard temperatures are above 18°C and breeders have observed that "shirt sleeve weather" during spring bloom gives the best fruit set during hybridizing. Experience from greenhouse forced flowering and from flowering in the tropics (Edwards, 1987; Rouse and Sherman, 2002) has shown that minimum night temperatures above 14°C during the time of flowering to shuck split reduces fruit set. For example, pollen germination (as affected by viable pollen production) of 'Flordared' peach trees forced to flower Oct. 22 at Oaxtepec, Mexico was 0%. Pollen germination on Nov. 8, Dec. 30 and Jan. 17 showed increases to 73% as minimum night temperature decreased (Ortiz, 1986). Variability exists for peach pollen germination under high temperatures. Ortiz found that 'Talisman' had 36% pollen germination vs. 9.5% for 'Flordared' on Nov. 8 at Oaxtepec. In fact, peach varieties at Gainesville that get winter chilling met in mid- to late Feb. and flower in mid-March do not set fruit if normal warm nights (above 14°C minimum) occur even though the bloom appears to be strong and uniform. Conversely, peach trees in the state of Michoacan, Mexico and in hill district just inland from Perth in Washington, Australia that exhibit severely delayed bloom and foliation due to inadequate chilling, will set adequate crop loads as minimum night temperatures are below 14°C (due to altitude) during bloom to shuck split. There appears to be genetic variability in our germplasm for fruit set in peach at 2 or 3°C above 14°C. However, if nighttime minimum temperatures are increased at twice the amount of daytime maximum temperatures in global warming (Houghton et al., 2001), then fruit set will become increasingly affected at higher latitudes.

Our hypothesis is that nature has influenced hu variability for adaptation. Thus, species that evolved high heat requirements to break endodormancy, like grape, kaki persimmon, pecan and walnut, bloom later (perhaps to escape spring freezes), and set fruit under higher night temperatures than early bloom, low heat requirement crops like apricot, almond and peach.

*Blind Nodes.* The degree of blind nodes (neither flower nor vegetative bud) in peach is regulated by genetic tendency of the cultivar (Boonprakob and Byrne, 1990) and is expressed in conditions of high temperature during rapid mid-summer shoot growth. The same varieties grown at cool summer climates of the high altitudes of north and central Mexico result in fewer blind nodes than at similar latitudes with a hot summer climate (high hu's) at a low altitude (Richards et al., 1994). We have observed that peach cultivars selected in a cool summer climate (usually at high altitudes) are more likely to have too many blind nodes and a resulting severe lack of leaves when grown in a hot summer climate. These trees are difficult to train as young trees and prune as mature trees and result in low yields. Oddly, peaches grown in a Mediterranean climate in which daily maximums exceed 38°C in summer usually have reduced blind nodes, presumably because of reduced shoot length occurring under such high temperatures. There is a large amount of genetic variability for blind nodes in peach and apple, and we select against it in our breeding program because it is annually expressed so well (Sherman et al., 1996).

*Bud Drop.* Stone fruit have shown the greatest tendency for bud drop, also referred to as bud failure and bud jump. Bud drop has also been reported in Asian pear (Nakasu et al., 1995), and in apple and pear (Zeller, 1973). Flower buds fail to swell in spring and dry up, abscising when other flowers on the tree are opening. Bud drop has been suggested to result from high autumn temperatures during flower bud formation (Brown, 1958), inadequate winter chilling or high temperatures during early endodormancy Layne et al., 1996), large fluctuations in winter temperatures (Nakasu et al., 1995), and high night temperatures in December and January (Weinberger, 1967). Apricots show bud drop the most of any stone fruit in the eastern US (Byrne et al., 2000), but bud drop has also been observed in peach in California and the southern US. Bud drop occurs every year in all apricots tested at Gainesville, Florida, even those that break dormancy with the low chill peaches Florida and is a severe problem preventing the cultivation of apricots in

the southern US Weinberger showed high variability in peach cultivars for bud drop at Fresno, California. We have observed genetic variability for bud drop in low chill peaches in Florida and regularly select against it (Sherman et al., 1996). Apricot germplasm introgressed with low-chill forms of *P. mume* Sieb. & Zucc. shows less susceptibility to bud drop than low chill apricots, under Florida conditions.

*Leafing With or Before Flowering.* Fruit crops that have vegetative and flower buds separately (not mixed buds as in pome fruits) usually flower before leafing. Thus, it has been speculated that flower buds have a lower chilling requirement than leaf buds or that leaf buds have a higher heat requirement than flower buds. In contrast, at given locations, some genotypes of low chill peaches and blueberries leaf with or before flowering. This phenomenon occurs in the lowest chill peach genotypes like 'Flordaprince' (150 cu) at Gainesville, Florida and 'Flordaking' (450 cu) at Byron, Georgia in years when the chilling requirement of the genotype is met, but temperatures remain low, but not freezing, for a period of ca. one month. We have made similar observations in low-chill blueberries at Gainesville. It may be that the leaf buds began accumulating hu's at a lower threshold than flower buds, and during prolonged cool weather the leaf buds get ahead of flower buds in heat accumulation and thus begin breaking dormancy earlier. Leafing before flowering gives an advantage in protection from a radiation frost in peaches, because the trees near full leaf in a late spring-frost trap more ground heat and shield fruit from exposure to the cold night sky. Early leafing does not give the blueberries as much frost resistance because the young fruit are often near the terminals and stick out above the leaves. In some blueberry genotypes at Gainesville, heavy flowering appears to inhibit the breaking of leaf buds and leafing with or before flowering makes for stronger leaf capacity to mature the crop. A significant disadvantage of early leafing in peaches is that in cool damp climates during leafing, peach leaf curl is more likely to be a major problem.

*Fruit Development Period (FDP).* Fruit growth from bloom to harvest also requires hu's and in peach the rate of fruit growth is in proportion to the rate of hu's accumulated. This relationship has been established in early ripening (less than 100 day FDP), low-chill peaches as about a 5 day advance or delay for each 1°C increase or decrease, respectively, in mean monthly temperature during the first 2 months following flowering (Weinberger, 1948; Topp and Sherman, 1989b; Bacon, 1999). Thus an 80-day cultivar in one location can become a 120-day cultivar in a cooler location. A grower can roughly predict the harvest date of this year's crop by knowing dates of bloom and mean monthly temperatures during fruit growth. In fine tuning harvest dates, one must consider the experience from forced flowering for early ripening, i.e. nights above 10°C and daytime below about 38°C promote the most rapid fruit growth, and thus the shortest time from flowering to harvest. Excessive heat units below 5°C decrease FDP in apricots and to a lesser extent in prune plums, but temperatures greater than 5°C in the last month prior to ripening have been shown to delay ripening in both crops (Baker and Brooks, 1944). We believe that temperatures above 38°C slow ripening in peach as we have observed that peach varieties ripening in June and July in Seville, Spain are delayed in ripening (compared to the same cultivars at Huelva where temperatures during the last month before ripening are ca. 6°C lower). These observations help explain yearly variability for time required from bloom to maturity at locations that have high temperatures during ripening.

Some fruits (such as apples and peaches) have genotypes that require so many hu's (long FDP) that they are not adapted to locations that have short growing seasons. 'Lady Williams' apple, superbly adapted to Western Australia, is high chilling and requires ca. 240 days to ripen from bloom. There are few climates in the world that receive such high chilling and still have so long a growing season. Similarly, 'GoldRush' apple is not adapted to Michigan because it ripens so late, but 'Pristine' apple ripens so early that it could be grown in Alaska. A similar claim could be made for the latest ripening peach cultivars like 'O'Henry' and the 180-day FDP canning peaches. It is obvious there is high genetic variability for FDP in most fruits and that variability must be

exploited for best adaptation of a variety in a particular location. Most pecan cultivars cannot be grown in the northern part of their native range (Illinois) because their FDP (lack of heat units) is too long for nuts to mature.

*Fruit Shape.* Fruit shape in some crops is certainly affected by hu's, but little data is available. In general, more elongated fruits are produced when temperatures are lower and rounder fruits are produced when temperatures are higher following bloom until ripening. For example, 'Delicious' apples grown in the Pacific NW US have longer shape with larger distal lobes than those grown in the warmer summer temperatures of the central northern states. In fact, it is possible to identify many apple genotypes by shape as affected by climatic conditions (Hauagge and Cummins, 2000). Berry shape in grapes is round or elongated depending upon whether night temperature is high or low (Kobayashi et al., 1965). Conversely, peach cultivars grown in the southern US and Australia, that are rated for higher chilling than they receive, often have an accentuated tip and suture bulge (Topp and Sherman, 1989a). Observation lead us to conclude that this is not due to inadequate chilling, but to high temperatures (hu's) during early fruit growth. Thus, peach varieties that are delayed in flowering due to inadequate chilling, have their early fruit growth later than normal and at a time when daily hu's are likely to be higher. Also, in places where periods of alternating cool and warm temperatures cause prolonged flowering, often over a period of a month, peach fruit with and without a tip are present on the same tree. Fruit shape in many crops is regularly selected for in most breeding programs, but shape often changes with climate. Thus, it is desirable to know the climates that give the most desirable shape if the fruit variety is going to be optimally adapted.

*Fruit Ripening.* Hu's during ripening can have major effects on commercial adaptation of fruits to given climates. 'Valencia' oranges over-winter on the trees before ripening in late spring, lose chlorophyll and color up in winter, and re-green when days of spring are warm enough. These fruit may be degreened with ethylene to give them the appearance of tree ripened. 'Valencia' oranges ripen later in spring in areas with less hu's accumulating during winter. Grapefruit and pineapple (Bartholomew and Malezieux, 1994) have lower fruit acidity and higher sugar content in climates that have warm winters and early springs when the fruit are ripening. That is why grapefruit are produced in southern Florida and southern Texas, but not in southern California, and why pineapple is produced in warm rather than cool tropical climates (Sanewski and Giles, 1997). 'Concord' grape is not adapted to the southern US, because berries ripen unevenly due to high night temperatures. Excessive heat results in skin burn and/or browning at the pit in some Japanese plum and prune cultivars, and thereby prohibit their production in locations that have excessively high temperatures during fruit ripening.

Red skin is an important marketing quality in many fruits and color development in most is improved when they experience relative cooler (lower hu's) rather than warmer night time temperatures during the last month prior to ripening. This is probably because high night temperatures increase respiration that decreases sugars which, in turn are precursors to the red anthocyanin pigment idaein (cyanidin-3-galactoside). Apples (Diaz, 1992) and grapes (Kliewer and Torres, 1972) have been shown to have less colored skins than the same cultivars grown under lower night temperatures. However, there appears to be variability for influence of night temperatures on skin color in apple with best color at 12°C in 'McIntosh', 13°C for in 'Fuji' and 15.5°C in 'Gala' (Hauagge and Cummins, 2000).

Vivipary (premature germination) in pecan is caused by high temperatures during nut ripening and is accelerated if the tree fruits excessively. Vivipary is a major problem in dry, low elevation areas of the southwestern US (Sparks, 2000). There is genetic variability among cultivars with 'Wichita' being particularly susceptible.

Some seedless grapes (stenospermocarpy) have a crunchy seed trace (later embryo abortion) in some locations and years, but not in other locations and years. Obviously, there is genetic variability for time of embryo abortion and therefore amount of lignification of the seed coat. However, the location influence is such that some seedless grape cultivars, developed in areas with cooler growing temperatures, tend to have

crunchy seed coat traces when grown in locations with warmer growing temperatures.

We have observed that peach pubescence is longer on the same cultivar when it ripens under high temperatures compared to when it ripens under low temperatures (i.e. southern Spain vs. southern France and central Florida vs high elevations in Mexico and central America). Nevertheless, there is genetic variability for density and length of pubescence in peach (Sherman, 1996) as we have observed short pubescence on many of the recent US peach cultivars.

*Seed Germination.* Subjecting early ripening stone fruit on the tree to higher temperatures stimulates embryo development more than fruit development, thereby yielding embryos of greater development at fruit maturity (Scorza and Sherman, 1996). Normal germinable peach embryos can be found in Florida genotypes ripening in 80 to 90 days FDP in years that have warmest spring temperatures. 'Springtime' peach embryos from New Jersey are reported to be more fully developed at fruit maturity than those in California. In sweet cherry, low temperatures during embryo growth had an adverse effect on embryo development (Braak, 1978). Our observations are that embryos of all early ripening peaches do not attain the same development, even if they bloom together at the same location.

We have observed seedling rosetting in most species of stone fruit, especially those from dry seed soaked in water and the seed coats removed for forced germination, but also from seed taken from the fruit in season and not allowed to dry before stratification. Rosetting appears to occur more in the highest chill peach genotypes, but even the lowest chill unit genotypes display near 100% rosetting if from current season's seed are sprouted in stratification and planted in flats during July and August under Florida conditions of 35°C day and 22°C night. Planting seed comparably stratified directly into growth chambers, and maintaining growing temperatures between 10° and 20°C, greatly reduces rosetting prior to planting in the field nursery.

*Tree Growth.* Low chill peach and apple genotypes have been observed to grow larger trees than high chill genotypes in areas of high chill. There is no reason to believe that low chill peaches grow any faster in mid summer than high chillers. It is obvious that in many high chill areas, the low chill genotypes will begin growing in spring up to one month before high chill genotypes and that low chill genotypes do not exhibit cessation of terminal growth in autumn as early as high chill genotypes. Thus, low chill genotypes have a functionally longer growing season compared to the high chill genotypes when grown in the same high chill location. Additionally, the low chill genotypes may have adaptation to growing at lower temperatures than high chill genotypes as they evolved in low chill areas where daylength was shorter and temperature was lower during spring bloom (Jan.) than in high chill climates at bloom time (May) at higher latitude.

## **Water**

Fruit crops usually show adaptation to lack of or excessive moisture in reactions to diseases and insects, but there are numerous examples of adaptation for plant vigor and growth in moisture extremes.

**1. Excess.** *Prunus* spp. and interspecific hybrids (Layne, 1987; Perry, 1987), apples (Ferree and Carlson, 1987), and pears (Lombard and Westwood, 1987) among other fruits, vary greatly in their tolerance to soil moisture. Plum and plum hybrid rootstocks are commonly used for peach, plum and apricots in heavy, wet soils of Eastern Europe for best adaptation, because almond, peach and apricot are not tolerant of wet soils. In fact, almond is the most sensitive of the stone fruits to "wet feet" (Kester and Gradziel, 1996). In citrus, some rootstocks such as sour orange are not deep rooted and tolerate wetter soils more than other rootstocks such as the deep rooted rough lemon which is adapted to the deep sandy soils of the Florida ridge (Castle, 1987). Even a liana (wide vessels) plant like kiwifruit, which requires high amounts of water, is sensitive to high water tables or wet feet (McAneney et al., 1989). Cactus fruit (prickly pear) are produced without irrigation in large quantities in the low rainfall, dry soils of upper elevation areas of north central Mexico.

**2. Deficiency.** Dates require near 60 cm of water annually, but are grown where it seldom rains more than 15 cm, because of fruit diseases, and thus either must be under tree irrigated or grown at oasis where there is available soil water. Apricots are thought of as drought resistant, but are sensitive to lack of soil moisture (Brown, 1952; Layne et al., 1996) even though they thrive in areas with low air humidity. Sweet cherries cannot be produced in areas where it rains during fruit ripening as fruit cracking renders the crop worthless. Fruit twinning, as occurs in some peach and sweet cherry genotypes, is induced by water stress during the summer when flower buds are initiated. Twinning can be overcome in susceptible peaches by irrigation in summer during drought and fruit thinning the following spring (Handley and Johnson, 2000). In the case of some sweet cherry genotypes, even irrigation is not enough to stop water stress induced twinning if summer temperatures are too high and humidity low, and that is why this crop is mostly grown in the central valley of California to the east of San Francisco, where the cool winds are drawn in from the coast by the heating of the valley to the north and south. Insufficient water during the Stage I of fruit growth (from bloom until shell length reaches full size—in mid May in California) in spring increases abnormal early splitting of pistachio nuts (Doster et al., 2001). Early split shells are frequently moldy and damaged by insects. Almond seedlings tend to produce taproots that grow deeply in well-drained soils and are adapted to drought and arid summer climates.

## Soil

Rootstocks for many crops have been made for climatic adaptation with various characteristics such as good anchorage, shallow wet and deep dry soils, pH tolerance, temperature tolerant, inducing precocity, disease and insect resistance in specific climates.

**1. Soil pH.** Blueberry and cranberry are fruits that are specifically adapted to acid soils with good organic content. However, there are related species that are adapted to moderately neutral pH soils of high mineral content and some ploidy bridging breeding work has begun to incorporate adaptation to these soils (Galletta and Ballington, 1996). Many fruit crops are not adapted to alkaline soils unless grafted on a rootstock that can obtain minor elements that are relatively less available at a high pH. For example, stone fruit grafted on peach rootstocks usually show Fe and Zn deficiencies in soils above pH 7.5, but almond, peach × almond hybrids (Kester and Gradziel, 1996), and some plums (Okie, 1987) convey less deficiency symptoms as these rootstocks are much better adapted (INRA, 1978). Pecan is native to deep alluvial, less than 7.0 pH soils of river valleys in the southwestern US. When planted on high pH soils in the same regions, pecan requires Zn to be applied to the leaves as Zn is rendered less available when applied to high pH soils. There exist variability among pecan seedlings for tolerance to alkaline soils, but there has been neither a breeding program to give homogenous lines nor a commercial clonal rootstock propagation method developed to take advantage of individual seedling adaptation to such soils.

**2. Soil Temperature.** There is evidence that rootstocks from high chill deciduous fruit crops require high soil temperatures to begin spring growth and thereby have an effect on the initial growth of the scion variety. For example, the ‘Golden Queen’ peach seedling rootstock delays bloom and ripening of low chill cultivars by 7–10 days, compared to ‘Okinawa’ and coastal peach seedlings, when soil temperatures warms up slowly in spring, but not in springs that warm up rapidly (Malcolm et al., 1999; George et al., 1986). Westwood and Chestnut (1964) have reported that ‘Bartlett’ pear blooms earlier on *Pyrus calleryana* Decne. than on *P. communis* L. rootstock. Even with inadequate chilling the ‘Bartlett’ bloomed earlier on the *P. calleryana* seedlings, indicating that soil temp earlier in spring may be more favorable to root growth in *P. calleryana* and thus promoting scion growth. The former is lower chill, but *P. calleryana* begins root growth earlier than *P. communis* as we have observed from growth of budlings dug from the nursery in spring.

Gur (2000) states that there is an optimal root temperature during the main growing season for temperate fruit crops and he discusses the effect of soil temperature

on morphological and anatomical features, respiration and photosynthesis, water supply, mineral nutrition and growth regulators. The effects of high root temperature on rootstock-scion incompatibility are also discussed. In fact, root growth in kiwifruit has been reported to have a lower optimum temperature (20°C) for growth than for other deciduous fruit crops (Buwalda and Hutton, 1988).

### **Unknown Factors**

There are unknown climatic factors associated with particular observations in fruit crops. For example, what causes the fruit size to increase and skin color to decrease when peach genotypes are taken from the eastern US to California (and vice versa for California peaches in the southeastern US)?

What causes many fruits to be more parthenocarpic as they are moved from eastern to western US? For example, many kaki persimmons set good crops in California without cross-pollination, but sporadically or none in the east. 'Bartlett' pear requires cross-pollination in the eastern US, but requires little or none in the Pacific Northwest. The need for cross pollination in apple appears to vary with location as 'Delicious' and 'Anna' set in some locations with little or no cross pollination, but not in other locations.

What factor results in "noninfectious bud failure" in western US almonds? What factors cause peach tree short life (SE-US), apoplexy in apricots (Europe), and blight of citrus (Florida and Brazil) in some, but not all major production areas? No infectious diseases are associated with any of these conditions. One could go on endless with obvious climatic (location) observations, for which we presently have no clear answers. Nevertheless, there appears genetic variability for each unknown.

## **FUTURE PROSPECTS**

### **Scion Cultivars**

Future prospects of cultivars in fruit crops are covered in most chapters in *Fruit Breeding: Vol. I. Tree and Tropical Fruits, Vol. II. Vine and Small Fruits, and Vol. III. Nuts*, edited by Janick and Moore (1996) and in *Outlines of Perennial Crop Breeding in the Tropics, Miscellaneous Papers 4*, edited by Ferwerda and Wit (1969). However, as new genes are found in non-crossable genotypes, cloned, transformed and activated into either cultivars or into crossable genotypes, and as single cell regeneration systems become a standard procedure for each fruit crop, then new characteristics will be available. These characteristics may be in areas of adaptation that were not previously possible. Thus, climatic adaptation to cold hardiness in tropical fruits and heat tolerance of temperate zone fruits in the tropics, pest (insect, bacteria, fungi, nematodes) resistance, herbicide resistance, drought and excess rainfall tolerance, photoperiod sensitivity, etc. will become a reality. In another light, if plants could be designed with reporter genes capable of responding to signals naturally developed in stressed plants, then management decisions could be made. The reporter genes, reacting to stress, may cause expression such as color change that could be easily monitored by remote sensing such as electromagnetic radiation. The resulting environmental impact would permit the geographical range of crop production to be extended.

### **Rootstocks**

Clearly there are genes for climatic adaptation in rootstocks for many crops and future prospects are reviewed in *Rootstocks for Fruit Crops* (Rom and Carlson, 1987). There is high probability that major new improvements and useful rootstocks will be discovered in or bred from genetically crossable genotypes, either to make fruits better adapted to the areas where they are currently grown or to make fruits adapted to new areas where they could not be previously grown due to lack of cold hardiness, lack of disease or nematode resistance, soils that are too wet, dry, alkaline or salty, etc. However, in many crops there is no adaptation available that is as good as the roots of native trees. In these cases we must rely on miracles of biotechnology. For example, mistletoe not

closely related to any of our fruits, has graft compatibility to a number of fruit crops and native trees. Mistletoe grows on crops such as pecan, apple, pear, walnuts, and jujube. There are other examples of compatibility in nature such as the primitive organelles in plant cells, the compatibility of algae and fungi in lichens, and parasitic mechanism of the quandong nut tree of Australia on roots of various plants. Perhaps biotechnology can find some compatibility genes from the “secrets of nature” that could be vectored into crop plants. This would permit fruit crops to be grafted onto native flora. Thus, we could take advantage of new adaptation in our mostly non-native fruits, and in other ways we have not even dreamed.

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