Breeding Peaches in North America for Cold Hardiness and Perennial Canker (*Leucostoma* spp.) Resistance — Review and Outlook

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Winter injury is an important factor influencing peach (*Prunus persica* [L.] Batsch) production in North America especially in the northerly areas, and is the major limiting factor affecting the northerly expansion of peach culture (2, 8, 9, 10, 13, 14). Perennial canker is a ubiquitous fungal disease of stone fruits (*Prunus* spp.) that is particularly damaging to peaches and nectarines in northerly areas of production except in the arid, irrigated regions of the Pacific northwest and southern British Columbia (4, 6, 19, 20). The disease is caused by two facultative wound parasites that enter the tree through dead and dying tissues (4). The causal fungi are *Leucostoma cincta* (Per. ex Fr.) Hohn (= *Valsa cincta*) and *L. persoonii* (Nits.) Hohn (*V. leucostoma*). Either or both fungi are involved in the canker disease depending on the geographic region. *L. cincta* tends to predominate in cooler regions while *L. persoonii* is more important in warmer regions (4, 12). Many biotic and abiotic factors predispose peaches to perennial canker infection (6, 7, 15, 17, 18, 19, 20) but winter injury appears to be the most important in more northerly areas of production (3, 6, 19, 20). Canker infected trees are commonly observed to be more susceptible to winter injury than healthy ones of the same cultivar. They appear to be especially susceptible to injury from freeze dessication induced by strong drying winds in exposed locations. Usually, the combined influence of low temperature stress and perennial canker is more damaging to peach trees than either acting alone (9). The resultant damage includes injury or death of flower buds, fruit bearing wood, major scaffold limbs and even entire trees (2, 3, 6, 10, 14, 19, 20). Such losses result in greatly reduced yields, shortened orchard life and lower returns to the grower. Losses from winter injury and perennial canker, while not confined to northerly areas, are usually greater there because at the higher latitudes the frequency and severity of low temperature stress is greater than regions further south (13, 14). While hardier peach cultivars with perennial canker resistance will be advantageous in most regions of production, the need for such cultivars is especially urgent in the northern United States and southern Canada. This paper will focus on the progress that has been made in breeding hardier cultivars of peach in North America and will assess the prospects for further genetic improvement of cold hardiness and perennial canker resistance.

Breeding for Cold Hardiness

The peach is the least cold hardy of the stone fruits grown commercially in North America for their edible fruit (14). Peach tissues and organs differ significantly in their relative cold hardiness at any stage of overwintering. At maximum hardiness levels, the most hardy of the stem tissues is the cortex, followed by the phloem, cambium and xylem. The leaf buds are the least hardy of the vegetative tissues and the flower buds are the least hardy of all above-ground tissues.

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Differences in cold hardiness of cultivars have been long recognized and believed to be under genetic control. The inheritance of flower bud and wood hardiness has been found to be quantitative on the basis of controlled freezing tests of selected peach progenies involving both North American and Asiatic germ plasm (2, 9).

Classification of peach cultivars and rootstocks into distinct hardiness groups is difficult because they differ in hardiness with respect to each other from fall to spring (9, 11, 16). They also differ in the rate and extent to which they deacclimate in mild, above-freezing weather and reacclimate in cold, below-freezing weather during overwintering. Thus, genetic discrimination of cold hardiness of field grown trees is usually best in mid-winter when cultivars are near maximum hardiness levels and when wide fluctuations in temperature are less frequent.

It may be possible to improve genetic discrimination of cold hardiness even further by controlled acclimation of detached shoots in a stepwise manner designed for induction of maximum hardiness levels prior to performing controlled hardiness tests (14). Cold hardiness of flower buds and shoot xylem are closely correlated when the shoots are fully acclimated to attain maximum hardiness but are not closely correlated when collected directly from outdoors without further acclimation (10). Thus it may be possible to select simultaneously for bud and wood hardiness if controlled freezing tests are done on fully acclimated shoots.

Flower buds and shoot xylem are the only peach tissues that exhibit deep supercooling of tissue water. Survival of these tissues appears critical to the northern extension of commercial peach culture in North America. The northern limits of Zone 6, corresponding to the average annual minimum isotherm temperature line of $-23.3°C$, appear to coincide with northern limits of commercial peach culture. This temperature closely corresponds to the average initiation temperature of cold injury to leaf buds and flower buds of peach at maximum hardiness (14). The most susceptible tissues (flower buds, leaf buds, shoot xylem), therefore, are the ones that must be critically assessed in classifying cold hardiness of cultivars and in developing improved testing and selection procedures for cold hardiness.

Peach roots in mid winter are more susceptible than above ground tissues because they can be damaged at milder temperatures ($\approx -10°C$) compared with above ground parts which are more commonly damaged at temperatures below $-18°C$ (8, 9). Fortunately soil temperatures usually do not get colder than $-10°C$ because of the insulation provided from snow and vegetation cover. However, in open winters, especially on light sandy soils and exposed knolls, deep frost penetration into the soil can readily occur during very cold weather and sometimes may result in severe winter injury or death of peach seedling rootstocks with comparatively little above ground injury (9). Although this type of injury is less frequent than above-ground injury, it can be devastating when it occurs (8, 9). Therefore, selection and/or breeding for cold hardiness of peach rootstocks is also of importance to successful peach culture, especially in the more northerly regions of production (8, 9). Special test procedures involving controlled freezing and regrowth tests with peach seedlings or rooted clones must be employed to select for root hardiness as a distinct and separate component of the hardiness complex (8, 9).

Despite the difficulty and complexity of breeding for improved cold hardiness in peach, progress has been made and there is good potential for increasing hardiness even further albeit by a few degrees at best (2, 8, 9, 10, 14, 16). The most important single barrier limiting the hardiness potential of peach cultivar is the existance of the freeze-avoidance mechanism in the flower bud primordia and xylem ray parenchyma mentioned earlier which involves the deep supercooling of tissue water (1, 14). This mechanism, while protective at moderately low temperatures (ca. −10°C to −20° C) becomes lethal at lower temperatures (ca −25 to −35°C) because the supercooled water in the presence of ice nucleators freezes instantaneously at these temperatures. The intracellular ice which forms is associated with injury and/or death of the tissues that possess the supercooling mechanism (14).

Deep supercooling of water in the flower primordia of peaches takes place because there is no vascular continuity between the shoot and the flower primordia except in late spring just before bloom (1). All peach flower buds exhibit the supercooling phenomenon and their maximum hardiness levels are limited by it. Cultivars may differ in rate of vascular development in early spring. Those that attain vascular continuity between the shoot and the flower primordia sooner may have a selection advantage in that the supercooling mechanism may be terminated earlier. This hypothesis needs to be tested to determine whether it may be a useful trait in selection for bud hardiness in peach.

The maximum hardiness which has been measured for fully acclimated peach flower buds is ≈ −30°C (13). It is unlikely, therefore, that peaches can be grown successfully in regions where such temperatures occur with moderate frequency because fruit production would not occur or at best would be inconsistent and uneconomic (13, 14). The maximum hardiness level attained by peach shoot xylem is ≈ −35°C (14). Thus, peach trees would not likely survive outdoors in regions where such temperatures occur with even moderate frequency (13, 14). Maximum hardiness levels that can be induced artificially indoors with detached shoots are not normally attained outdoors under natural conditions (10, 14). Thus, the hardiness limit in midwinter for peach flower buds outdoors is likely to fall between −25° and −30°C and that for shoot xylem between −30 and −35°C.

These lower limits will not likely be exceeded by peach breeders if all breeding and selection is done at the intraspecific level because genetic resources for achieving this within *P. persica* are unknown. If such resources exist, it is likely that they may be found in China near the northern limit of geographic distribution of the wild peach. Hardy cultivar introductions from Harbin Province in northern China (Chui Lum Tao, Tzim Pee Tao) and an open pollinated selection (Siberian C) made at Harrow from a hardy Chinese seed source, possess significantly hardier shoot xylem than North American germ plasm. They are valuable genetic sources of wood hardiness because this hardiness is heritable and has been successfully transmitted when crossed to less hardy North American cultivars (2, 9). The Chinese introductions (Chui Lum Tao, Tzim Pee Tao) and Siberian C are also among the most bud hardy peaches in the Harrow collection. A North American cultivar, Bailey, appears to be equally bud hardy and others including Babygold 5, Late Redhaven, Harrow Blood, Troy, Reliance, Early Elberta, Siberian C, Kalamazoo, Olinda and Harbrite while less hardy, are among the more bud hardy cultivars evaluated at Harrow and each is hardier than Redhaven (10). There are several seedling and second test selections that equal or surpass the hardiness of these including: H6744005, HW 242, HW 213, H7121084, HW 225 and HW 229 (10). Thus, there is good potential now for developing cultivars that exceed the cold hardiness of Redhaven peach, generally considered the standard for cold hardiness among commercially important peach cultivars (8, 9).

The challenge to the breeder is to ensure that new hardy peach cultivars also possess other desirable tree and fruit characteristics, adequate disease resistance, and other pomologically important characteristics necessary and/or desirable for profitable commercial production. To achieve this quickly, it will be important to use a multiple selection index for the most important characters and employ a breeding strategy that maximizes segregation for the characters undergoing selections (9). A combination of recurrent mass selection and backcrossing appears to be the most efficient breeding strategy to produce commercially acceptable cultivars with improved cold hardiness (2, 9). Large populations on which to base selection will be necessary because various levels of selection will be needed.

Wood hardiness is more important than flower bud hardiness for ultimate tree survival, thus, the first level of selection should be to eliminate all seedlings that lack adequate wood hardiness. Flower bud hardiness is essential for consistent croping, thus, all selections lacking adequate bud hardiness should be eliminated. The remaining selections possessing a combination of wood and bud hardiness could then be intermated to provide large F_2 populations that will produce the desired recombinant types containing many favorable hardiness alleles and a moderate level of commercial type genes. The best F_2 plants should then be backcrossed to elite commercial cultivars to produce the desired hardy commercial genotypes (2, 9). As pointed out earlier, it may be possible to select for flower bud and wood hardiness simultaneously, provided that the seedling shoots are fully acclimated. Only when the shoots are fully acclimated is there a good correlation between bud and wood hardiness (Layne, unpublished).

All *Prunus* spp. that have been investigated have been found to possess the deep supercooling, freeze avoidance mechanism in the flower buds and xylem rays (14). Thus, the potential for breeding peaches that will withstand ambient temperatures colder than −40°C (the homogeneous nucleation point of pure water) is remote. However, there are other *Prunus* spp., notably *P. besseyi*, which have been shown to be hardy to between −38 and −45°C for flower buds and −40 to −44°C for shoot xylem (14). Hybrids of *P. besseyi* x *P. persica* and *P. tenella* x *P. persica* have been found to be substantially more hardy than cultivars of *P. persica* and are intermediate in hardiness between the hardy wild species and peach (14). It should be possible, therefore, to utilize the hardiness present in these species and interspecific hybrids to improve cold hardiness in peach. Complicating factors include hybrid sterility which makes backcrossing to peach difficult. When we learn how to regenerate whole plants from fused protoplasts of *Prunus* and to use other genetic engineering techniques, it may become easier to overcome some of the sterility barriers posed by interspecific hybridization.

Breeding for Canker Resistance

There has been no major effort to breed specifically for perennial canker resistance in peach. Nevertheless, breeders select for some measure of canker resistance (tolerance) either directly or indirectly by choosing the healthiest and best seedlings for advanced trials. While such mild selection pressure has been applied, its intensity has presumably been too low to result in major genetic improvement of canker resistance of cultivars being grown today (5, 12, 17). However, cultivars definitely differ in their levels of canker resistance (5, 7, 12), although no highly resistant or immune selections have been identified (5). A complicating factor in utilizing these sources of canker resistance is that there is a significant cultivar x year interaction with respect to canker progression (5). Thus it may become necessary to screen for canker resistance in a semi- or fully- controlled environment as opposed to screening outdoors in order to improve precision in selection. As mentioned earlier, it may also be necessary to seek higher levels of canker resistance than what can be found in peach, such as from other related species, and transfer this resistance to peach by interspecific hybridization in much the same way as may be required for improving cold hardiness.

A further complicating factor is that two species of the canker pathogen (4) are involved *(L. cincta, L. persoonii)*. In some regions such as Ontario, *L. cincta* is the most important of the two (4), thus evaluation of cultivar or seedling resistance in Ontario would have to give this pathogen primary consideration. In other regions such as Colorado (12), *L. persoonii* is the common canker pathogen. We do not know whether the same or different genes are involved in canker resistance to the two pathogens. This information is needed to improve chances of success in selecting for canker resistance. Does a cultivar that has some resistance to *L. cincta* (e.g. Sunhaven) also have a measure of resistance to *L. persoonii*? If resistance to each pathogen is inherited independently, it may be necessary to screen for resistance to each pathogen separately. Is it possible to use mixed inoculum and screen for both pathogens simultaneously? Furthermore, do we know what mechanism of resistance is needed? Presumably, because canker is a wound pathogen and does not penetrate intact epidermis directly (3, 4, 12), the resistance mechanism likely to be most useful would be one in which resistance is expressed at the biochemical level.

Already it has been shown that cultivars differ in their time of defoliation (15) and rate of wound compartmentalization (17) which in turn may relate to host resistance (18). Host resistance based on such mechanisms is expected to be most effective during the growing season when periderm formation is more rapid. However, these mechanisms may be of little value during the dormant period when very little wound periderm is formed. Is there a biochemical basis for host resistance in *Prunus* which is expressed year-round and is functional during the dormant period when the other resistance mechanisms may be nonfunctional? Can this be transferred to peach? Recent evidence from forest trees indicates that the ability of injured trees to compartmentalize wounds is an important feature of their survival (18). There is some evidence that the ability to compartmentalize wounds is under genetic control. Peach cultivars may also differ in their wound compartmentalizing ability (17). It may be possible to use this trait as a means of selecting indirectly for canker resistance in peach (18).

Much has been learned about the best time to inoculate plants for assessment of canker resistance (3, 4, 5, 6, 12), types of inoculation procedures that are efficient and effective in obtaining good infection (5, 6, 12), tissue age and type best suited for inoculation (6, 20), and optimum length of time needed for disease progression in order to maximize discrimination of differences in canker resistance (12). We do not know if canker resistance can be selected for *in vitro*. Is it possible to screen for canker resistance at the tissue culture level? More basic information is needed on perennial canker resistance, resistance mechanisms and screening techniques in order to maximize progress in breeding for canker resistance in peach.

Of course there are other factors besides winter injury that predispose peach to perennial canker. Injuries from oriental fruit moth predispose peach twigs to canker infection (19, 20). Perennial cankers on peach trunks serve as breeding grounds for the lesser peach tree borer. The larvae feed on surrounding callus tissue and extend canker margins in early spring. Rootstocks also influence canker resistance of scion cultivars (7). Consideration of these factors during selection may indirectly serve to reduce canker infection and severity.

Conclusions

Definite progress has been made in improving the cold hardiness of peach cultivars through breeding. The potential for further progress is good although limited by the level of hardiness present in *P. persica* germ plasm. Gene transfer from very hardy *Prunus* spp. such as *P. besseyi, P. tenella, P. tomentosa* and their interspecific hybrids with peach offer the best potential for major advances in cold hardiness but will likely involve several backcrosses to peach in order to recover commercially acceptable cultivars. New technology in genetic engineering of plants may provide a valuable approach to reducing the time needed to effect gene transfer from very hardy *Prunus* species and interspecific hybrids to peach.

Only modest progress has been made in improving canker resistance of peach cultivars. Several factors may account for this including the possibility that the existing level of canker resistance in North American peach germ plasm is probably quite low and the selection pressure that has been applied has been insufficient to result in appreciable genetic advance in canker resistance. A wider search is needed of peach and other *Prunus* germ plasm to identify higher levels of canker resistance that might be transferred to peach. Interspecific hybridization and genetic engineering techniques may have a role to play here as well.

Wounds of any kind predispose peach to infection by peach canker. Canker infected trees are more cold susceptible than healthy ones. Therefore, it may be equally important to select peaches for ability to compartmentalize wounds quickly.

Research directed in the above areas may hold the key to developing significantly hardier, canker resistant, wound tolerant peach cultivars of the future.

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Fruit Survival Ratings of Peaches and Nectarines Following Late Spring Freezes During Two Years[1]

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Abstract

Fifty-one peach and nectarine cultivars and selections growing in a grower cooperator test plot in the piedmont section of South Carolina were rated for amount of crop following −5°C on March 27, 1982, and −3.3°C on April 20 and 23, 1983. In both years, cultivar ratings ranged from no crop to those that needed heavy thinning. Generally, cultivars developed in climates similar to South Carolina's performed best.

In the South, dormant peach flower buds are seldom injured by midwinter temperatures. However, flowers and developing fruit are often injured by spring frosts. Varietal differences in spring frost hardiness have been reported (1, 7). Hardiness at this stage of bud development is not always correlated with hardiness of dormant flower buds (2). Generally, bud survival is correlated with time of bloom (2). However, late blooming cultivars have sometimes been injured more by late frosts than earlier blooming cultivars (1, 7).

Controlled freezing tests have been used to a limited degree to determine differences in cultivar hardiness (8). However, most information on cultivar hardiness has been based on natural freezes (1, 2, 4, 5, 6, 7). Hardiness of seedling populations has also been evaluated after natural freezes (3, 6). To fully evaluate spring frost hardiness of a cultivar it is important to test it over a number of years and at

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