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Genetic and temporal variation in abscission zone formation in peach  
leaves in relation to peach canker disease

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## **Abstract**

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Leaf scars from 13 peach cultivars and clones with varying susceptibility to peach canker disease were collected during the period November, 1986, through May, 1987, and were examined histologically. Leaf scar sections were examined with light and fluorescence microscopy for tissue changes related to wound healing, including depth and width of the polysaccharide-impregnated zone, the timing and tissue depth at which the ligno-suberized layer occurred, the thickness and numbers of cells in the ligno-suberized layer, the longitudinal length of the lignosuberized layer and whether or not the tissue was complete in longitudinal section through the leaf scar, the presence and numbers of phellem cells in the wound periderm and whether or not the periderm was complete across the longitudinal section of the leaf scar. The percentage of leaf scars with a complete polysaccharide-impregnated zone varied by date with 94 to 96% of the leaf scars exhibiting the zone in January and April. The thickness of the polysaccharide-impregnated zone also varied by date, reaching its thickest in January and April. Percentages of lignified leaf scars were mostly similar among cultivars at 4 of the 5 dates; however, on 1 May, there was considerable variation among cultivars with percent lignification ranging from 0 to 100%. The proportion of leaf scars with lignification was not significantly correlated with the field susceptibility rankings for peach canker disease at any of the five dates. The proportion of leaf scars with complete ligno-suberized layers varied by date only, with the highest values observed on 12 January and 14 May. The lowest values was observed on 1 May,

and this was significantly less than that observed on 7 November and 10 April. The highest percentage of leaf scars possessing periderm occurred on 12 January (74%), with all the other dates not significantly different from each other (ranging from 29 to 40%). Analysis of cultivar across all dates combined indicated that Candor generally showed the highest percentages of leaf scars with periderm (64%), and this was significantly higher than Sunhaven (24%), Earlired (14%), and V68101 (13%), which were not different from each other. The proportion of leaf scars with periderm was not significantly correlated with the field susceptibility rankings for peach canker disease at any of the five dates.

Key words: *Prunus*, wounding, *Leucostoma*

### **Introduction**

Peach canker, a fungal disease caused by *Leucostoma cincta* (Pers. ex Fr.) Höhn. (anamorph = *Leucocytophora cincta* (Sacc.) Höhn.) and *L. personii* (Nits.) Höhn. (anamorph = *L. leucostoma* (Pers.) Höhn.), continues to be a major limiting factor in peach production in the northern areas of North America. The pathogens initiate disease in wounds created by pruning, leaf abscission, winter injury, and insect damage (21). The disease appears as perennial cankers on trunks, scaffold limbs, and branches, and causes crop losses mainly through reduction in bearing surface and premature tree death. Leaf scars have been identified as the major site of entry for *L. cincta* and this fungus is considered to be the primary canker pathogen of 1-year-old twigs in the Niagara Peninsula of Ontario (14,27). *Leucostoma personii*, the pathogen associated with the destructive phase of the disease, is isolated only rarely from such twigs and usually is

present in perennial cankers on older branches, scaffold limbs, and trunks (12,19,20). All the currently grown peach cultivars are susceptible to these pathogens (14), and there is no known treatment which will prevent infection over the long term (5).

Resistance to infection, invasion, and colonization is associated with rate of formation of new tissues associated with defense and repair in the bark (1,3,4,6). The formation of tissue zones, predominant in either polysaccharides (gum and callose) or lignin and suberin, has been demonstrated in peach bark either wounded or wounded and inoculated with *L. cincta* or *L. personii* (1,3). Rate of formation of new tissue layers in mature bark and leaf scars also is influenced strongly by temperature (2,7).

Many factors have impeded progress in breeding peach trees for increased resistance to the canker pathogens, including regional variation in cultivar performance (14), cultivar by year variation in susceptibility to pathogens (10), lack of standardized inoculation procedures (15), lack of knowledge regarding pathogen variation, lack of breeding material in *Prunus* with immunity to the pathogens, and the land- and labor-intensive nature of conventional fruit tree breeding. A rapid, reliable and economically efficient method to detect pathogen resistance would expedite development of new, *Leucostoma*-resistant peach cultivars.

Willison (22) noted that the cultivar Rochester was highly susceptible to leaf scar infections relative to Elberta, a moderately resistant cultivar. Rate of leaf fall and the temperature during the leaf abscission period were considered to be critical factors affecting outbreaks of the disease. Weaver (18) observed marked differences among cultivars in rate of leaf fall and that rapid leaf abscission was correlated with moderate levels of pathogen resistance. He concluded that natural infection would be greatly reduced by the selection of breeding lines that exhibited rapid

defoliation (18). Given the potential importance of this observation to peach breeding programs, the objective of the present study was to document the gross tissue changes in the leaf scar following abscission and examine the correlation between the measured anatomical parameters and the known susceptibility of several different peach cultivars and clonal selections to the peach canker pathogens.

### **Materials and Methods**

**Orchard sites.** Peach (*Prunus persica* (L.) Batsch.) orchards were established at the Agriculture Canada experimental farm in Jordan Station, Ont., (Jordan) and at the experimental farm of the Horticultural Research Institute of Ontario in Vineland Station, Ont., (Victoria) in May of 1984 and 1985, respectively. The Jordan farm is about 3 km east of the Victoria farm. Soils on both farms are imperfectly drained Vineland fine sandy loam and are typical of peach orchard soils in the Niagara Peninsula. The Jordan orchard was established with 1-yr-old, virus-tested, canker-free nursery stock on cultivar Bailey rootstock. Cultivar Boone County rootstocks were used at the Victoria site, except for the combination of cultivar Madison on Halford. Trees on the Victoria farm were canker-free although not virus-tested. Tree spacing was 1.5 X 4.0 m and 3.0 X 5.0 m at the Jordan and Victoria farms, respectively. Orchards were managed with clean cultivation in the spring followed by a rye grass cover crop planted in July. Fungicides and insecticides were applied as needed to control peach leaf curl, brown rot, and oriental fruit moth (ferbam, captan, phosmet, respectively). The trees were planted in randomized complete blocks at each orchard site. Cultivars were selected to represent a range of susceptibility to Leucostoma spp. based on historical field performance ratings with visual assessment and a 1 to 10 numerical

rating system (6, R.E.C. Layne, personal communication). The field performance ratings for the Jordan cultivars were determined at the Agriculture Canada Harrow Research Station in Harrow, Ontario. For those cultivars established at the Victoria site, field performance ratings were determined in an adjacent planting at the same site. None of the cultivars selected for these experiments was immune to the pathogens because known sources of immunity are not available. Therefore, the cultivars selected ranged from highly susceptible to moderately resistant.

Eleven peach cultivars and two clones from Chinese germplasm, V68101 and V68051, were used in this study. Cultivars were selected to represent a range of susceptibility to Leucostoma spp. based on historical field performance ratings with visual assessment and a 1 to 10 numerical rating system: 1 = no canker observed; 2 = trace in 1- or 2-year-old wood; 3 = canker very light in major limbs of tree; 4 = canker light to moderate in trunk, crotch, and lower scaffold; 5 = canker moderate in trunk, crotch, and lower scaffold, but severe in minor branches; 6 = canker severe in one of trunk, crotch, or scaffold; 7 = canker severe in two of trunk, crotch, or scaffold; 8 = tree alive but canker likely to become major cause of death, disease severe in trunk, crotch, and scaffold; 9 = tree dying, canker severe and judged to be the major cause of dying; 10 = tree dead, canker severe and judged to be the major cause of death (R. E. C. Layne, personal communication). The order of cultivars and clones from moderately resistant to highly susceptible was determined to be: V68101, V68051, 'Veeglo', 'Babygold 5', 'Sunhaven', 'Redhaven', 'Garnet Beauty', 'Loring', 'Vanity', 'Candor', 'Madison', 'Vivid', and 'Earlired'.

Five leaf scars, from each of three replicate trees/cultivar from Jordan and five replicate trees/cultivar from Vineland, were collected on five dates, 7 Nov. 1986, 12 Jan. 1987, 10 April

1987, 1 May 1987, and 14 May 1987. All leaf scars were collected from the middle portions of the one-yr-old stems. Samples were fixed in FAA and prepared for light and fluorescence microscopic examination as described previously (1). Data were recorded for nine histological features based on the deposition of reaction zones and new tissues in peach bark as described previously (1). Histological features measured were: depth and width of the polysaccharide-impregnated zone (PSZ), the timing and tissue depth at which the ligno-suberized layer (LSL) occurred, the thickness and numbers of cells in this layer, the longitudinal length of the LSL tissue and whether or not the tissue was complete across the longitudinal section of the leaf scar, the presence and numbers of phellem cells in the wound periderm and whether or not it was complete across the longitudinal section of the leaf scar.

**Data analysis.** All data were analysed with a general linear models procedure (SAS Institute, Cary, NC, GLM procedure) based on a completely randomized design. Main effect means for the treatments were separated with Duncan's multiple range test (16). Where significant interactions of cultivar and leaf scar collection date were observed, separate analyses of cultivar main effects were conducted for each leaf scar collection date. These additional analyses were necessary due to the dynamic nature of host tissue differentiation in response to leaf abscission and environmental influences. Spearman's nonparametric rank correlation procedure was used to determine the significance of the association between individual anatomical parameters and the known relative susceptibility of the cultivars to peach canker disease.

## **Results and Discussion**

The percentage of leaf scars with a complete PSZ varied by date, but not by cultivar (Table

1), with 94 to 96% of the leaf scars exhibiting the PSZ in January and April (Table 2). The thickness of the PSZ also varied by date, but not by cultivar (Table 1), reaching its thickest in January and April (Table 2). For thickness, the interaction of cultivar x date was significant (Table 1).

The percentage of leaf scars exhibiting complete lignification varied by cultivar and date, with a significant interaction between these variables (Table 1). Percentage of lignified leaf scars were similar among cultivars at 7 November, 12 January, and 14 May (Table 3). On 10 April, only clone V68051 was significantly different from the other cultivars; whereas on 1 May, there was considerable variation among cultivars with percent lignification ranging from 0 to 100% (Table 3). Cultivars Babygold 5, Garnet Beauty, Sunhaven, and Veeglo exhibited 100% lignified leaf scars, significantly greater ( $P > 0.05$ ) than cultivars Earlired, Madison, and clone V68101 which exhibited 0% lignification (Table 3). The variability in lignification at leaf scars at this time could be interpreted as a period of susceptibility to infection by *L. cincta*. This interpretation is supported by the observations of Royse and Ries (13) who found higher percentages of *L. cincta* in twig elements in spring versus fall samples. The proportion of leaf scars with lignification was not significantly correlated with the field susceptibility rankings for peach canker disease at any of the five dates.

After lignification occurs and just prior to the initiation of necrophylactic periderm, part of the lignified layer also becomes suberized. The proportion of leaf scars with complete ligno-suberized layers varied by date only (Table 1), with the highest values observed on 12 January and 14 May (Table 2). The lowest values was observed on 1 May, and this was significantly less than that observed on 7 November and 10 April.

The percentage of leaf scars exhibiting complete periderm formation varied by date and cultivar, and there was a significant interaction between these two variables (Table 1). For date, the highest percentage of leaf scars possessed periderm on 12 January (74%), with all the other dates not significantly different from each other (ranging from 29 to 40%) (Table 4). There was variation in periderm formation among cultivars at all dates except on 7 November (Table 4). Analysis of cultivar across all dates combined indicated that Candor generally showed the highest percentages of leaf scars with periderm (64%), and this was significantly higher than Sunhaven (24%), Earlired (14%), and V68101 (13%), which were not different from each other (data not shown). The proportion of leaf scars with periderm was not significantly correlated with the field susceptibility rankings for peach canker disease at any of the five dates.

Very often, examination of the leaf scar revealed the presence of more than one periderm layer. Leaf scars with more than one periderm layer were more likely to be observed on 12 January (significantly different from the other four dates which were similar to each other (data not shown)). Mean numbers of periderm layers varied among cultivar (Table 1), with Babygold 5 and Madison exhibiting more periderm layers than Earlired and Vivid (Table 5). All other cultivars were similar to the four previously mentioned and to each other. For the most recently formed periderm layer, the cultivars Candor and Madison had greater numbers of suberized phellem cells than the cultivar Earlired (Table 5). All other cultivars were similar to the three previously mentioned and to each other.

Genetic and temporal variability in leaf scar anatomy is demonstrated for peach. The anatomical modifications associated with peach leaf abscission were similar to those described for *Castanea* (11). Lee considered this a simple and apparently primitive type of abscission. In both

peach and chestnut, the ligno-suberized layer and necrophyllactic periderm are not formed until after leaf fall. However, Lee describes chestnut as possessing a small area around the leaf scar that was unprotected by cork layers over winter (11). In peach, this was variable with 100% of all leaf scars being lignified in January, 94% possessed ligno-suberized tissues at this time, and, among cultivars, presence of necrophyllactic periderm varied from 0 to 100%.

In an earlier study on the anatomy of peach leaf scars, Biggs and Northover (7), maintained that rate and extent of tissue changes in leaf scars could be practical determinants for studying susceptibility to the pathogens which colonize via leaf scars or mechanical wounds. Although the present study detected genetic variability within peach for lignification and necrophyllactic periderm formation, cultivar responses were not related to the known relative susceptibility of the cultivars and clones examined.

The present study is the third investigation in these orchards to investigate the association between wound-related events in autumn and susceptibility to the peach canker pathogens. Biggs and Miles (6) reported that the rate of suberin accumulation in mechanically wounded peach twigs was correlated significantly with susceptibility to the peach canker pathogens but only when wounds were inflicted and suberin determined during the months of May and June. Wounds created and examined for suberin in September and October showed significant genetic variation, although no correlation of suberin with susceptibility. These authors suggested that the wound system employed in the earlier study inadequately represented events associated with abscission. Next, in a study of leaf abscission rate at the same site, the results did not substantiate earlier observations (18) on the association of leaf abscission rate with susceptibility to the peach canker disease (9). Tekauz and Patrick (17), also unable to support Weaver's observations, demonstrated

that all nodes on a twig are equally susceptible to inoculation with *L. cincta* and concluded that early defoliation by itself did not confer resistance to infection. (4,6,15). Finally, in the present study, no relationship could be demonstrated between changes at the infection court and the known relative susceptibility of the cultivars and clones to *Leucostoma* spp. From the results of all three studies, it can be concluded that wound-related events in the leaf scar are probably not associated with cultivar variation in susceptibility to the peach canker pathogens. The absence of a relationship between leaf abscission parameters and susceptibility to disease is unfortunate because measuring rate of leaf scar changes is relatively easy when compared with other techniques for evaluating resistance to *Leucostoma* spp.

One caveat to the above discussion is related to the influence of temperature on the rate of formation and the physical condition of leaf scars. The interaction of temperature with rate of leaf abscission, as observed by Willison (21), and the effects of cold temperatures on periderm integrity require further study. Temperature has been shown to influence the rate of boundary zone and periderm formation in peach bark (2) and leaf scars (7). In the latter study, periderm formation in leaf scars was delayed for up to 16 days at 7.5 C relative to 17.5 C. It is possible, as Willison indicated, that fungal infection proceeds at low temperatures even though resistance mechanisms in leaf scars have been impeded by low temperatures. In addition, periderms in leaf scars might be sensitive to cold temperatures, resulting in cracks or other physical discontinuities that could provide avenues of ingress for *Leucostoma* spp. that were previously confined to outer tissues by the intact periderm.

In summary, the present investigation confirmed the presence of genetic variation in wound healing in leaf scars among peach cultivars and clones. However, variation in wound

healing parameters, as demonstrated in earlier studies of wounded bark tissue (4,6,9), is useful as an expression of partial resistance to *Leucostoma* spp. only if it can be established that a significant association exists between a specific anatomical parameter and relative cultivar susceptibility to the pathogens. Unfortunately, this relationship could not be demonstrated over the course of the current investigations. Given the results of the present study and earlier reports (4,6,8), the importance of leaf scar infection by *L. cincta* and the role of this fungus in tree decline and death should be evaluated further.

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Table 1. *F*-statistic and level of significance from analysis of variance data for abscission zone wound reaction parameters in various peach cultivars and clones

| Variable        | Leaf scars with polysaccharide zone (%) | Thickness of polysaccharide zone | Leaf scars with complete lignified zone (%) | Leaf scars with complete primary lignosuberized zone (%) | Leaf scars with complete periderm (%) | Number of suberized phellem cells | Number of periderm layers |
|-----------------|---|----------------------------------|---|--|---------------------------------------|-----------------------------------|---------------------------|
| Date            | 7.55*** <sup>z</sup>                    | 7.55***                          | 5.25 ***                                    | 5.66***  | 2.33*                                 | 0.35                              | 1.29                      |
| Cultivar        | 1.01                                    | 0.74                             | 2.18**                                      | 1.46   | 2.55**                                | 1.74                              | 2.22*                     |
| Site            | 1.37                                    | 0.01                             | 0.22  | 0.15   | 1.21                                  | 0.44                              | 0.59                      |
| Date x cultivar | 1.27                                    | 1.44                             | 1.59*                                       | 1.03   | 1.36                                  | 1.09                              | 1.17                      |
| Date x site     | 2.36                                    | 0.53                             | 1.98  | 0.59   | 0.31                                  | 1.56                              | 0.43                      |

<sup>z</sup> Asterisks indicate level of significance of the *F*-statistic: \*\*\* =  $P \leq 0.001$ , \*\* =  $P \leq 0.01$ , \* =  $P \leq 0.05$

Table 2. Percentage of leaf scars with a polysaccharide zone, the thickness of the zone in longitudinal orientation, and percentage of leaf scars with a primary lignosuberized layer

| Date            | Leaf scars with polysaccharide zone (%) | Thickness ( $\mu\text{m}$ ) of polysaccharide zone | Leaf scars with primary lignosuberized layer (%) |
|-----------------|---|--|--|
| 7 November 1986 | 57.8 <sup>c<sup>y,z</sup></sup>         | 271.7 b  | 68.1 b   |
| 12 January 1987 | 94.3 ab                                 | 391.4 a  | 94.2 a   |
| 10 April 1987   | 96.4 a                                  | 480.4 a  | 61.8 b   |
| 1 May 1987      | 50.8 c                                  | 199.5 bc   | 39.0 c   |
| 14 May 1987     | 79.7 b                                  | 167.1 c  | 84.8 a   |

<sup>y</sup> Values are the means of 45, 35, 56, 59, and 59 observations for 7 November, 12 January, 10 April, 1 May, and 14 May, respectively.

<sup>z</sup> Different letters in columns denote significant differences according to Duncan's multiple range test ( $P \leq 0.05$ ).

Table 3. Percentage of leaf scars with a complete lignified zone

| Cultivar or clone | Date                   |              |               |            |             |
|-------------------|------------------------|--------------|---------------|------------|-------------|
|                   | 7 Nov. 1986            | 12 Jan. 1987 | 10 April 1987 | 1 May 1987 | 14 May 1987 |
| Babygold 5        | 100.0 a <sup>y,z</sup> | 100.0 a      | 100.0 a       | 100.0 a    | 100.0 a     |
| Candor            | 100.0 a                | 100.0 a      | 87.5 a        | 62.5 ab    | 87.5 a      |
| Earlired          | 100.0 a                | 100.0 a      | 100.0 a       | 0.0 b      | 100.0 a     |
| Garnet Beauty     | 100.0 a                | 100.0 a      | 100.0 a       | 100.0 a    | 80.0 a      |
| Loring            | 40.0 a                 | 100.0 a      | 100.0 a       | 60.0 ab    | 100.0 a     |
| Madison           | 100.0 a                | 100.0 a      | 100.0 a       | 0.0 b      | 100.0 a     |
| Redhaven          | 87.5 a                 | 100.0 a      | 100.0 a       | 75.0 a     | 100.0 a     |
| Sunhaven          | 100.0 a                | 100.0 a      | 75.0 a        | 100.0 a    | 40.0 b      |
| Vanity            | 75.0 a                 | 100.0 a      | 100.0 a       | 75.0 a     | 100.0 a     |
| Veeglo            | 100.0 a                | 100.0 a      | 100.0 a       | 100.0 a    | 100.0 a     |
| Vivid             | 66.7 a                 | 100.0 a      | 100.0 a       | 66.7 ab    | 100.0 a     |
| V68051            | 100.0 a                | 100.0 a      | 33.3 b        | 66.7 ab    | 100.0 a     |
| V68101            | -----                  | -----        | -----         | 0.0 b      | 100.0 a     |

<sup>y</sup> Values in columns for each cultivar are a mean of 3 to 8 observations.

<sup>z</sup> Different letters in columns denote significant differences according to Duncan's multiple range test ( $P \leq 0.05$ ).

Table 4. Percentage of leaf scars with complete periderm on different collection dates

| Cultivar      | Leaf scar collection date |              |               |            |             |
|---------------|---------------------------|--------------|---------------|------------|-------------|
|               | 7 Nov. 1986               | 12 Jan. 1987 | 10 April 1987 | 1 May 1987 | 14 May 1987 |
| Babygold 5    | 0.0 a                     | 100.0 a      | 100.0 a       | 100.0 a    | 33.3 ab     |
| Candor        | 75.0 a                    | 100.0 a      | 50.0 ab       | 37.5 ab    | 62.5 ab     |
| Earlired      | 33.0 a                    | 50.0 ab      | 0.0 b         | 0.0 b      | 0.0 b       |
| Garnet Beauty | 25.0 a                    | 100.0 a      | 60.0 ab       | 60.0 ab    | 20.0 ab     |
| Loring        | 0.0 a                     | 100.0 a      | 20.0 b        | 20.0 b     | 40.0 ab     |
| Madison       | 50.0 a                    | 100.0 a      | 50.0 ab       | 0.0 b      | 100.0 a     |
| Redhaven      | 71.4 a                    | 40.0 ab      | 50.0 ab       | 25.0 b     | 25.0 ab     |
| Sunhaven      | 50.0 a                    | 0.0 b        | 50.0 ab       | 0.0 b      | 20.0 ab     |
| Vanity        | 14.3 a                    | 83.3 ab      | 12.5 b        | 50.0 ab    | 50.0 ab     |
| Veeglo        | 33.3 a                    | 100.0 a      | 33.3 ab       | 0.0 b      | 0.0 b       |
| Vivid         | 0.0 a                     | 33.3 ab      | 0.0 b         | 0.0 b      | 33.3 ab     |
| V68051        | 0.0 a                     | 50.0 ab      | 0.0 b         | 33.3 ab    | 66.7 ab     |
| V68101        | -----                     | -----        | -----         | 0.0 b      | 100.0 a     |

<sup>y</sup> Values in columns for each cultivar are the mean of 3 to 8 observations.

<sup>z</sup> Different letters in columns denote significant differences according to Duncan's multiple range test ( $P \leq 0.05$ ).

Table 5. Mean number of periderm layers and mean numbers of cells in the most recently formed periderm in leaf scars of peach cultivars and clones

| Cultivar      | Number of               |                           |
|---------------|-------------------------|---------------------------|
|               | suberized phellem cells | Number of periderm layers |
| Babygold 5    | 1.7 ab <sup>y,z</sup>   | 0.64 a                    |
| Candor        | 2.5 a                   | 0.63 ab                   |
| Earlired      | 0.3 b                   | 0.14 b                    |
| Garnet Beauty | 1.9 ab                  | 0.54 ab                   |
| Loring        | 0.8 ab                  | 0.32 ab                   |
| Madison       | 2.9 a                   | 0.67 a                    |
| Redhaven      | 2.0 ab                  | 0.54 ab                   |
| Sunhaven      | 0.8 ab                  | 0.24 ab                   |
| Vanity        | 1.4 ab                  | 0.46 ab                   |
| Veeglo        | 0.7 ab                  | 0.33 ab                   |
| Vivid         | 0.8 ab                  | 0.13 b                    |
| V68051        | 1.2 ab                  | 0.33 ab                   |
| V68101        | 1.1 ab                  | 0.50 ab                   |

<sup>y</sup> Values in columns for each cultivar are the mean of 3 to 8 observations.

<sup>z</sup> Different letters in columns denote significant differences according to Duncan's multiple range test ( $P \leq 0.05$ ).