Susceptibility of Peach Cultivars to Rusty Spot and Characterization of Susceptibility Groups

Norman Lalancette¹ and Daniel L. Ward

Department of Plant Biology and Pathology, Rutgers University, Rutgers Agricultural Research and Extension Center, 121 Northville Road, Bridgeton, NJ 08302-5919

Joseph C. Goffreda

Department of Plant Biology and Pathology, Rutgers University, Rutgers Fruit and Ornamental Research and Extension Center, 283 Route 539, Cream Ridge, NJ 08514-9634

Additional index words. disease resistance, fungus, *Podosphaera leucotricha*, powdery mildew, *Prunus persica*

Abstract. A field study was conducted during the 2007 and 2008 growing seasons to determine and compare the susceptibility of 33 peach (*Prunus persica* L. Batsch) cultivars and advanced selections to rusty spot caused by *Podosphaera leucotricha*. During each season, the progression of peach rusty spot was monitored on three cultivars of varying susceptibility to determine when the epidemics had terminated. At that time, disease incidence and severity were estimated as percent infected fruit and number of lesions per fruit, respectively, for all cultivars in the study. Observations were recorded on fruit sampled from four replicate trees of each cultivar located in experimental plantings at the Rutgers Agricultural Research and Extension Center, Bridgeton, NJ. No fungicide sprays were applied to the trees during the study. Overall disease incidence values, estimated by averaging data from both years, varied widely across cultivars, ranging from 5% to 68% fruit infected. The three most susceptible cultivars were Autumnnglo, Jerseyqueen, and Bounty, whereas the three least susceptible cultivars were Gloria, Harrow Beauty, and Sugar May. Results of Tukey-Kramer mean separation groupings and relative susceptibility rankings across both years were used to place cultivars into five disease susceptibility categories. The most susceptible cultivars were characterized as having yellow flesh with normal melting flesh texture and acidity, whereas less susceptible cultivars tended to have white-fleshed stony-hard subacid fruit. Among eight quantitative fruit characteristics examined for association with disease levels, ripening date, fruit weight at pit hardening, and fruit pubescence were found to be positively correlated with rusty spot development. Finally, the relationship between disease incidence and lesion density within the 0 to 0.5 incidence range, based on data from all cultivars in the study, agreed closely with former models derived from only a single cultivar.

Rusty spot is an important disease of peach (*Prunus persica* L. Batsch) that occurs in many fruit-growing regions of the world (Dolovac et al., 2009; Grove, 1995b; Jankovics et al., 2011). Although the disease was first described in 1941, early attempts to identify the causal agent were thwarted as a result of sparse pathogen growth on fruit (Blodgett, 1941). Eventually, results from an inoculation study provided evidence that the causal agent may be *Podosphaera leucotricha* (Ellis & Everh.) E. S. Salmon, the apple powdery

mildew pathogen, but results were not definitive (Manji, 1972). Subsequent field studies examining disease gradients in peach orchards adjacent to apple orchards provided further support for *P. leucotricha* as the causal agent (Daines and Trout, 1977; Ries and Royse, 1978). Recent molecular-based research examining the rDNA internal transcribed spacer sequences of fungal thallus from rusty spot lesions has confirmed the pathogen to be *P. leucotricha* (Jankovics et al., 2011).

Unlike peach powdery mildew, caused by *Sphaerotheca pannosa*, rusty spot symptoms only occur on fruit and not on leaves or shoots (Grove, 1995a, 1995b). Symptoms on young fruit consist of small, mostly round, orange-brown lesions that typically increase in size as the fruit grows. In disease-favorable seasons, lesions can cover large areas of the fruit surface and multiple lesions often coalesce. As the lesions age, the epidermis becomes necrotic and the trichomes detach. The resulting

lesion surface becomes smooth and russeted, often rendering the fruit unmarketable. On highly susceptible cultivars, estimates of yield loss have been as high as \$504 per hectare in disease-favorable growing seasons (Polk et al., 1997).

Temporal analyses of rusty spot epidemics revealed that disease increases in a logistic fashion from the shuck-off stage of fruit development until approximately 60 d after full bloom, a period ranging from 17 to 30 d (Furman et al., 2003a). This period coincides with the first stage of fruit development, which is characterized by rapid cell division (Flore, 1994; Tukey, 1933). As fruit growth slows and approaches initiation of pit hardening toward the end of this stage, the rate of disease increase slows and approaches zero. Given this pattern of disease and fruit growth, the optimum timing for fungicidal control consists of three to five applications beginning at 90% to 100% petal fall (Furman et al., 2003b). Subsequent efficacy studies have demonstrated that four fungicide sprays, applied at petal fall, shuck-split, first cover, and second cover, provide adequate control in most years (Lalancette et al., 2006; Lalancette and Foster, 2001). These studies also showed that demethylation inhibitor fungicides were much more effective than sulfur and that some quinone outside inhibitors also exhibited good efficacy. A recent evaluation of biorational materials known to be effective against powdery mildew pathogens revealed that some of these materials can consistently reduce rusty spot development (Lalancette et al., 2013). However, although these products significantly reduced disease, their level of control was low relative to conventional fungicides.

As outlined previously, much progress in understanding the etiology, epidemiology, and control of peach rusty spot has been made over the last decade. However, little information is available on the relative susceptibility of peach cultivars to rusty spot. Differences in disease levels among cultivars are often observed in any given year, but quantitative comparisons have not been performed. Consequently, the major objective of this study was to determine the relative susceptibility of commercial cultivars and advanced selections by comparing their disease levels over two growing seasons. The resulting susceptibility ratings will not only aid commercial growers in cultivar selection, but also provide important additional information for implementation of integrated disease management programs. A secondary objective was to characterize susceptible cultivars by identifying those horticultural traits that are associated with disease development. Finally, because a wide variation in disease levels was observed across the cultivars, the quantitative relationship between disease incidence and severity was investigated.

Materials and Methods

Orchard site. The study was conducted during 2007 and 2008 in an experimental peach cultivar orchard located at the Rutgers Agricultural Research and Extension Center,

Received for publication 19 Dec. 2013. Accepted for publication 15 Mar. 2014.

This research was funded in part by the New Jersey Agricultural Experiment Station.

We thank Alison Burnett, Kathleen Foster, Gail Lokaj, and Gary Glatfelter for their technical assistance.

¹To whom reprint requests should be addressed; e-mail lalancette@njaes.rutgers.edu.

Bridgeton, NJ. All cultivar scions in the block were grafted on 'Lovell' peach rootstock and planted at a tree by row spacing of 3 m × 6.1 m. Standard commercial practices for tree management, insect control, and weed control were followed throughout the study (Hamilton et al., 2007). No fungicides were applied before or during the rusty spot epidemics in each year of the study.

Experimental design. The rectangular experimental orchard was divided into four quadrants, each containing cultivars belonging to one of four harvest maturity classifications: early season, early midseason, late midseason, and late season. Four single-tree replicates of each cultivar were planted within each quadrant; tree locations were randomly chosen. This planting arrangement was originally created to facilitate application of fungicides for management of brown rot during the pre-harvest ripening period. However, for evaluation of rusty spot susceptibility in this study, a completely randomized design was considered the best possible fit for analyses. Because all inoculum for rusty spot epidemics is believed to be airborne and to originate from outside the orchard (Grove, 1995b), and no known point sources of inoculum existed nearby, it was assumed that restricted randomization of replicate location within the block would not bias estimation of disease levels.

Cultivars. A total of 33 commercially available cultivars and advanced selections were chosen for evaluation of rusty spot susceptibility. Only those advanced selections that were considered good candidates for eventual release, based on horticultural performance, were included in the study. Chosen cultivars and selections, referred to collectively as cultivars, in the early-season maturity classification were Desiree™ ('NJ350'), 'Sentry', 'Sugar May', Scarlet Rose™ ('NJ355'), and L12-4; in the early midseason category were 'Melik Early Topaz', 'Raritan Rose', 'Redhaven', 'White Lady', TangOs® ('NJF16'), H11-59, H11-76, H11-79, H13-11, J19-28, and L13-18; in the late midseason category were 'Bounty', Gloria™ ('NJ351'), John Boy® (limb mutation of 'Loring'), Messina™ ('NJ352'), Saturn ('N.J. F-2'), 'Sugar Lady', 'Suncrest', D88-59, and 7-28; and in the late-season category were 'Autumnlo', 'Encore', 'Harrow Beauty', 'Jerseyglo', 'Jerseyqueen', 'Laurol', 'Snow Giant', and Victoria™ ('NJ353'). All numbered selections were from the Rutgers Tree Fruit Breeding Program with the exception of selection 7-28, which was from Dr. Masao Yoshida in Japan. Saturn ('N.J. F-2') was initially marketed exclusively as Stark® Saturn Peach (Stark Brothers Nurseries & Orchards, Inc., Louisiana, MO).

Although 'Autumnlo', 'Jerseyglo', and 'Suncrest' trees were not situated in the test orchard, they were included in the study to further broaden the mixture of cultivars being evaluated. Solid blocks of each of these three cultivars were located on the research farm within 0.4 km of the test orchard. In addition, trees from a nearby 'Encore' block also located on the farm, designated as 'Encore101', were

Fig. 1. Progression of peach rusty spot disease incidence on 'Autumnlo', 'Laurol', and 'White Lady' fruit during the 2007 and 2008 growing seasons. Data points are means based on assessment of 160 fruit (four replicate trees × 40 fruit/tree); vertical bars are SEMs. Day of year corresponds to the number of consecutive days from 1 Jan.

Table 1. Results of analyses of variance on rusty spot disease incidence and lesion density dependent variables for 34 peach cultivars evaluated during 2007 and 2008.

Source	Degrees of freedom		Disease incidence ^a		Lesion density ^a	
	Numerator	Denominator	F-value	P > F	F-value	P > F
Year	1	177	45.39	<0.0001	37.68	<0.0001
Cultivar	33	177	11.83	<0.0001	13.41	<0.0001
Year × cultivar	33	177	1.10	0.3325	1.26	0.1753

^aResults of Type III tests of fixed effects; incidence = % infected fruit; lesion density = no. of lesions/fruit.

included for direct comparison to 'Encore' trees situated within the test orchard. This addition of 'Encore101' to the data set augments the number of cultivar "treatments" in the study from 33 to 34. All cultivars used in the study were mature trees planted between 1996 and 2002 (age 5 to 12 years at evaluation).

Disease assessment. Peach rusty spot epidemics in southern New Jersey typically begin in mid-May and end in mid-June, following a logistic pattern of growth (Furman et al., 2003a). However, varying weather patterns, inoculum levels, or other factors can alter the timing of these epidemics. Therefore, the progression of disease development was tracked in each year of this study by performing successive assessments at 3- to 5-d intervals on three cultivars of varying susceptibility, namely 'White Lady', 'Laurol', and 'Autumnlo'. When disease development on these three cultivars achieved their maximum, which corresponded to 13 and 17 June in 2007 and 2008, respectively, assessments were performed on all cultivars in the study. This approach was taken to ensure that the full extent of disease development was observed on each cultivar.

Each assessment sample consisted of 40 fruit that were picked from each replicate tree of each cultivar. Fruit were arbitrarily selected from throughout the canopy of the tree. The total number of rusty spot lesions and weight was recorded for each sampled peach. From these data, disease incidence was calculated as the percentage of infected fruit and

lesion density, a measure of disease severity, as the average number of lesions per fruit.

Cultivar characterization. Three qualitative and seven quantitative horticultural traits of each cultivar were examined for their association with rusty spot susceptibility. The qualitative traits and categories were flesh color (yellow, white), firmness (normal, stony-hard), and acidity (normal, subacid), where yellow flesh, stony-hard firmness, and normal acidity are homozygous recessive traits (Scorza and Sherman, 1996). The quantitative traits, either measured directly or estimated using a 1 to 5 rating scale, were ripening date; fruit size at harvest (diameter); fruit blush (percent surface area); fruit pubescence (1 = very light, 5 = very heavy); pit adhesion (1 = cling, 5 = free); fruit firmness (1 = very soft, 5 = stays firm); and overall fruit quality (1 = poor, 5 = excellent). Because firmness from the stony-hard trait was evaluated separately as a qualitative trait, stony-hard selections were excluded from the fruit firmness characterization.

All cultivar characterization data were recorded from trees in the Rutgers Tree Fruit Breeding Program located at the Rutgers Fruit and Ornamental Research and Extension Center, Cream Ridge, NJ. Given that cultivars were added and subtracted from the breeding program over time, the amount of quantitative trait data used to calculate the means varied among the different cultivar-trait combinations. Nevertheless, 206 of the 224 cultivar-quantitative trait combinations (92%) were assessed over a minimum of

Table 2. Relative susceptibility of peach cultivars to rusty spot based on fruit disease incidence.

Cultivar	LSMean ^z		Difference <i>P</i> > <i>F</i>	Overall LSMean ^z	SE	Tukey-Kramer grouping ^y
	2007	2008				
Autumnglo	58.8	78.1	0.0311	68.4	4.46	a
Jerseyqueen	50.4	78.8	0.0027	64.6	4.46	ab
Bounty	34.4	51.3	0.0600	42.8	4.46	bc
Lauro	27.5	48.1	0.0218	37.8	4.46	cd
Jerseyglo	35.6	37.5	0.8336	36.6	4.46	cde
Encore101	30.0	37.6	0.3931	33.8	4.46	cdef
Suncrest	30.6	35.6	0.5755	33.1	4.46	cdefg
Victoria TM	20.8	41.9	0.0302	31.4	4.81	cdefgh
Raritan Rose	16.9	40.8	0.0080	28.8	4.46	cdefghi
JohnBoy [®]	25.7	27.5	0.8435	26.6	4.46	cdefghi
Sentry	15.7	35.6	0.0269	25.7	4.46	cdefghi
Desiree TM	23.1	24.4	0.8919	23.7	4.81	cdefghi
Melik Early Topaz	24.1	22.5	0.8580	23.3	4.46	cdefghi
Messina TM	14.2	30.0	0.0787	22.1	4.46	cdefghi
Encore	11.7	30.8	0.0642	21.3	5.15	cdefghi
Redhaven	1.9	32.5	0.0007	17.2	4.46	defghi
L13-18	14.2	20.0	0.5716	17.1	5.15	cdefghi
H11-79	6.0	25.8	0.0558	15.9	5.15	defghi
H13-116	6.7	21.7	0.1468	14.2	5.15	defghi
Snow Giant	12.1	13.8	0.8519	12.9	4.46	efghi
H11-76	4.2	21.3	0.0777	12.7	4.81	defghi
D88-59	2.7	20.0	0.1152	11.4	5.46	defghi
J19-28	11.8	10.6	0.8967	11.2	4.46	fghi
White Lady	1.9	19.2	0.0742	10.5	4.81	fghi
Scarlet Rose TM	0.0	20.4	0.0232	10.2	4.46	fghi
TangOs [®]	2.5	17.5	0.1218	10.0	4.81	fghi
L12-4	5.6	8.4	0.7734	7.0 ^x	4.81	hi
Sugar Lady	2.8	10.6	0.3793	6.7 ^x	4.46	hi
7-28	5.0	8.3	0.7464	6.7 ^x	5.15	hi
Saturn	10.0	2.5	0.4672	6.3 ^x	5.15	hi
H11-59	5.8	6.4	0.9623	6.1 ^x	5.75	ghi
Sugar May	3.5	7.5	0.7265	5.5 ^x	5.75	ghi
Harrow Beauty	5.8	5.0	0.9272	5.4 ^x	4.46	i
Gloria TM	2.5	7.5	0.6042	5.0 ^x	4.81	i

^zLeast squares means for percent infected fruit.^yOverall LSMeans not having the same letter are significantly different at *P* ≤ 0.05.^xCultivar LSMeans not significantly different from zero (*P* > 0.05).

three growing seasons; 42% of these combinations were assessed for at least 10 years. The remaining 8% of the combinations were assessed for only 1 or 2 years, and the majority of these data were from L13-18 and 'Harrow Beauty'. Quantitative fruit characteristic data were not available for 'Melik Early Topaz'.

An eighth quantitative trait, fruit weight at pit hardening, was also examined for association with rusty spot susceptibility. Unlike the characterization data obtained from the breeding program, these fruit weights were recorded at the time of disease assessment in the test block. Thus, the data set consisted of paired fruit weight means and disease incidence values calculated across all 40 fruit from each replicate tree.

Statistical analysis. Analyses of variance were performed separately on the disease incidence and lesion density-dependent variables with year, cultivar, and year × cultivar as the fixed main effects. Calculations were performed using the MIXED procedure of the Statistical Analysis System (Version 9.3) with denominator degrees of freedom estimated through the Kenwardroger approximation (SAS Institute, Cary, NC). As a result of missing trees and/or poor fruit set, 10 and 11 of the 33 cultivars in 2007 and 2008, respectively, had only three replicate data values as opposed to the designated four replicates. Furthermore, one cultivar in 2007 (D88-59)

and two cultivars in 2008 (Sugar May, H11-59) had only two replications. Given this unbalanced design, all cultivar comparisons were performed on least squares means (LSMeans) using the Kramer approximation of the Tukey mean comparison procedure.

The association between the two disease measures, incidence and severity, and the various horticultural traits was performed by calculating Pearson correlation coefficients using the CORR procedure of SAS Version 9.3. In these analyses, each of the quantitative fruit characteristics derived from the breeding program was paired with the overall disease measure LSMeans calculated across both years of the study. The association between the disease measures and fruit weight recorded at pit hardening was similarly quantified by calculating Pearson correlation coefficients. However, in this case, the data set consisted of paired LSMeans for both disease measure and fruit weight variables. Furthermore, because fruit weight data were recorded for each year of the study, the correlation analyses were performed on separate yearly LSMeans rather than the overall experimental mean.

Incidence-lesion density relationship. The quantitative relationship between fruit disease incidence and lesion density was expressed by fitting the zero intercept version of the exponential model, $d = a[e^{bi} - 1]$, where

d = lesion density, *i* = disease incidence, and *a* and *b* are model parameters. The model was fit using nonlinear regression analysis with the marquardt iterative method (NLIN procedure; SAS Version 9.3). This model was previously determined to provide the best overall fit for this relationship on 'Jerseyqueen' (Furman et al., 2003b). In this study, data consisted of incidence and lesion density estimates from each replicate tree of each cultivar. Data from both years were pooled.

Results

Disease progression. The majority of the increase in disease incidence in both years was observed between Days 140 and 155 (Fig. 1). After Day 155, disease levels fluctuated somewhat but remained fairly constant, thereby indicating that the maximum or upper asymptote had been reached. Comparison of these maximums indicated that disease pressure in 2008 was higher than in 2007. For all three cultivars examined, maximum disease levels in 2008 were approximately 15%, 17%, and 8% higher than in 2007 for 'Autumnglo', 'Lauro', and 'White Lady', respectively. Similar results were obtained for the lesion density disease progress curves (not shown).

Analyses of variance. Analyses of the combined 2007 and 2008 data for the disease incidence and lesion density-dependent variables yielded highly significant year and cultivar main effects, thereby indicating significant differences between years and among cultivars (Table 1). However, because the year × cultivar interactions were not significant, the specific treatment (cultivar) comparisons were performed on the pooled data from both years. Examination of standardized residuals indicated that data conformed to the assumptions of the analyses of variance without using transformations.

Cultivar and year comparison. Overall cultivar LSMeans for disease incidence and severity, estimated across both years, ranged from 5% to 68% fruit infected and 0.05 to 1.3 lesions/fruit, respectively (Tables 2 and 3). In general, these levels represent a moderate to high disease incidence and low to moderate disease severity. Nine Tukey-Kramer groupings (A to I) were calculated for incidence, whereas only five (A to E) occurred for severity, resulting in a somewhat greater mean separation for the former variable. The most susceptible cultivars, Autumnglo and Jerseyqueen, and to some extent 'Bounty', had significantly higher disease levels than most other cultivars. Cultivars in the 30% to 40% incidence range were also significantly different from some of the least susceptible cultivars, but fewer of these differences were significant for disease severity. All of the cultivars in the low to moderate range of 5% to 30% incidence had statistically similar disease levels. Furthermore, eight cultivars with the lowest disease incidence and 13 with the lowest disease severity had disease levels that were not significantly different from zero.

Table 3. Relative susceptibility of peach cultivars to rusty spot based on fruit disease severity.

Cultivar	LSMean ²		Difference <i>P</i> > <i>F</i>	Overall LSMean ²	SE	Tukey-Kramer grouping ³
	2007	2008				
Autumnglo	1.22	1.44	0.1628	1.33	0.08	a
Jerseyqueen	0.80	1.59	<0.0001	1.20	0.08	a
Bounty	0.52	0.85	0.0352	0.68	0.08	b
Laurol	0.33	0.76	0.0063	0.54	0.08	bc
Jerseyglo	0.50	0.54	0.7796	0.52	0.08	bcd
Encore101	0.33	0.61	0.0795	0.47	0.08	bcde
Suncrest	0.41	0.44	0.8729	0.43	0.08	bcde
Raritan Rose	0.21	0.58	0.0185	0.39	0.08	bcde
Victoria TM	0.25	0.49	0.1500	0.37	0.08	bcde
JohnBoy [®]	0.33	0.38	0.7577	0.35	0.08	bcde
Sentry	0.19	0.46	0.0834	0.33	0.08	bcde
Melik Early Topaz	0.33	0.31	0.9327	0.32	0.08	bcde
Desiree TM	0.27	0.28	0.9714	0.27	0.08	bcde
Messina TM	0.18	0.36	0.2506	0.27	0.08	bcde
Encore	0.12	0.42	0.0978	0.27	0.09	bcde
Scarlet Rose TM	0.00	0.42	0.0077	0.21	0.08	cde
Redhaven	0.02	0.40	0.0156	0.21	0.08	cde
L13-18	0.18	0.23	0.7818	0.21	0.09	cde
H11-79	0.06	0.35	0.1096	0.21	0.09	cde
H13-116	0.08	0.28	0.2686	0.18	0.09	cde
H11-76	0.05	0.30	0.1399	0.18	0.08	cde
D88-59	0.03	0.29	0.1650	0.16 ^x	0.10	cde
Snow Giant	0.15	0.16	0.9469	0.16 ^x	0.08	cde
J19-28	0.12	0.14	0.9316	0.13 ^x	0.08	cde
TangOs [®]	0.03	0.22	0.2579	0.12 ^x	0.08	cde
White Lady	0.02	0.20	0.2838	0.11 ^x	0.08	cde
7-28	0.05	0.11	0.7466	0.08 ^x	0.09	cde
Sugar Lady	0.03	0.13	0.5338	0.08 ^x	0.08	e
L12-4	0.06	0.08	0.8986	0.07 ^x	0.08	e
H11-59	0.06	0.08	0.9279	0.07 ^x	0.10	cde
Saturn	0.11	0.03	0.6444	0.07 ^x	0.09	de
Harrow Beauty	0.06	0.06	0.9903	0.06 ^x	0.08	e
Sugar May	0.03	0.08	0.8417	0.05 ^x	0.10	cde
Gloria TM	0.03	0.08	0.7671	0.05 ^x	0.08	e

²Least squares means for lesion density (no. of lesions/fruit).³Overall LSMeans not having the same letter are significantly different at *P* ≤ 0.05.^xCultivar LSMeans not significantly different from zero (*P* > 0.05).

Because the main effects of year in the analyses of variance were significant, some cultivars were expected to have significant differences in disease levels across the 2 years. Of the 34 cultivar selections examined, 30 (88%) had higher disease incidence in 2008 than 2007 (Table 2). Eight of these 30 increases in disease incidence were significant (*P* ≤ 0.05). The remaining four selections had lower incidences in 2008, but none of these decreases were significant. Similar year-to-year differences were observed for lesion density (Table 3). A total of 31 (91%) of the cultivar selections had higher lesion densities in 2008, of which six were significant (*P* ≤ 0.05). Furthermore, all six of these cultivars also had significantly higher incidences in 2008. Finally, all cultivar selections showing significant yearly increases in either or both disease measures were situated in the upper 50% of cultivars ranked from highest to lowest overall LSMean (Tables 2 and 3).

Cultivar characterization. When ranked from highest to lowest levels of disease incidence, cultivars that were the most susceptible had yellow flesh with normal melting flesh texture and acidity (Table 4). The only exception to this rule was 'Raritan Rose' with its white flesh. Conversely, cultivars sustaining lower levels of disease tended to have white-fleshed stony-hard subacid fruit.

However, in this category, there were more exceptions to this rule, particularly for the flesh texture characteristic.

Given the eight quantitative fruit characteristics examined for association with disease levels, three were observed to have significant correlations with both disease incidence and severity (Table 5; Fig. 2). All three of these traits, namely ripening date, fruit weight at pit hardening, and fruit pubescence, were found to be positively correlated with disease. A graph of disease incidence versus fruit weight at pit hardening indicated that the association was similar in both years (Fig. 2); comparable results were observed for lesion density (not shown).

Incidence-lesion density relationship. The zero-intercept exponential model provided an excellent fit to the observed 2007–08 data, explaining 92% of the variation in lesion density (Fig. 3). An equivalent scatter of data points for each year occurred above and below the predicted curve for incidence values ranging from 0 to 0.5. For disease incidence values within this range, predicted values from the newer 2007–08 model agree closely with those from the former 1999–2001 and 2000 models. The incidence-lesion density relationship within this range is nearly linear. As a result of lower disease pressure, fewer data points were available at higher incidences in 2007.

Discussion

Overall results from this study, which summarized data from two seasons of differing disease pressures, identified cultivars with a high degree of susceptibility as well as others with moderate and low degrees of susceptibility. Disease incidence levels across all cultivars ranged from a low of 5% to a high of 68% fruit infected. In total, the susceptibility levels of 33 commercial cultivars and advanced selections were determined. Furthermore, because all selections were evaluated under the same environmental conditions in each year, the quantitative data collected in this study allowed direct comparisons of relative susceptibility. Although similar quantitative comparisons of cultivar disease levels have not been previously conducted, rusty spot has been reported to occur on a variety of peach cultivars, including 'Rio-Oso-Gem', 'Summer Queen', 'Goldeneast', and 'Loring' (Daines and Trout, 1977); 'Jerseyqueen' (Furman et al., 2003a); and most recently 'Summerset', 'Suncrest', and 'Fayette' (Jankovics et al., 2011). In each of these studies, the severity of disease development and/or level of yield loss was observed to be high, indicating that these cultivars have a high degree of susceptibility. Two of these cultivars, Jerseyqueen and Suncrest, were also observed in the current study to sustain relatively high amounts of disease. Specifically for 'Jerseyqueen', the 2-year mean disease incidence in this study was 64.6%, whereas the 3-year mean from a former study, estimated as the upper asymptote, *K*, of the logistic model, was 75.5% (Furman et al., 2003a).

In addition to analyses of overall results, comparison of 2007 and 2008 disease levels for each cultivar provided further insight into their susceptibility to rusty spot. Although only eight and six cultivars had statistically significant increases in disease incidence and severity, respectively, between 2007 and 2008, most cultivars had numerically higher disease levels in 2008. These results indicate that one or more non-host factors such as environment or inoculum level limited the extent of infection in the first year. Indeed, disease development in 2008 was also probably limited by similar factors. Recent highly disease-favorable conditions in 2012, possibly as a result of above-normal temperatures during early spring, resulted in record levels of rusty spot. 'Suncrest' and 'Autumnglo' trees sustained 79% and 99% fruit infection with 2.0 and 5.4 lesions/fruit, respectively (McFarland and Lalancette, 2013; N. Lalancette, unpublished data). Clearly, like with many plant diseases, environment and pathogen-related factors cause wide seasonal variations in the severity of rusty spot epidemics. Thus, classification of cultivars for susceptibility based on absolute disease thresholds is difficult given these interacting factors.

Although cultivar disease levels varied between years, the relative ranking of cultivars, when placed in categories, remained

Table 4. Association of qualitative fruit characteristics with peach rusty spot disease incidence.

Cultivar	Overall LSMean ^y	Fruit characteristic ^z		
		Flesh color	Flesh texture	Acidity
Autumnglo	68.4	* Yellow *	* Normal *	* Normal *
Jerseyqueen	64.6	* Yellow *	* Normal *	* Normal *
Bounty	42.8	* Yellow *	* Normal *	* Normal *
Lauro	37.8	* Yellow *	* Normal *	* Normal *
Jerseyglo	36.6	* Yellow *	* Normal *	* Normal *
Encore101	33.8	* Yellow *	* Normal *	* Normal *
Suncrest	33.1	* Yellow *	* Normal *	* Normal *
Victoria TM	31.4	* Yellow *	* Normal *	* Normal *
Raritan Rose	28.8	White	* Normal *	* Normal *
John Boy [®]	26.6	* Yellow *	* Normal *	* Normal *
Sentry	25.7	* Yellow *	* Normal *	* Normal *
Desiree TM	23.7	* Yellow *	* Normal *	* Normal *
Melik Early Topaz	23.3	* Yellow *	* Normal *	* Normal *
Messina TM	22.1	* Yellow *	* Normal *	* Normal *
Encore	21.3	* Yellow *	* Normal *	* Normal *
Redhaven	17.2	* Yellow *	* Normal *	* Normal *
L13-18	17.1	* Yellow *	Stony-hard	Subacid
H11-79	15.9	White	Stony-hard	Subacid
H13-116	14.2	White	Stony-hard	Subacid
Snow Giant	12.9	White	* Normal *	Subacid
H11-76	12.7	White	Stony-hard	Subacid
D88-59	11.4	White	* Normal *	Subacid
J19-28	11.2	White	Stony-hard	Subacid
White Lady	10.5	White	* Normal *	Subacid
Scarlet Rose TM	10.2	White	Stony-hard	Subacid
Tango [®]	10.0	* Yellow *	* Normal *	* Normal *
L12-4	7.0	White	Stony-hard	Subacid
Sugar Lady	6.7	White	* Normal *	Subacid
7-28	6.7	White	Stony-hard	Subacid
Saturn	6.3	White	* Normal *	Subacid
H11-59	6.1	White	Stony-hard	Subacid
Sugar May	5.5	White	* Normal *	* Normal *
Harrow Beauty	5.4	* Yellow *	* Normal *	* Normal *
Gloria TM	5.0	* Yellow *	Stony-hard	Subacid

^zTraits that tend to be associated with high levels of disease are marked with asterisks.^yLeast squares means for percent infected fruit calculated across both years.

Table 5. Correlation of peach cultivar fruit characteristics at maturity with rusty spot disease incidence and lesion density over the 2007 and 2008 growing seasons.

Fruit characteristic ^y	Units or rating scale	Disease incidence ^z		Lesion density ^z	
		<i>r</i>	<i>P</i> > <i>r</i>	<i>r</i>	<i>P</i> > <i>r</i>
Ripening date	Day of year	0.542	0.0013	0.522	0.0022
Size	cm	0.307	0.0876	0.254	0.1600
Blush	Percent surface area	-0.179	0.3266	-0.143	0.4345
Pubescence	Light-heavy (1-5)	0.460	0.0092	0.408	0.0229
Pit adhesion	Cling-free (1-5)	0.232	0.2012	0.212	0.2436
Firmness ^x	Soft-firm (1-5)	-0.304	0.1694	-0.293	0.1852
Quality, overall	Poor-excellent (1-5)	-0.169	0.3554	-0.139	0.4494

^zPearson correlation coefficients, *r*, and significance; *n* = 32.^yValues of cultivar characteristics derived from the fruit breeding program were paired with least squares means for disease incidence and lesion density calculated across both years (overall LSMeans).^xAnalysis of firmness characteristic excludes stony-hard selections; *n* = 22.

reasonably constant across both years. For example, assume that the cultivars are ranked each year according to their disease incidence LSMeans and divided into three categories of high, moderate, and low susceptibility with 11 cultivars per category. Given this structure, eight of the high and low susceptibility cultivars and four of the moderate susceptibility cultivars, a total of 20 cultivars or 61%, were ranked in these same categories both years. Five and seven “intermediate” cultivars were ranked 1 year in the high and low categories, respectively, and the other year in the moderate category. Only one cultivar, Redhaven, was ranked 1 year in the low category and 1 year in the high category.

One possible classification scheme for this rank-based structure would have five categories (Table 6). The very high, moderate, and very low categories in this proposed scheme include those cultivars that remained in the previous high, moderate, and low categories both years. The new high and low categories include the “intermediate” cultivars that switched between the original high and moderate and original low and moderate categories, respectively.

In general, cultivars having subacid white-fleshed fruit containing the stony-hard trait tended to have a lower susceptibility to rusty spot. Overall fruit disease incidence for these cultivars ranged from 5% to 16% with

a maximum incidence of 26% in disease-favorable 2008. However, all three of these characteristics were part of the selection criteria being emphasized in the breeding program. Consequently, the observed low susceptibility may be associated with only one or two of these traits.

The positive correlations between both disease measures and ripening date in this study agrees with observations in other locations showing significant yield losses from rusty spot in late-maturing cultivars (Jankovics et al., 2011). However, because rusty spot epidemics occur much earlier in the growing season, between the shuck-split and pit-hardening stages, the association with late ripening does not appear to be direct (Furman et al., 2003a). One possible explanation is that late-ripening cultivars bloom later in spring, thereby exposing the fruit to warmer, more favorable conditions for infection. However, an analysis of associations between various peach fruit characteristics clearly showed that bloom date and ripening data are not correlated (de Souza et al., 1998). Thus, some other factor or trait related to time of ripening must increase susceptibility to rusty spot.

Two possible hypotheses are proposed for explaining the positive correlation observed between disease development and fruit pubescence. The first hypothesis is that the trichomes serve as an important, if not sole, infection court for *P. leucotricha* conidia. The fact that rusty spot has not been observed on nectarine supports this hypothesis. An earlier histological study of rusty spot lesions did not observe the presence of mycelium or spores but did note the eventual necrosis of peach “hairs” (Sprague and Figaro, 1956). Of course, the epidermal cells could have been infected first, eventually resulting in death of the trichomes. A second possible hypothesis is that fruit trichomes function as spore traps. Higher numbers or densities of peach hairs might result in more efficient trapping and therefore greater likelihood of infection.

Stage one fruit growth, which encompasses the period from fertilization to pit hardening, consists principally of cell division (Flore, 1994). In this study, fruit weight at pit hardening, which also coincides with termination of the rusty spot epidemic, was positively correlated with rusty spot development. This finding suggests that cultivars supporting rapid cell division during this period, thereby resulting in larger fruit, are more susceptible to rusty spot. This hypothesis agrees with available data showing that susceptibility of a plant part such as leaves or fruit often occurs during the growth period of that part (Populer, 1978). Furthermore, factors that artificially augment plant growth such as overfertilization often result in highly susceptible, succulent growth. A classic example is the increased susceptibility of vigorously growing apple shoots to fire blight infection after nitrogen fertilization (van der Zwet and Keil, 1979). However, it is entirely possible that the higher disease level observed on larger fruit is simply the result of

Fig. 2. Relationship between early fruit size during Stage I, assessed as fruit weight at pit hardening, with incidence of rusty spot at termination of the 2007 and 2008 epidemics. Data points are paired means based on assessment of 160 fruit (four replicate trees $\times$ 40 fruit/tree) for each of 34 cultivars examined in the study. Data from both years were pooled for calculation of the Pearson correlation coefficient (r).

Fig. 3. Peach rusty spot disease severity, measured as fruit lesion density, expressed as a function of disease incidence. The solid line represents predicted values of the zero intercept exponential model fit to pooled 2007 and 2008 data obtained from all cultivars (equation shown). The dashed lines represent predicted values of the same model fit to 'Jerseyqueen' data observed during the 1999, 2000, and 2001 epidemics (Furman et al., 2003b). Each data point represents the incidence and severity calculated for a single tree (40 fruit/tree). The coefficient of determination was calculated as $R^2 = 1 - (\text{SSE} / \text{SST}_{\text{corrected}})$. SSE = sum of squares for error; SST = total sum of squares.

Table 6. Proposed classification scheme for rusty spot susceptibility based on ranking of disease incidence means in 2007 and 2008.

Very Low	Low	Moderate	High	Very High
White Lady	Snow Giant	Messina TM	Raritan Rose	Autumn glo
TangOs [®]	H11-76	L13-18	John Boy [®]	Jerseyqueen
L12-4	D88-59	H11-79	Sentry	Bounty
Sugar Lady	J19-28	H13-116	Desiree TM	Laurel
7-28	Scarlet Rose TM	Redhaven ^z	Melik Early Topaz	Jerseyglo
Sugar May	Saturn	Encore ^y		Suncrest
Harrow Beauty	H11-59			Victoria TM
Gloria TM				

^z'Redhaven' classified as moderate based on similarity of overall LSmean to cultivars in this category.

^yRanking results for 'Encore' were used instead of 'Encore101'.

their greater surface area intercepting more airborne inoculum.

The quantitative relationship between disease incidence and lesion density, derived from observations on all 33 cultivars, was

successfully modeled using the zero intercept version of the exponential function. This same model, based on data from a single cultivar, was previously shown to provide the best overall fit for this relationship (Furman

et al., 2003b). Predictions of lesion density from the current and prior models were nearly identical in the low to moderate disease incidence range of $0 \leq i \leq 0.5$, whereas considerable divergence occurred at higher disease incidences. The near linear relationship and high degree of correlation between the two disease measures indicates that only one dependent variable, the more easily assessed incidence, needs to be examined when disease pressures are low to moderate. Conversely, at high disease incidence levels, lesion density cannot be readily predicted from incidence, and inclusion of this variable in the analyses will provide additional information on the severity of the epidemic.

Knowledge of peach cultivar susceptibility to rusty spot aids growers in their selection of cultivars for new orchard plantings. Given two or more cultivars of similar horticultural characteristics, selection of resistant cultivars contributes to a reduction in fungicide use, particularly because fungicides active against rusty spot are often added to current programs. However, because rusty spot is readily controlled by fungicides, choice of cultivars is perhaps more importantly based on desired horticultural characteristics or resistance to diseases that are difficult to control such as bacterial spot. In fact, for these same reasons, rusty spot resistance was not a selection characteristic in the breeding program that created the cultivars examined in this study. Nevertheless, knowledge of the degree of rusty spot susceptibility is still useful. For example, some biorational fungicides have been shown to provide consistent but only partial control of rusty spot (Lalancette et al., 2013). Such fungicides would presumably be good candidates for use with cultivars having low or moderate susceptibility. The integration of these two forms of controls would allow reduction in conventional fungicides. Similarly, substitution of biorational fungicides for some conventional fungicide applications in a rusty spot program may be feasible for moderate and perhaps even highly susceptible cultivars (Lalancette et al., 2004). Additional data are needed to verify the integration of cultivar resistance, biorational fungicides, and conventional fungicides for effective management of peach rusty spot.

Literature Cited

- Blodgett, E.C. 1941. Rusty spot of peach. Plant Dis. Rptr. 25:27-28.
- Daines, R.H. and J.R. Trout. 1977. Incidence of rusty spot of peach as influenced by proximity to apple trees. Plant Dis. Rptr. 61:835-836.
- de Souza, V.A.B., D.H. Byrne, and J.F. Taylor. 1998. Heritability, genetic and phenotypic correlations, and predicted selection response of quantitative traits in peach: II. An analysis of several fruit traits. J. Amer. Soc. Hort. Sci. 123:604-611.
- Dolovac, N., V. Gavrilović, and N. Miletić. 2009. Control of rusty spot of peach in Serbia. 7th Int. Peach Symp. Lleida, Spain [abstract].
- Flore, J.A. 1994. Stone fruit, p. 234-262. In: Schaffer, B. and P.C. Andersen (eds.). Handbook of environmental physiology of fruit crops, vol. I: Temperate crops. CRC Press, Boca Raton, FL.

- Furman, L.A., N. Lalancette, and J.F. White, Jr. 2003a. Peach rusty spot epidemics: Temporal analysis and relationship to fruit growth. *Plant Dis.* 87:366–374.
- Furman, L.A., N. Lalancette, and J.F. White, Jr. 2003b. Peach rusty spot epidemics: Management with fungicide, effect on fruit growth, and the incidence-lesion density relationship. *Plant Dis.* 87:1477–1486.
- Grove, G.G. 1995a. Powdery mildew, p. 12–14. In: Ogawa, J.M., E.I. Zehr, G.W. Bird, D.F. Ritchie, K. Uriu, and J.K. Uyemoto (eds.). *Compendium of stone fruit diseases*. The Amer. Phytopathol. Soc., St. Paul, MN.
- Grove, G.G. 1995b. Rusty spot, p. 15. In: Ogawa, J.M., E.I. Zehr, G.W. Bird, D.F. Ritchie, K. Uriu, and J.K. Uyemoto (eds.). *Compendium of stone fruit diseases*. The Amer. Phytopathol. Soc., St. Paul, MN.
- Hamilton, G.C., J.R. Heckman, N. Lalancette, B.A. Majek, J.B. Paulin, P.W. Shearer, and D.L. Ward. 2007. *The New Jersey commercial tree fruit production guide*. N. J. Agric. Exp. Stn. Rutgers Coop. Ext. Bul. E002.
- Jankovics, T., N. Dolovac, A. Bulajić, B. Krstić, T. Pascal, M. Bardin, P.C. Nicot, and L. Kiss. 2011. Peach rusty spot is caused by the apple powdery mildew fungus, *Podosphaera leucotricha*. *Plant Dis.* 95:719–724.
- Lalancette, N. and K.A. Foster. 2001. Integration of biorational fungicides for management of peach rusty spot, 2000. *F&N Tests* 56, STF3. Online publication. doi: 10.1094/FN56.
- Lalancette, N., K.A. Foster, and E. Murday. 2006. Comparison of fungicides for full season management of peach diseases, 2005. *F&N Tests* 61, STF013. Online publication. doi: 10.1094/FN61.
- Lalancette, N., L.A. Furman, and J.F. White. 2004. Integrated management of rusty spot of peach. *Phytopathology* 94(6):S165 [abstract].
- Lalancette, N., L.A. Furman, and J.F. White. 2013. Management of peach rusty spot epidemics with biorational fungicides. *Crop Protection* 43:7–13.
- Manji, B.T. 1972. Apple mildew on peach. *Phytopathology* 62:776 [abstract].
- McFarland, K.A. and N. Lalancette. 2013. Management of peach scab with Quadris Top and Inspire Super, 2012. *Plant Disease Management Reports* 7:STF019. Online publication, doi: 10.1094/PDMR07.
- Polk, D., D. Schmitt, E. Rizio, and K. Peterson. 1997. The economic impact of peach pests in New Jersey 1996–1997. *N. J. State Hort. Soc. Hort. News* 78:3–10.
- Populer, C. 1978. Changes in host susceptibility with time, p. 239–262. In: Horsfall, J.G. and E.B. Cowling (eds.). *Plant disease, an advanced treatise*, vol. II. How disease develops in populations. Academic Press, New York, NY.
- Ries, S.M. and D.J. Royse. 1978. Peach rusty spot epidemiology: Incidence as affected by distance from a powdery mildew infected apple orchard. *Phytopathology* 68:896–899.
- Scorza, R. and W.B. Sherman. 1996. Peaches, p. 325–440. In: Janick, J. and J.N. Moore (eds.). *Fruit breeding*, vol. I. Tree and tropical fruits. Wiley, New York, NY.
- Sprague, R. and P. Figaro. 1956. Rusty spot, powdery mildew and healthy skin of peach fruits compared histologically. *Phytopathology* 46:640 [abstract].
- Tukey, H.B. 1933. Growth of the peach embryo in relation to growth of fruit and season of ripening. *Proc. Amer. Soc. Hort. Sci.* 30:209.
- van der Zwet, T. and H.L. Keil. 1979. Fire blight—A bacterial disease of rosaceous plants. *U.S. Department of Agriculture, Agriculture Handbook* No. 510.