Scab Susceptibility of a Provenance Collection of Pecan in Three Different Seasons in the Southeastern United States

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Abstract

Bock, C. H., Grauke, L. J., Conner, P., Burrell, S. L., Hotchkiss, M. W., Boykin, D., and Wood, B. W. 2016. Scab susceptibility of a provenance collection of pecan in three different seasons in the southeastern United States. *Plant Dis.* 100:1937-1945.

Pecan scab (caused by *Fusicladium effusum*) is the most economically destructive disease of pecan in the Southeast United States. Wet, humid conditions typical of the Southeast are known to provide conditions conducive to epidemics. A provenance collection of pecan from 19 locations representing the native range of the tree is located in Byron, Georgia, and was assessed for pecan scab severity in 1998, 2013, and 2014. There were significant differences among the 19 provenances ($F = 5.6$ to 62.5 , $P < 0.0001$). Provenances from wetter locations (generally north of Texas) had the greatest proportion of scab resistant trees, while provenances from the drier southern areas (Texas and Mexico) tended to be the most susceptible to scab. The association with rainfall was borne out by correlation analysis ($r = -0.625$ to -0.823 [$P < 0.0001$ to 0.004]). Other factors consistently associated with scab severity included leaflet tilt and droop angle ($r = -0.533$ to -0.883 [$P < 0.0001$ to 0.02]). Multiple regression

analysis demonstrated that leaflet droop angle was a particularly good predictor of provenance susceptibility. Leaflet characteristics vary with provenance location, and whether there is a direct relationship between scab severity and leaflet characteristics is not established. Estimates of heritability were not entirely consistent among years, but different methods were used to assess scab severity in 1998 (a 1 to 5 category scale) compared with 2013 and 2014 (the percent ratio scale). Despite using different methods, there was generally good agreement among years in regard to severity of disease on individual trees. In conclusion, trees from more northern populations (in areas with greater annual rainfall) are most likely to provide valuable and diverse sources of resistance to scab. The provenance collection contains a range of scab-resistant genotypes from diverse locations that can contribute to genetic improvement regarding scab resistance.

Pecan scab (caused by the plant pathogenic fungus *Fusicladium effusum* G. Winter) is the most destructive disease of pecan (*Carya illinoensis* [Wangenh.] K. Koch) in the Southeast United States. Yield loss can be substantial (Gottwald and Bertrand 1982, 1988; Sanderlin 1995; Stevenson and Bertrand 2001), and much of the acreage in the Southeast is planted to susceptible and moderately susceptible cultivars. Not only does scab cause yield loss, but due to the stress it causes the tree, it can initiate cycles of alternate bearing with consequent production issues for growers. Scab epidemics are favored by warm, wet weather (Gottwald 1985; Gottwald and Bertrand 1982, 1983; Latham 1982), which is typical in the Southeast during the summer.

Several methods are used to manage scab, including application of fungicides, careful selection of orchard location and tree management (for example, thinning and hedge pruning), and the use of resistant cultivars. Unfortunately, *F. effusum* has now developed insensitivity to several classes of fungicide (Seyran et al. 2010; Stevenson 1999; Stevenson et al. 2004), and development of new chemistries is hampered by environmental sensitivity to use of pesticides for agriculture. Furthermore, scab can be particularly troublesome to control in the upper canopy of tall trees where spray equipment is unable to deliver sufficient fungicide (Bock et al. 2013, 2015). Orchard location, tree thinning, or hedge pruning can offer some measure of disease reduction, but are not solutions to the problem (Bock et al. 2014b; Cooper

and Johnson 1985). With many resistant cultivars that have been released, there is a history of resistance gradually declining over time (Cole and Gossard 1956; Goff et al. 1996), and the pathogen appears to adapt to the resistance presented by the host (Thompson and Grauke 1994). Indeed, the scab fungus is known to be genetically diverse throughout its range (Bock et al. 2014a, c), and there are several examples demonstrating pathogenic specialization of the pathogen to specific cultivars, or to a small range of generally related cultivars (Conner 2013; Conner and Stevenson 2004; Converse 1960; Demaree and Cole 1929). Nonetheless, in the long term, resistant cultivars are the single most desirable method for managing scab. However, there are many issues to resolve before a fully informed approach can be developed to optimize use of the range of available sources of resistance. Indeed, the number and diversity of resistance genes involved is yet to be characterized.

Breeding for scab resistance is a slow process, taking approximately 25 years from the initial cross to the time of release (Thompson and Grauke 1994). A tree of a resistant cultivar, once released, is continuously exposed to the pathogen population for decades or more, providing ample time for the fungus to adapt. Thus, it is desirable for any resistant cultivars developed to be based on a choice of resistance that will be durable. Currently there is no knowledge of the genetics of resistance as only limited crosses have been done, precluding the identification and tracking of specific resistance genes in any crosses. Nonetheless, some progress has been made in crossing various parental lines, which seems to indicate heritability of scab resistance is fairly high ($h^2 \sim 0.50$) (Thompson and Grauke 1994).

Although a linkage map has been developed for pecan (Beedanagari et al. 2005), and a few molecular markers have been developed (Conner and Wood 2001; Grauke et al. 2003a), these have only been used for cultivar identification and are not linked specifically to traits of interest for breeding purposes, such as scab resistance. This is unlike in apple, where linkage groups are becoming better characterized in relation to resistance genes in the host and virulence genes in the apple scab pathogen, *Venturia inaequalis* (for example, Erdin et al. 2006; Xu et al. 2009).

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*The e-Xtra logo stands for “electronic extra” and indicates that three supplementary tables and five supplementary figures are available online.

Accepted for publication 29 March 2016.

<http://dx.doi.org/10.1094/PDIS-12-15-1398-RE>

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A provenance collection of pecan representing the native geographic range of the species is planted in Byron, GA (and partially duplicated in Burleson and Brown counties, TX). The genetic diversity represented in the provenance collection is comparable to that of wild populations (Rüter et al. 1999). The collection has been described previously, and characteristics of the trees have been described in relation to source locations (Grauke et al. 1989, 2011; Rüter et al. 1999; Wood et al. 1998). However, the collection has not been assessed for resistance to pecan scab. The location in Byron, GA, has regular summer rainfall and frequent epidemics of scab. Characterizing the relationship between scab susceptibility and provenance may help provide insights into the locations where useful germplasm with novel sources of resistance to *F. effusum* may be found.

The objective of this study was to assess patterns of scab susceptibility in relation to the geographic range of pecan. Specifically, it was to identify those provenances and families within provenances that had greater resistance to scab, thereby indicating sources and locations of material of potential value to pecan breeding programs.

Materials and Methods

The provenance collection. The pecan provenance collection located at the USDA-ARS-SEFTNRL in Byron, GA (32°39'54" N, 83°44'31" W), has been described in detail previously (Grauke et al. 1989; Rüter et al. 1999; Wood et al. 1998). The site has an elevation of ~156 m and ~240 days freeze-free growing period and annual precipitation of ~118 cm, and has Faceville sandy loam soils (FoA; fine, Kaolintic, thermic Typic Kandudult soil). The provenances, their locations, physical characteristics, and some characteristics of the foliage are shown (Table 1). The trees represent collections of wild pecans from 19 provenances from locations in Missouri in the northern United States to Oaxaca in southern Mexico. As previously described in detail (Wood et al. 1998), nuts from five to six arbitrarily selected trees were sampled in each provenance. At each provenance location, intertree distance (50 m to 10 km) was maximized during the sampling process to reflect the genetic nature in that area. Nuts from each tree sampled within a provenance thus represented a "family" (further details of the collection and planting are found in Grauke et al. 1989, 2011; Wood et al. 1998).

Nuts from each of the five to six trees in each of the provenances were subsequently germinated in March 1989 (Wood et al. 1998),

and were planted in the field. A completely randomized design was imposed to allow analysis of traits among provenances, with replicates (10) being represented by the seedlings from each of the five parent trees (families) within each of the 19 provenances ($n = \sim 960$). Inter tree distance is 10.5 m within row and 10.5 m between rows. Orchard management is typical for pecans in Georgia (Wells et al. 2015), although no pesticides were applied.

Apart from source location and environmental conditions at source location, various other morphological parameters have been measured on these trees (Wood et al. 1998). Specifically included in this study were date of bud break (day of the year), leaflet droop angle, and leaflet tilt angle. Based on four leaves sampled in the lower canopy, Wood et al. (1998) measured droop angle as the angular distance between the abaxial planes of opposite leaflets at the center of a compound leaf (flat compound leaves have a large droop angle, while leaves that droop to form a "rib-cage" appearance have smaller droop angles). The leaflet tilt angle is the angular distance the plane of the base of leaflets project above the plane of the rachis of the compound leaf to which the leaflet is attached.

The orchard was transplanted from the original location to a second location at the USDA-ARS-SEFTNRL farm in March 2007. Approximately the same design was maintained and trees were replanted in a similar tree and replicate sequence as at the original site, although the row length and number of rows was different, and some trees were missing due to tree death, although tree survival after transplant was close to 100%. A few of the trees were placed in different replicates at the new planting. If trees were not matched in each replicate with the original planting, they were not included in comparisons between years. Trees were trimmed back to the main trunk to reduce transplant shock and aid survival. Site characteristics and tree management were as described for the first planting site. Trees were drip-irrigated at both locations following standard management practice for pecans.

Weather conditions. Weather data were recorded close to the provenance planting using weather stations (Campbell Scientific, Logan, UT) and was downloaded from the Georgia Automated Environmental Monitoring Network (<http://www.weather.uga.edu/>). Mean temperature, relative humidity, and total rainfall were reported from 1 March to 31 July in 1998 (Fort Valley State University, Fort Valley, Peach County, GA), 2013 and 2014 (USDA-ARS-SEFTNRL, Byron, Peach County, GA). This period ensures covering those months during which leaves would be susceptible to infection.

Table 1. The latitude, elevation, and climatic conditions prevailing at sample sites of pecan provenances collected throughout the native range of the tree, and some foliar characteristics of the trees possibly associated with scab susceptibility^y. Locations listed by latitude, from north to south

Country	State	County	Code	Latitude	Elevation (m)	Precipitation (mm, Mar-Jul) ^z	Max temp (°C)	Min temp (°C)	Budbreak (day of year)	Leaflet droop (°)	Leaflet tilt (°)
U.S.	Missouri	Livingston	MO-L	39.083	213	542.8	12.4	-24.5	93	135	50
U.S.	Illinois	Jersey	IL-J	39.000	192	488.2	11.4	-24.5	93	142	53
U.S.	Missouri	Vernon	MO-V	37.083	226	632.2	13.9	-22.0	93	143	47
U.S.	Kentucky	Webster	KY-W	37.050	226	523.0	13.8	-22.0	94	139	50
U.S.	Kansas	Cowley	KS-C	37.033	347	566.9	14.6	-22.0	96	135	48
U.S.	Kansas	Cherokee	KS-K	37.000	274	604.3	14.3	-22.0	94	138	46
U.S.	Tennessee	Lake	TN-L	36.033	94	597.7	14.8	-19.0	93	144	53
U.S.	Mississippi	Washington	MS-W	33.883	39	545.8	17.4	-10.5	94	134	49
U.S.	Texas	Bowie	TX-B	33.550	119	440.9	17.1	-10.5	90	148	52
U.S.	Texas	Tom Green	TX-T	31.367	580	242.1	18.7	-13.5	85	122	43
U.S.	Texas	Val Verde	TX-V	30.000	313	248.9	21	-8.0	81	110	38
U.S.	Texas	Gonzales	TX-G	29.500	95	395.7	19.8	-8.0	77	135	45
U.S.	Texas	Kinney	TX-K	29.233	227	282.2	21.9	-8.0	80	117	39
U.S.	Texas	Zavala	TX-Z	28.883	341	294.6	21	-5.5	79	122	43
Mexico	Tamaulipas	Jaumave	MX-J	23.367	884	327.0	24.4	-2.5	71	125	38
Mexico	S.L.P	Santa Catarina	MX-C	22.067	1219	195.1	17.9	-2.5	82	125	39
Mexico	Hidalgo	Ixmiquilpan	MX-I	20.483	1829	244.5	14.2	0.5	81	126	39
Mexico	Jalisco	Sayula	MX-S	19.917	1372	288.3	19.1	3.0	80	121	43
Mexico	Oaxaca	Oaxaca	MX-O	17.083	1737	425.5	20.6	3.0	78	113	43

^y Table and additional data from Wood et al. (1998).

^z Rainfall is based in the period from 1 March to 31 July, when foliage would be susceptible across the geographic range.

Disease severity data. Disease severity was estimated differently in 1998, 2013, and 2014. In 1998, trees were approximately 7 m tall, and in 2013 and 2014, they were 10 to 12 m tall. Assessments were made from 1 to 31 July in 1998, 12 July to 10 August in 2013, and 10

June to 28 July in 2014, respectively. In 1998, a total of 954 trees in all 10 replicates were assessed; in 2013, only seven replicates were assessed, totaling 588 trees, and in 2014, eight replicates were assessed totaling 756 trees. Replicate size varied as some replicates

Fig. 1. The proportion of the total trees assessed each year in each provenance with consistent severity of pecan scab indicating **A**, resistance (a rating score of 1, or $\leq 0.1\%$ leaf area diseased) or **B**, susceptibility (a rating score of 4 or 5, or $\geq 0.5\%$ leaf area diseased). The individual trees with these scored are presented in Supplementary Tables S2 and S3, respectively.

Table 2. Pecan scab severity by provenance in 1998, 2013, and 2014 at Byron, GA. In 1998, a 1 to 5 score was given to each plant based on an assessment of the scab on the single most severely infected leaf using the Hunter-Roberts scale 1 = no infection, 2 = one to several lesions restricted in size, 3 = several large lesions on leaflets, 4 = numerous leaflet and rachis lesions, some stem lesions may be present, and 5 = leaflet and rachis lesions more numerous than above, stem lesions usually present. This was also converted to a percent severity based on the midpoint method. In 2013 and 2014, a sample of 10 leaves was taken from each plant and each was assessed for the % area with scab symptoms

Provenance (by latitude, N→S)	Scab severity (1 to 5)	Scab severity (%) ^z		
	1998	1998	2013	2014
MO-L	1.737 def	0.500 f	0.067 de	0.145 d
IL-J	1.487 ef	0.162 f	0.081 de	0.166 d
MO-V	1.612 def	0.321 f	0.086 de	0.151 d
KY-W	1.587 def	0.221 f	0.033 e	0.202 d
KS-C	2.346 cdef	1.873 ef	0.172 cde	0.199 d
KS-K	1.745 def	0.345 f	0.089 de	0.199 d
TN-L	1.359 f	0.141 f	0.012 e	0.146 d
MS-W	1.776 def	0.651 f	0.033 e	0.120 d
TX-B	1.562 def	0.218 f	0.008 e	0.191 d
TX-T	4.496 a	30.951 a	1.204 ab	0.200 d
TX-V	4.291 a	23.774 ab	0.829 abc	0.390 bcd
TX-G	2.602 cd	2.066 ef	0.073 de	0.250 cd
TX-K	4.324 a	24.251 ab	1.319 ab	1.009 abc
TX-Z	4.102 a	19.984 bc	1.436 a	0.392 bcd
MX-J	2.490 cde	1.953 f	0.019 e	0.197 d
MX-C	4.352 a	26.649 ab	0.719 abcd	1.312 ab
MX-I	3.062 bc	8.864 d	0.386 bcde	0.538 abcd
MX-S	4.017 ab	17.373 bcd	0.38 bcde	1.613 a
MX-O	3.409 abc	9.741 cde	0.416 abcde	0.453 abcd
F-value (<i>P</i> value)	30.7 (<0.0001)	62.5 (<0.0001)	11.4 (<0.0001)	5.6 (<0.0001)

^z The % area diseased estimates were square root transformed. Back transformed values are presented with means separation for the transformed values. Means separation was based on Tukey's HSD ($\alpha = 0.05$).

had more than one tree represented from each family. Complete replicate sets were collected and assessed in each year.

1998. In each tree, the leaf with the most severe scab was selected and severity was estimated based on the Hunter-Roberts category scale (Hunter and Roberts 1978), where 1 = no infection, 2 = one to several lesions restricted in size, 3 = several large lesions on leaflets, 4 = numerous leaflet and rachis lesions, some stem lesions may be present, and 5 = leaflet and rachis lesions more numerous than above, stem lesions usually present. Raters placed the sample leaf in the category most appropriate to the severity of the symptoms. These category data were converted to a percent severity based on

the midpoint method (Campbell and Madden 1990), by using the severity depicted on the guide leaves provided by Hunter and Roberts (1978) which was measured by image analysis (Lamari 2008).

2013 and 2014. Raters estimated severity visually based on the percent ratio scale, which is a continuous scale. Severity was estimated as the percent area diseased with scab symptoms on the whole leaf. Ten leaves were sampled arbitrarily per tree to represent the range of leaf ages on terminals. The raters used a standard area diagram series of scab symptoms on whole leaves to interpolate estimates as an aid for the assessments (C. H. Bock, unpublished data). Standard area diagrams are demonstrated to increase accuracy

Table 3. Pecan scab severity by family and provenance in 1998, 2013, and 2014 at Byron, GA. In 1998, a 1 to 5 score was given to each plant based on an assessment of the scab on the single most severely infected leaf using the Hunter-Roberts scale 1 = no infection, 2 = one to several lesions restricted in size, 3 = several large lesions on leaflets, 4 = numerous leaflet and rachis lesions, some stem lesions may be present, and 5 = leaflet and rachis lesions more numerous than above, stem lesions usually present. This was also converted to a percent severity based on the midpoint method (Campbell and Madden 1990). In 2013 and 2014, a sample of 10 leaves was taken from each plant and each was assessed for the % area with scab symptoms

Provenance (by latitude, N→S)	Family	Scab severity (1 to 5)		Scab severity (%) ^y	
		1998	1998	2013	2014
MO-L	1	1.231 tu	0.033 rs	0.138 nopqrstvw	0.093 uwyz(2)abe
MO-L	3	2.400 fghijklmnopqrstu	1.776 klmnopqrs	0.022 qrstvw	0.242 jklmnopqrstuvwxyz(2)ac
MO-L	4	1.750 ijklmnopqrstu	0.397 nopqrst	0.079 nopqrstvw	0.119 qrstuwyz(2)abde
MO-L	5	1.786 lmnopqrstu	0.466 qrs	0.053 nopqrstvw	0.142 stuwyz(2)abe
IL-J	1	1.539 opqrstu	0.191 qrs	0.081 nopqrstvw	0.141 tuwyz(2)ae
IL-J	2	1.714 mnoopqrstu	0.343 qrs	0.105 nopqrstvw	0.167 stuwyz(2)ae
IL-J	3	1.385 rstu	0.120 qrs	0.059 opqrstvw	0.161 stuwyz(2)ae
IL-J	4	1.250 tu	0.039 rsw	0.063 opqrstvw	0.164 stuwyz(2)ae
IL-J	5	1.539 opqrstu	0.201 qrs	0.100 nopqrstvw	0.197 qrstuwyz(2)ade
MO-V	1	2.000 cdefghijklmnopqrstu	0.749 ghijklmnopqrsx	0.045 nopqrstvw	0.116 nopqrstuvwxyz(2)abd
MO-V	2	1.600 mnoopqrstu	0.254 qrs	0.114 nopqrstvw	0.162 qrstuwyz(2)abde
MO-V	3	1.800 klmnopqrstu	0.495 pqrs	0.053 opqrstvw	0.175 qrstuwyz(2)ade
MO-V	4	1.546 nopqrstu	0.246 qrs	0.171 mnoopqrstvw	0.132 stuwyz(2)abe
MO-V	5	1.333 pqrstu	0.069 qrs	0.073 nopqrstvw	0.166 qrstuwyz(2)abde
KY-W	1	1.000 uy	0.000 rsw	0.043 opqrstvw	0.098 uwyz(2)abe
KY-W	2	1.333 jklmnopqrstu	0.069 mnoopqrs	0.003 rstvw	0.250 ijklmnopqrstuvwxyz(2)ac
KY-W	3	2.000 klmnopqrstu	0.775 pqrs	0.065 nopqrstvw	0.137 stuwyz(2)abe
KY-W	4	1.500 mnoopqrstu	0.156 pqrs	0.027 qrstvw	0.144 stuwyz(2)abe
KY-W	5	2.000 ijklmnopqrstu	0.665 opqrsu	0.058 mnoopqrstvw	0.493 cdefghijklmnopqrstuvwxyz
KS-C	1	1.750 ijklmnopqrstu	0.351 nopqrst	0.025 nopqrstvw	0.121 noqrstuvwxyz(2)abd
KS-C	2	3.500 abcdefghijklmnopqrstu	5.449 abcdefghijklmnopqrs	0.507 cdefghijklmnopqrstvw	0.209 ijklmnopqrstuvwxyz(2)abc
KS-C	3	3.000 cdefghijklmno	3.311 klmnopqrs	0.342 hijklmnopqrstvw	0.312 hijklmnopqrstuvwxyz(2)c
KS-C	4	1.833 klmnopqrstu	1.066 opqrs	0.145 mnoopqrstvw	0.140 qrstuwyz(2)abde
KS-C	5	2.182 jklmnopqrstu	1.133 opqrs	0.041 nopqrstvw	0.221 noqrstuvwxyz(2)ad
KS-K	1	1.167 opqrstu	0.017 pqrs	0.103 nopqrstvw	0.205 noqrstuvwxyz(2)ad
KS-K	3	1.714 klmnopqrstu	0.416 opqrs	0.020 qrstvw	0.121 stuwyz(2)abe
KS-K	4	2.333 jklmnopqrstu	1.275 opqrs	0.155 nopqrstvw	0.263 noqrstuvwxyz(2)d
KS-K	5	1.546 nopqrstu	0.197 qrs	0.098 nopqrstvw	0.210 qrstuwyz(2)ade
TN-L	1	1.111 u	0.007 s	0.003 vw	0.119 uwyz(2)abe
TN-L	3	1.200 tu	0.024 qrs	0.002 vw	0.092 wyz(2)ab
TN-L	4	1.462 pqrstu	0.150 qrs	0.020 qrstvw	0.090 wxyz(2)ab
TN-L	5	1.556 mnoopqrstu	0.207 qrs	0.085 nopqrstvw	0.114 tuwyz(2)abe
TN-L	6	2.000 abcdefghijklmnopqrstu	0.625 abcdefghijklmnopqrs	0.001 nopqrstvw	0.535 abcdefghijklmnopqrstuvwxyz(2)ab
MS-W	1	3.000 abcdefghijklmnopqrstu	3.000 abcdefghijklmnopqrs	- ^z	-
MS-W	2	1.429 qrstu	0.114 qrs	0.038 nopqrstvw	0.100 qrstuwyz(2)abde
MS-W	3	2.600 dfghijklmnopqrstu	2.068 jklmnopqrs	0.057 nopqrstvw	0.149 noqrstuvwxyz(2)abd
MS-W	4	1.667 klmnopqrstu	0.277 opqrs	0.008 rstvw	0.157 qrstuwyz(2)abde
MS-W	5	1.000 mnoopqrstux	0.000 nopqrs	0.043 nopqrstvw	0.074 qrstuwyz(2)abde
TX-B	1	2.000 klmnopqrstu	0.686 pqrs	0.007 stvw	0.233 noqrstuvwxyz(2)ad
TX-B	2	1.455 opqrstu	0.139 qrs	0.043 pqrstvw	0.173 qrstuwyz(2)ade
TX-B	3	1.667 lmnopqrstuw	0.347 pqrs	0.011 rstvw	0.274 klmnopqrstuvwxyz
TX-B	4	1.273 tu	0.046 qrs	0.002 tvwy	0.157 qrstuwyz(2)abde
TX-B	5	1.417 pqrstu	0.108 qrs	0.000 w	0.133 tuwyz(2)abe
TX-T	1	4.083 abcdfg	19.878 abcdefghijkmt	0.307 inopqrstvw	0.000 (2)ab
TX-T	2	4.667 abe	39.172 abc	1.763 bcde	0.408 fghijklmnopqrstu
TX-T	3	4.636 abe	34.113 abcdefg	1.691 bcdefg	0.415 fghijklmnopqrstu

(continued on next page)

^y The % area diseased estimates were square root transformed. Back transformed values are presented with means separation for the transformed values. Means separation was based on Tukey's HSD ($\alpha = 0.05$). Where (2) is indicated, the means separation spans a second run of the alphabet for that means comparison.

^z Missing values.

of disease estimates (Yadav et al. 2013). Scab severity on leaves is generally closely related to that on fruit (Nutter et al. 1985), so is an appropriate measure of scab susceptibility to compare germplasm (Goff et al. 2003; Nesbitt et al. 1996; Sanderlin et al. 1981).

Statistical analysis. SAS V9.3 (SAS Institute, Cary, NC) was used for all the statistical analyses.

Differences among provenances and families. All scab severity data (1998 scale and converted % area data, and 2013 and 2014 % area severity data) were analyzed using a general linear mixed model. To compare provenance means, a general linear mixed model was used with fixed effects of provenance and random effects of family nested in provenance and replicate nested in provenance (as families within provenances were not necessarily equally susceptible, and the five families are not the same for each provenance). To compare family means within provenance, the same general linear mixed model was used, but with fixed effects of both provenance and family nested in provenance. The Akaike (and Akaike improved) and

Bayesian information criteria were checked during model selection in relation to random effects. Type III fixed effects were checked to confirm significance. Almost all % severity estimates were <30%, and variance was proportional to the mean, so data were square root transformed to improve normality and homoscedasticity prior to analysis. Residuals were inspected, and results of the analysis were back-transformed for presentation. Category scale data were not transformed. A pairwise comparison of genotypes was made using Tukey-Kramer adjusted pairwise comparisons and was converted to letter groupings using an SAS macro (PDMIX800), which takes the probability values for differences among means and converts the information to letter groups, where means with a common letter are not statistically different at $\alpha = 0.05$ (Saxton 1998).

Correlation analysis was used to compare severity of disease among families (averaged across replicate trees with each family within a provenance) and provenances (averaged across families within each provenance) in the different years; where category scale

Table 3. (continued from preceding page)

Provenance (by latitude, N→S)	Family	Scab severity (1 to 5)		Scab severity (%) ^a	
		1998	1998	2013	2014
TX-T	4	4.588 abe	31.595 abcdeg	1.544 bcdefg	0.612 efghijklmnopqrstuv
TX-T	5	4.500 abe	31.789 abcdeg	0.974 bcdefghijklm	0.039 yz(2)ab
TX-V	1	3.778 abcdgghi	7.124 hijkmnopqrs	0.532 cdefghijklmnopqr	0.016 (2)b
TX-V	2	3.846 abcdgfh	17.104 bcdefghijkmn	0.486 fklmnopqx	0.259 otuwy(2)de
TX-V	3	4.444 abcd	24.650 abcdefghijk	1.336 bcdeghi	1.171 abcdefghi
TX-V	4	4.833 abc	45.420 abcd	0.782 cdefghijklmn	0.604 cdefghijklmnopqrstuv
TX-V	5	4.643 abe	34.460 abcdeg	1.227 bcdefghij	0.744 cdefghijklmnopqr
TX-G	1	3.000 abcdefghijklmnopqrstu	3.000 bcdefghijklmnopqrs	0.107 klmnopqrstvw	0.184 jklmnopqrstuvwxyz(2)abc
TX-G	2	2.750 ghijklmnopqr	2.441 nopqrs	0.034 qrstvw	0.290 jklmnopqrstuvwxyz(2)c
TX-G	3	2.182 jklmnopqrstu	0.978 opqrs	0.041 qrstvw	0.193 qrstuvwxyz(2)ade
TX-G	4	2.571 hijklmnopqrstu	1.896 opqrs	0.129 nopqrstvw	0.288 mqrstuvwxyz(2)d
TX-G	5	2.733 ghijklmnopq	2.329 opqrs	0.085 nopqrstvw	0.297 klmnopqrstuvwxyz
TX-K	1	4.000 abcdgfv	12.584 cdefghijklmnop	1.267 bcdefghij	0.709 dfgghijklmnopqrstv
TX-K	3	4.333 abcd	22.446 abcdefghijk	1.682 bcd	0.613 dfgghijklmnopqrstuvx
TX-K	4	4.733 ab	39.478 ab	2.274 ab	1.938 ab
TX-K	5	4.444 abcd	28.495 abcdefghi	0.541 efghijklmnopqru	1.590 abce
TX-K	6	4.083 abcdg	22.244 abcdefghijk	1.058 cdefghijkl	0.541 fghijklmnopqrstuv
TX-Z	1	4.308 abcd	23.596 abcdefghijl	1.610 bce	0.285 lstuwy(2)d
TX-Z	2	4.900 a	49.613 a	4.164 a	0.663 cdefghijklmnopqrstuv
TX-Z	3	3.556 abcdgghij	10.092 defghijklmnopqw	0.681 dfgghijklmnou	0.000 z(2)ab
TX-Z	4	3.583 abcdgghij	9.099 fhijklmnopqx	0.455 ghijklmnopqrsxy	0.852 bcdefghijklmnopqr
TX-Z	5	4.167 abcdgfh	18.122 abcdefghijklmno	1.566 bcdef	0.710 cdefghijklmnopqrstuv
MX-J	1	2.000 klmnopqrstu	0.720 pqr	0.004 tw	0.197 qrstuvwxyz(2)ade
MX-J	2	2.455 hijklmnopqrstu	1.772 opqrs	0.061 nopqrstvw	0.126 tuwyz(2)abe
MX-J	3	2.833 fghijklmnop	2.621 nopqrs	0.046 nopqrstvw	0.205 nopqrstuvwxyz(2)ad
MX-J	4	2.929 fghijklmn	3.027 nopqrs	0.032 qrstvw	0.315 jklmnopqrstuvwxyz(2)c
MX-J	5	2.231 jklmnopqrstu	2.098 opqrs	0.000 w	0.169 stuvwxyz(2)ae
MX-C	1	4.100 abcdg	19.966 abcdefghijklmn	0.815 bcdefghijklmnop	1.197 abcdefghijklm
MX-C	2	4.600 abc	36.127 abcdeg	0.796 bcdefghijklmno	1.169 abcdefghijklm
MX-C	3	4.000 abcdefghijklmnopqrs	21.307 abcdefghijklmnopqrs	0.487 cdefghijklmnopqrstvw	1.579 abcdefghi
MX-C	4	4.500 abcd	30.850 abcdefgh	0.796 cdefghijklmn	1.323 abcdefgh
MX-I	1	1.375 stu	0.099 rs	0.130 nopqrstvw	0.195 rwyz(2)ade
MX-I	2	4.267 abcd	28.284 abcdefgh	1.127 bcdefghijk	1.025 abcdefhijp
MX-I	3	3.429 bcdgghij	11.243 efghijklmnopv	0.482 efghijklmnopqru	0.633 cdefghijklmnopqstu
MX-I	4	3.917 abcdgfh	21.423 abcdefghijklm	0.232 lmnopqrstvw	0.628 cdefghijklmnopqrstuv
MX-I	5	2.385 ijklmnopqrstu	1.616 opqrs	0.257 lmnopqrstvw	0.401 gklmnopqrstuvwxyz(2)c
MX-S	1	3.429 abcdgghijkw	5.225 hijklmnopqrs	0.280 hijklmnopqrstvw	2.582 a
MX-S	2	4.000 abcdefghi	8.624 cdefghijklmnopqrs	0.455 cdefghijklmnopqrstv	1.694 abcde
MX-S	3	4.800 abcd	43.393 abcdef	0.169 lmnopqrstvw	1.209 bcdefghijkl
MX-S	4	4.167 abcdgfh	30.134 abcdefghij	0.409 cdefghijklmnopqrstvw	1.142 bcdefghijklmno
MX-S	5	3.750 abcdefghijkl	12.539 abcdefghijklmnopqrs	0.734 bcdefghijklmnopqrst	1.754 abcdefg
MX-O	1	3.333 abcdgghijklm	11.627 bcdefghijklmnopqr	0.792 bcdefghijklmnopq	0.151 nopqrstuvwxyz(2)abd
MX-O	2	2.546 hijklmnopqrstvy	2.872 nopqrst	0.112 mqrstuvwxyzvw	0.077 uwyz(2)abe
MX-O	3	3.333 abcdgghijkx	4.805 ijklmnopqrs	0.217 jklmnopqrstvw	0.239 jklmnopqrstuvwxyz(2)ac
MX-O	4	4.000 abcdefghijklmnopqrstu	8.624 abcdefghijklmnopqrs	1.103 abcdefghijklmnopqrs	2.736 abcd
MX-O	5	4.429 abcd	28.860 abcdefghij	0.383 bcdefghijklmnopqrstvw	0.543 bcdefghijklmnopqrstuvwxyz
F-value (<i>P</i> value)		3.97 (<0.0001)	3.96 (<0.0001)	6.50 (<0.0001)	10.89 (<0.0001)

data were used, Spearman's rank correlation was applied, but for continuous data, Pearson's correlation was used. Due to non-independence of data, associations of individual tree assessments between years were not subject to correlation analysis. In addition, correlation analysis was used to relate provenance scab severity to latitude, elevation, precipitation, temperature, budbreak date, leaflet droop angle, and leaflet tilt angle. *P*-values were inspected to ascertain associations between variables. A stepwise multiple regression analysis was applied to determine those physical factors (latitude, rainfall, mean maximum and mean minimum temperatures, and elevation) and those foliar characteristics (budbreak date, leaflet droop angle, and leaflet tilt angle) contributing most as predictors of scab severity among the different provenances (averaged across families within each provenance). An unweighted paired grouping of mathematical averages (UPGMA) cluster analysis was performed to assess the relationship among the various provenances based on scab severity data in each year.

Heritability. Heritability (Holland et al. 1998; Wright 1976) was calculated using a mixed model based on the same general linear mixed model described above, but with all sources modeled as random effects. Random effects of replicate and replicate $\times$ provenance were estimated to be zero and were removed from the model to simplify the analysis. Thus a reduced model based solely on provenance and family within provenance was used. The variance components of the model were obtained and used to estimate heritability as described in Holland et al. (1998) and on the website <http://www4.ncsu.edu/~jholland/heritability/OneEnvironRCBDHeritability.sas>. Heritability for both individual trees and families was calculated. As previously described (Wood et al. 1998), trees in the same family were assumed to be half-sibs as selfing in maternal trees was unlikely due to broad outcrossing. Each tree genotype was tested at only a single site (Byron, GA), precluding a separation of genotype-environment interactions from genetic variation among families and individuals, which thus slightly overestimates heritability (Wright 1976).

Results

Weather. Although mean maximum (27.9, 25.8, and 27.2°C), mean minimum (14.8, 14.0, and 14.4°C), and mean temperatures (21.1, 19.4, and 20.4°C) were fairly similar during the period recorded in 1998, 2013, and 2014, respectively, rainfall was markedly different (288.3, 860.3, and 549.4 mm, respectively). In 1998, there were relatively dry conditions during the growing season, but in 2013, conditions were particularly wet, and in 2014 they were moderately wet.

Estimates of severity. Despite different assessment methods used in 1998 (1 to 5 scale), and in 2013 and 2014 (the percentage ratio scale), there was a clear relationship between methods of assessment (Supplementary Fig. S1A to C). However, the frequency of severities in 1998, 2013, and 2014 showed different trends (Supplementary Fig. S2). Estimates based on the category scale were spread relatively evenly across the five categories. However, estimates in 2013 and 2014 indicated a preponderance of very low severities in both years (<0.5% leaf area). The frequency of trees that had extreme susceptibility in 2013 and 2014 (>2% leaf area) was relatively low. There was general agreement among severity estimates on individual trees from all years (Supplementary Fig. S3), although there were a few outliers between 2013 and 2014, and in 1998 trees scored as a 4 or a 5 (susceptible) did not necessarily have much leaf area diseased in 2013 and 2014. Assessment on individual trees among years shows the range of rating score in 1998 and of estimates of % area in 2013 and 2014 (Supplementary Table S1). Thus, comparing only the trees that were common to all three years, in 1998, there were 165 trees that had a score of 1 (no scab) and 101 with a score of 5. However, in 2013, there were 117 trees with a severity of <0.2%, and only 3 with a severity (% leaf area) >12.5%, while in 2014 there were 134 trees with a severity of <0.2%, and only 4 with a severity (% leaf area) >12.5%. In most cases, trees had comparable severity among years. Examples of individual trees that showed inconsistent results between years are: #284 (IL-J-2), which was scored as 1, 2.1%, and 0.1% in 1998, 2013, and 2014, respectively; #364 (TX-V-3), which was scored as 5, 4.7%, and 0.7% in 1998, 2013, and 2014,

respectively; #448 (TX-T-3), which was scored as 5, 11.4%, and 0.9% in 1998, 2013, and 2014, respectively; and #616 (TX-B-2), which was scored as 1, 2.4%, and 0.1% in 1998, 2013, and 2014, respectively. An example of a tree with consistent severity is #118 (MO-L-5), which was scored as 1, 0.0%, and 0.1% in 1998, 2013, and 2014, respectively. Indeed, the majority of trees were highly consistent in regard to severity rating. Thus, there were 66 trees that were consistently highly resistant across years and had a rating score of 1 or $\leq 0.1\%$ area diseased (Supplementary Table S2). Similarly, there were 147 trees consistently scored as highly susceptible across years and had a severity score of 4 or 5 or $\geq 0.5\%$ leaf area diseased (Supplementary Table S3). The consistency among these scores in regard to source provenance is demonstrated when considering these trees as a proportion of total trees assessed in each provenance in each year (Fig. 1). The greatest proportion of scab resistant trees were consistently found in provenances MO-L, IL-J, MO-V, KY-W, KS-K, TN-L, MS-W (more northerly provenances with higher rainfall), and TX-B, and to a lesser extent MX-J and MX-I. Conversely, the greatest proportion of scab susceptible trees were consistently found in provenances TX-T, TX-V, TX-K, TX-Z, MX-C, MX-S, and MX-O, and to a lesser extent MX-I, all drier, more southerly provenances.

Provenance and family scab resistance. In all three years, the severity of scab depended on provenance ($F = 5.6$ to 62.5 , $P < 0.0001$, Table 2). In 1998, the severity score ranged from 1.359 (TN-L) to 4.496 (TX-T), in 2013 the mean leaf area diseased ranged from 0.008% (TX-B) to 1.436% (TX-Z), and in 2014 from 0.120% (MS-W) to 1.613% (MX-S). Although there were some differences among ranking with provenances among years, nine provenances consistently had the most resistant genotypes in all years (TN-L, IL-J, TX-B, KY-W, KS-K, KS-C, MO-L, MO-V, and MS-W), while two provenances, MX-C and MX-O (when based on the scale in 1998) were consistently in the most susceptible group; TX-T, TX-V, TX-Z, MX-C, and MX-S were also grouped together with TX-K, and MX-O in 1998. Other provenances had intermediate scab severity. When ranking changed for a provenance between years, the change was never to extreme susceptibility or resistance. The UPGMA showed that certain provenances consistently clustered together (Supplementary Fig. S4). In all three seasons, there were two groupings, one comprising provenances with more scab susceptible trees (TX-T, TX-V, TX-K, and TX-Z, rainfall March to July = 242.1 to 294.6 mm), and the other with provenances having trees that tended to be more resistant (MO-L, MS-W, IL-J, KY-W, TX-B, TN-L, MO-V, KS-K, KS-C, MX-J, and TX-G, rainfall March to July = 327.0 to 632.2 mm).

Among families nested within provenance, there was also a range of susceptibilities in all three years ($F = 3.96$ to 10.89 , $P < 0.0001$, Table 3). The means separation was similar among years, although ranking differed slightly, and the severities followed a similar pattern to that described for provenances. One of the provenances with the most resistant families was TN-L. In 1998, the severity scores ranged from 1.111 to 2.000, and the severity estimates in 2013 and 2014 were 0.001 to 0.085 and 0.090 to 0.535, respectively. For a more susceptible provenance, for example, TX-K, the severity scores for families in 1998 ranged from 4.000 to 4.733, and the severity estimates in 2013 and 2014 were 0.541 to 2.274% and 0.541 to 1.938%, respectively. The frequency of trees with different severities within provenances had a similar pattern among years (Supplementary Fig. S5), with those more susceptible provenances consistently having greatest frequency of trees with a high scab severity, and the more resistant provenances consistently having a greater frequency of trees with less severe scab. There was consistent correlation among provenances between years ($r = 0.891$ to 0.955 , $P < 0.0001$), and between families within provenances ($r = 0.821$ to 0.896 , $P < 0.0001$).

Provenance and severity of pecan scab in relation to environmental and host variables. In 1998, severity of pecan scab was negatively correlated with provenance source latitude ($r = -0.693$ [$P = 0.001$], Table 4), but there was no association with latitude in 2013 or 2014. However, scab severity was negatively associated with precipitation at the provenance source location in all three seasons ($r = -0.625$ to -0.823 [$P < 0.0001$ to 0.004]), indicating that trees tended to be more resistant from locations where rainfall was higher. Scab

severity was positively correlated with maximum temperature at the source location in all three seasons ($r = 0.491$ to 0.677 [$P = 0.002$ to 0.03]), but with minimum temperature only in 1998. Similarly, provenance source elevation was positively associated with scab severity only in 1998. Severity was negatively correlated with budbreak in 1998, but not in 2013 or 2014. Scab severity was negatively correlated with both leaflet droop ($r = -0.700$ to -0.883 [$P < 0.0001$ to 0.0004]) and leaflet tilt ($r = -0.533$ to -0.844 [$P < 0.0001$ to 0.02]) in all three years. The multiple regression analysis indicated precipitation and leaflet droop were good predictors of provenance scab susceptibility (Table 5).

Tree and family heritability of pecan scab resistance. Estimates of heritability varied among years and to a lesser degree assessment method (Table 6). Whereas family heritability was comparatively high when based on the 1 to 5 category scale in 1998, they were relatively low in 2013 and 2014 when based on the 0 to 100% scale. However, converting the percent scale data to the category scale improved the heritability estimates of scab resistance for 2013 and 2014. Single tree heritability was consistently lower in all years, and followed a similar pattern in relation to assessment method to that for family heritability.

Discussion

There was a substantial range in scab susceptibility in the pecan provenance collection. The collection is known to be genetically diverse (Grauke et al. 1995, 2003b; Rüter et al. 1999; Sagaram et al. 2011; Wood et al. 1998), and the reaction of trees from the different provenances to naturally developing epidemics of pecan scab at this location in Byron, GA, confirms this genetic diversity. The environmental conditions experienced at the source locations by these trees will most likely affect the frequency of specific alleles associated with traits such as scab susceptibility. In areas where scab pressure is high, the trees experience selection to develop and maintain scab resistance. This is particularly true when considering the toll that scab can take on reproductive capacity of a tree (Gottwald and Bertrand 1982, 1988; Sanderlin 1995; Stevenson and Bertrand 2001). Highly susceptible trees might not produce any offspring in severe scab epidemic seasons. However, where scab is not an issue, selection for scab resistance would be unlikely to be sufficient for these traits to become predominant in the pecan population.

Rainfall at the provenance location was consistently correlated with the severity of scab. Rainfall is known to be the driving force

behind epidemics (Gottwald and Bertrand 1982, 1983; Latham 1982), and it is those provenances with the least rainfall that tended to have the more scab susceptible trees (TX-Z, TX-T, TX-V, TX-K, MX-O, MX-I, MX-S, and MX-C). Grauke et al. (1995) commented that in Arkansas, the climatic conditions in early spring are generally conducive to scab epidemics, and thus trees in that area may have adapted by developing resistance to the pathogen. The results of the current study bear out this observation—locations with higher rainfall tend to have a preponderance of trees that are more resistant to scab. Trees in these areas provide a valuable resource for resistance to scab. Indeed, it is material from these areas that have been utilized by the USDA in the scab resistance screening program (Thompson and Grauke 1991). Elevation has been shown to affect severity (Sparks et al. 2009), although only in 1998 was elevation found to be associated with scab severity in the current study. Similarly, temperature was associated with scab severity in 1998, but budbreak date, and in particular leaflet droop angle and leaflet tilt angle, were consistently negatively associated with the severity of scab among provenances. Both leaflet droop angle and leaflet tilt angle are positively correlated with latitude and rainfall (Wood et al. 1998), and thus the association between scab and leaflet characteristics may be spurious and due to other co-related factors, rather than leaflet characteristics directly affecting scab severity per se.

Within each provenance, trees from the different families exhibited a range of severity, demonstrating the diversity of scab resistance among related trees at local spatial scales. The genetics of resistance

Table 6. Heritability of pecan scab severity by family (H_f^2) and by tree (H_t^2) based on either scale data (1998), percentage area diseased (2013 and 2014), or scale data converted to midpoint data (1998) or percentage area diseased converted to scale data (2013 to 2014).

Year		Family		Single tree	
		H_f^2	SE ^z	H_t^2	SE
1998	Scale	0.714	0.050	0.202	0.040
	% area - midpoint	0.703	0.053	0.194	0.040
2013	Scale (converted)	0.196	0.137	0.036	0.031
	% area	0.147	0.156	0.026	0.032
2014	Scale (converted)	0.323	0.109	0.055	0.026
	% area	0.069	0.136	0.009	0.019

^z Standard error.

Table 4. Correlation analysis^z between severity of pecan scab in Byron, GA, in 1998, 2013, and 2014 and environmental variables (Table 1) from each provenance location

Year	Latitude (°)	Precipitation (cm year ⁻¹)	Max temp (°C)	Min temp (°C)	Elevation (m)	Bud break	Leaflet droop (°)	Leaflet tilt (°)
1998 (scale)	-0.693 (0.001)	-0.823 (<0.0001)	0.677 (0.002)	0.633 (0.004)	0.663 (0.002)	-0.560 (0.01)	-0.883 (<0.0001)	-0.844 (<0.0001)
1998 (%)	-0.564 (0.01)	-0.868 (<0.0001)	0.524 (0.02)	0.566 (0.01)	0.426 (0.07)	-0.549 (0.02)	-0.803 (<0.0001)	-0.730 (0.0004)
2013	-0.267 (0.3)	-0.716 (0.0006)	0.508 (0.03)	0.313 (0.2)	0.093 (0.7)	-0.413 (0.08)	-0.728 (0.0004)	-0.611 (0.006)
2014	-0.187 (0.4)	-0.625 (0.004)	0.491 (0.03)	0.251 (0.3)	0.017 (0.9)	-0.371 (0.1)	-0.700 (0.0009)	-0.533 (0.02)

^z With scale (category) data, Spearman's rank correlation was used. With continuous data (%), Pearson's correlation was used. Values in parentheses are *P*-values.

Table 5. Stepwise multiple regression^x between scab severity on pecan trees from different provenances in three different years and provenance location environmental variables and pecan foliage characteristics

Year	Total R ²	Partial R ² y (beta coefficient) ^z					
		Precipitation	Elevation	Latitude	Minimum temp	Budbreak	Leaflet droop
1998 (scale)	0.89	0.77 (-0.63)	ns	ns	ns	0.02 (0.22)	0.11 (-0.56)
1998 (%)	0.89	0.74 (-0.86)	ns	ns	ns	0.09 (0.50)	0.06 (-0.52)
2013	0.86	0.12 (-0.79)	0.13 (-0.47)	ns	ns	0.08 (0.49)	0.53 (-0.74)
2014	0.81	0.14 (-0.61)	ns	0.19 (0.85)	ns	ns	0.49 (-0.85)

^x Results of ANOVA by year: 1998 (scale) model F-value 42.7 = ($P < 0.0001$), 1998 (%) model F-value = 37.2 ($P < 0.0001$), 2013 model F-value = 22.0 ($P < 0.0001$), 2014 model F-value = 21.9 ($P < 0.0001$).

^y The partial R² value describes the proportion of the variance accounted for by that predictor in the model.

^z The beta coefficient (also known as the standardized estimate) allows direct comparison of the relative strength of the various predictors within the model (the beta coefficient is measured in standard deviations, not the actual units of the variables, so they can be compared directly to one another).

to scab in pecan is not understood, but diversity in susceptibility of progeny in families has been noted previously (Thompson and Grauke 1994). Heritability of scab resistance is considered to be sufficiently high to allow breeding to make reasonable progress (Thompson and Grauke 1994). The results of the current study on heritability were not consistent. In 1998, family heritability was 0.714, indicating good heritability, and comparable to that found by Thompson and Grauke (~0.500). However, in 2013 and 2014 (using the percentage scale), family heritability was rather low (0.147 and 0.069, respectively), but improved slightly if the % data were converted to the 1 to 5 rating scale (0.196 and 0.323, respectively). Further work is needed to establish heritability of pecan scab. Using a 1 to 5 rating scale and basing that score on the maximum severity encountered in a canopy may offer some advantages in estimating heritability in this respect, as well as being a more rapid approach to disease assessment. However, these types of category scales have been shown to be associated with a greater risk of type II error (Bock et al. 2010; Chiang et al. 2014). The similarity in results among the three years shows that both methods were adequate to demonstrate differences among provenances and among families in provenances. Differences among years might, at least in part, be due to the different assessment methods used to compare trees, “escapes” from infection, prevailing weather conditions, the individual raters in different years, or changes in the pathogen population. Pecan leaves develop over a period of several weeks, and remain susceptible only during the period of leaf expansion (generally April through June, but for individual leaves this lasts only 10 to 14 days). Lack of sufficient inoculum during leaf production and development would reduce infection. Finally, the different individual raters involved could also be a source of variation between years; interrater variability is one of the sources of error in plant disease assessment (Bock et al. 2008; Nutter et al. 1993).

The study was conducted at a single location. Pathogenic specialization exists in *F. effusum* (Conner 2013; Conner and Stevenson 2004; Converse 1960; Demaree and Cole 1929), and it is known to be genetically diverse (Bock et al. 2014a, c). Thus, those trees resistant at Byron in 1998 and again 16 and 17 years later will not necessarily be resistant if exposed to the scab pathogen at other locations. The Byron location has 600 acres of pecan with numerous cultivars that are known to have varying susceptibility to scab (Thompson and Grauke 1994), ensuring that at least to some degree, these trees have been exposed to a wide range of pathogenic variants of *F. effusum*. But the risk of resistance failing at another location should be considered prior to utilizing any of the material identified herein.

The results of this study are consistent, but analysis based on an assessment of scab severity on the fruit in the same trees should be conducted to corroborate observations on foliage. Fortunately there is a good relationship between severity of scab on leaves and fruit (Goff et al. 2003; Nesbitt et al. 1996; Nutter et al. 1985; Sanderlin et al. 1981). However, not all trees have produced fruit, and some have severe alternate bearing, making a comprehensive collection problematic. As the trees get older, bearing may become more consistent on more trees.

The results of this study confirm the range in scab susceptibility that exists within the pecan metapopulation. Much of this variation is likely due to rainfall at the source location for the genotype, which drives scab epidemics. This genetic variation in regard to scab susceptibility is important to characterize as it is a basis for selection of material likely to have favorable traits conferring scab resistance. Thus certain populations or source areas of pecan are more likely to have scab resistance compared with others as a result of selection where rainfall and other local conditions are conducive to regular scab epidemics. Those materials most likely to contribute to genetic improvement regarding scab resistance are identified in the provenance collection.

Acknowledgments

We acknowledge the time and input of Shirley Anderson, Jacob Werner, and Kaylee Carson, who helped with sample collection, assessment, and data input. We also appreciate the contributions of Dr. Charles ‘Chuck’ Riley for his work

on the 1998 collections and insights into the provenance collection in relation to scab. We appreciate the funding support of the USDA-ARS through CRIS project 6042-21220-012-00. This article reports the results of research only. Mention of a trademark or proprietary product is solely for the purpose of providing specific information and does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture and does not imply its approval to the exclusion of other products that may also be suitable.

Literature Cited

- Beedanagari, S. R., Dove, S. K., Wood, B. W., and Conner, P. J. 2005. A first linkage map of pecan cultivars based on RAPD and AFLP markers. *TAG Theor. Appl. Genet.* 110:1127-1137.
- Bock, C. H., Cottrell, T. E., Hotchkiss, M. W., and Wood, B. W. 2013. Vertical distribution of scab in large pecan trees. *Plant Dis.* 97:626-634.
- Bock, C. H., Endalew, T. T., Biswas, B. K., Yadav, A. K., Sittler, V., Hotchkiss, M. W., Stevenson, K. L., and Wood, B. W. 2014a. A comparison of UP-PCR and RAPD markers to study genetic diversity of the pecan scab fungus (*Fusicladium effusum* G. Winter). *For. Pathol.* 44:266-275.
- Bock, C. H., Gottwald, T. R., Parker, P. E., Ferrandino, F., Welham, S., van den Bosch, F., and Parnell, S. 2010. Some consequences of using the Horsfall-Barratt scale for hypothesis testing. *Phytopathology* 100:1030-1041.
- Bock, C. H., Hotchkiss, M. W., Cottrell, T. E., and Wood, B. W. 2015. The effect of sample height on spray coverage in mature pecan trees. *Plant Dis.* 99:916-925.
- Bock, C. H., Hotchkiss, M. W., Brenneman, T. B., Stevenson, K. L., Goff, W., Smith, M. W., Wells, L., and Wood, B. W. 2014b. Hedging – does it affect the severity of pecan scab? *Pecan Grower* 25:48-58.
- Bock, C. H., Parker, P. E., Cook, A. Z., and Gottwald, T. R. 2008. Visual rating and the use of image analysis for assessing different symptoms of citrus canker on grapefruit leaves. *Plant Dis.* 92:530-541.
- Bock, C. H., Stevenson, K. L., Arias, R. S., and Wood, B. W. 2014c. Genetic diversity and population structure of *Fusicladium effusum* on pecan in the U.S.A. *Plant Dis.* 98:916-923.
- Campbell, C. L., and Madden, L. V. 1990. Monitoring epidemics: Environment. Pages 43-73 in: *Introduction to Plant Disease Epidemiology*. Wiley, London.
- Chiang, K.-S., Liu, S.-C., Bock, C. H., and Gottwald, T. R. 2014. What interval characteristics make a good categorical disease assessment scale? *Phytopathology* 104:575-585.
- Cole, J. R., and Gossard, A. C. 1956. Increased virulence of scab (*Cladosporium effusum* Wint. Demaree) on Stuart pecan in Mississippi and its presence in Louisiana. *Plant Dis. Rep.* 40:1120.
- Conner, P. J. 2013. Evaluation of response to pecan scab pathogen race using a detached leaflet protocol. *HortScience* 48:63-67.
- Conner, P. J., and Stevenson, K. L. 2004. Pathogenic variation of *Cladosporium caryigenum* isolates and corresponding differential resistance in pecan. *HortScience* 39:553-557.
- Conner, P. J., and Wood, B. W. 2001. Identification of pecan cultivars and their genetic relatedness as determined by randomly amplified polymorphic DNA analysis. *J. Am. Soc. Hortic. Sci.* 126:474-480.
- Converse, R. H. 1960. Physiologic specialization in *Fusicladium effusum* and its evaluation in vitro. *Phytopathology* 50:527-531.
- Cooper, J. N., and Johnson, J. D. 1985. The influence of tree spacing and fungicide use on the susceptibility of ‘Western’ to pecan scab. Pages 37-38 in: *Proceedings of the 63rd and 64th Texas Pecan Growers Association Annual Conferences*, San Antonio, Texas, 8-11 July, 1984 and Galveston, Texas, 7-10 July, 1985.
- Demaree, J. B., and Cole, J. R. 1929. Behavior of *Cladosporium effusum* (Wint.) Demaree on some varieties of pecan. *J. Agric. Res.* 38:363-370.
- Erdin, N., Tartarini, S., Broggin, G. A. L., Sansavini, S., Gessler, C., and Patocchi, A. 2006. Mapping the apple scab-resistance gene *Vb*. *Genome* 49:1238-1245.
- Goff, W. D., McVay, J. R., and Gazaway, W. S. 1996. Page 222 in: *Pecan production in the Southeast*. Alabama Cooperative Extension System Circular ANR-459. Auburn University, Auburn, AL.
- Goff, W. D., Nesbitt, M. L., and Browne, C. L. 2003. Incidence of scab and foliage condition on pecan cultivars grown without fungicide or insecticide sprays in a humid region. *HortTech.* 13:381-384.
- Gottwald, T. R. 1985. Influence of temperature, leaf wetness period, leaf age, and spore concentration on infection of pecan leaves by conidia of *Cladosporium caryigenum*. *Phytopathology* 75:190-194.
- Gottwald, T. R., and Bertrand, P. F. 1982. Patterns of diurnal and seasonal airborne spore concentrations of *Fusicladium effusum* and its impact on a pecan scab epidemic. *Phytopath.* 72:330-335.
- Gottwald, T. R., and Bertrand, P. F. 1983. Effect of time of inoculation with *Cladosporium caryigenum* on pecan scab development and nut quality. *Phytopath.* 73:714-718.
- Gottwald, T. R., and Bertrand, P. F. 1988. Effects of an abbreviated pecan disease control program on pecan scab disease increase and crop yield. *Plant Dis.* 72:27-32.
- Grauke, L. J., Iqbal, M. J., Reddy, A. S., and Thompson, T. E. 2003a. Development of microsatellite DNA markers in pecan. *J. Am. Soc. Hortic. Sci.* 128:374-380.
- Grauke, L. J., Mendoza-Herrera, M., Miller, A., and Wood, B. W. 2011. Geographic patterns of genetic variation in native pecans. *Tree Gen. Geno.* 7:917-932.
- Grauke, L. J., Payne, J. A., and Wood, B. W. 1989. North American pecans: A provenance study. *Annu. Rep. N. Nut Growers Assoc.* 80:124-131.

- Grauke, L. J., Storey, J. B., Thompson, T. E., and Wood, B. W. 2003b. Leaf structure and nutrient content vary in native pecan populations. *Proc. Tex. Pecan Growers Assoc.* 70:59-60.
- Grauke, L. J., Thompson, T. E., and Marquard, R. D. 1995. Evaluation of pecan [*Carya illinoensis* (Wangenh.) K. Koch] germplasm collections and designation of a core subset. *HortSci.* 30:950-954.
- Holland, J. B., Uhr, D. V., Jeffers, D., and Goodman, M. M. 1998. Inheritance of resistance to southern corn rust in tropical-by-corn-belt maize populations. *Theor. Appl. Genet.* 96:232-241.
- Hunter, R. E., and Roberts, D. D. 1978. A disease grading system for pecan scab. *Pecan Q.* 12:3-6.
- Lamari, L. 2008. ASSESS 2.0: Image Analysis Software for Plant Disease quantification. APS Press, St. Paul, MN.
- Latham, A. J. 1982. Effects of some weather factors and *Fusicladium effusum* conidium dispersal in pecan scab occurrence. *Phytopathology* 72:1339-1345.
- Nesbitt, M., Goff, W. D., Hale, T., Thompson, T., Reynolds, K. L., and O'barr, R. D. 1996. Screening 147 pecan cultivars for scab resistance. *Proc. Se Pecan Growers Assoc.* 89:90-97.
- Nutter, F. W., Jr., Gleason, M. L., Jenco, J. H., and Christians, N. L. 1993. Accuracy, intra-rater repeatability, and inter-rater reliability of disease assessment systems. *Phytopathology* 83:806-812.
- Nutter, F. W., Jr., Gottwald, T. R., and Bertrand, P. F. 1985. Relationship between pecan scab disease progression on leaves versus nuts in three pecan cultivars. *Phytopathology* 75:1369 (abstract 722).
- Rüter, B., Hamrick, J. L., and Wood, B. W. 1999. Genetic diversity within provenance and cultivar germplasm collections versus natural populations of pecan (*Carya illinoensis*). *J. Hered.* 90:521-528.
- Sagaram, M., Lombardini, L., and Grauke, L. J. 2011. Variation in anatomical characteristics in leaves of pecan seedstocks from Mexico and the United States. *J. Am. Soc. Hortic. Sci.* 136:103-108.
- Sanderlin, R. S. 1995. Effect of nut scab on pecan yield and quality components. Pages 45-49 in: *Sustaining Pecan Productivity into the 21st Century: Second National Pecan Workshop Proceedings*, Wagoner, Oklahoma, 23-26 July, 1994. U.S. Dept. Agric., Agriculture Research Service.
- Sanderlin, R. S., Hunt, A. S., and Young, W. A. 1981. Reaction of pecan varieties to scab disease in Louisiana. *Pecan South* 8:6-9.
- Saxton, A. M. 1998. A macro for converting mean separation output to letter groupings in PROC MIXED. Pages 1243-1246 in: *Proc. 23rd SAS Users Group Intl.*, Nashville, TN, 22-25 March. (<http://www2.sas.com/proceedings/sugi23/Stats/p230.pdf>).
- Seyran, M., Brenneman, T. B., and Stevenson, K. L. 2010. A rapid method to monitor fungicide sensitivity in the pecan scab pathogen, *Fusicladium effusum*. *Crop Prot.* 29:1257-1263.
- Sparks, D., Yates, I. E., Bertrand, P. F., and Brenneman, T. B. 2009. The relative importance of elevation and rainy days on the incidence of scab damage of pecan nuts in the southeastern USA. *J. Hortic. Sci. Biotechnol.* 84:137-142.
- Stevenson, K. L. 1999. Fungicide resistance management in pecans. *South East Pecan Growers Association* 92:58-64.
- Stevenson, K. L., and Bertrand, P. F. 2001. Within-season dynamics of yield loss due to pecan scab fruit infections. *Phytopathology* 91:S85.
- Stevenson, K. L., Bertrand, P. F., and Brenneman, T. B. 2004. Evidence for reduced sensitivity to propiconazole in the pecan scab fungus in Georgia. *Phytopathology* 94:S99.
- Thompson, T. E., and Grauke, L. J. 1991. Pecans and hickories (*Carya*). Pages 839-904 in: *Genetic Resources of Temperate Fruit and Nut Crops*. J. N. Moore and J. R. Ballington, eds. International Society for Horticultural Science, Wageningen, Netherlands.
- Thompson, T. E., and Grauke, L. J. 1994. Genetic resistance to scab disease in pecan. *HortScience* 29:1078-1080.
- Wells, L., Brenneman, T., Brock, J., Culpepper, A. S., Hudson, W., and Mitchem, W. 2015. 2015 Commercial pecan spray guide. University of Georgia Extension. Bulletin 841. <http://www.caes.uga.edu/commodities/fruits/pecan/documents/2015-Pecan-Spray-Guide.pdf>
- Wood, B. W., Grauke, L. J., and Payne, J. A. 1998. Provenance variation in pecan. *J. Am. Soc. Hortic. Sci.* 123:1023-1028.
- Wright, J. W. 1976. Provenance testing. Pages 253-265 in: *Introduction to Forest Genetics*. Academic Press, New York.
- Xu, X.-M., Roberts, T., Barbara, D., Harvey, N. G., Gao, L.-Q., and Sargent, D. J. 2009. A genetic linkage map of *Venturia inaequalis*, the causal agent of apple scab. *BMC Res. Notes* 2:163.
- Yadav, N. V. S., de Vos, S. M., Bock, C. H., and Wood, B. W. 2013. Development and validation of standard area diagrams to aid assessment of pecan scab symptoms on fruit. *Plant Pathol.* 62:325-335.