Temporal Progress of Septoria Leaf Spot on Rabbiteye Blueberry (*Vaccinium ashei*)

P. S. Ojiambo and H. Scherm, Department of Plant Pathology, University of Georgia, Athens 30602

ABSTRACT

Ojiambo, P. S., and Scherm, H. 2005. Temporal progress of Septoria leaf spot on rabbiteye blueberry (*Vaccinium ashei*). Plant Dis. 89:1090-1096.

Septoria leaf spot, caused by *Septoria albopunctata*, is an important disease on blueberry in the southeastern United States, yet its epidemiology is largely unknown. Disease severity and dissemination of pycnidiospores were monitored from 2002 to 2004 in a planting of susceptible Premier rabbiteye blueberry to characterize the temporal progress of the disease and determine the effect of inoculum dynamics and selected leaf attributes on disease development. Disease onset was observed between late April and mid-June, followed by a rapid increase in disease severity until mid- to late September; thereafter, disease severity decreased until the end of the season due to abscission of severely infected leaves. A logistic model was fitted to disease severity data using nonlinear regression, and parameter estimates were used to compare the effects of leaf position on the shoot and shoot location in the canopy on disease progress. Based on this model, the highest absolute rate of disease increase and the highest upper asymptote of disease severity were predicted for leaves in intermediate positions on the shoot and for shoots in the lower canopy. Data collected with funnel spore samplers showed that splash-dispersed pycnidiospores of *S. albopunctata* were available throughout most of the period from April through late October. Final disease severity on individual leaves was more strongly correlated with cumulative spore numbers throughout the entire season (from leaf emergence to the end of the assessment period in November) than with cumulative spore numbers during shorter periods around the time of leaf emergence; this suggests that infection is not limited to young, expanding leaves, but rather that leaves at all developmental stages can become infected by *S. albopunctata* season-long. Disease incidence on leaves of potted trap plants exposed to natural inoculum in the field during rain events in 2003 and 2004 was >70.0% irrespective of leaf developmental stage at the time of exposure. Taken together, the results of this study indicate that inoculum of *S. albopunctata* is present throughout most of the growing season and that infection can occur season-long on leaves of any age, giving rise to a polycyclic epidemic.

Septoria leaf spot, caused by *Septoria albopunctata*, is the most prevalent foliar disease of blueberry (*Vaccinium* section *Cyanococcus*) in Georgia (21) and in other southeastern states (7). Most southern highbush blueberry (*Vaccinium corymbosum* hybrids) cultivars and a number of rabbiteye blueberry (*V. ashei*) cultivars are highly susceptible to the disease. Symptoms appear as small circular leaf lesions with white to tan centers and purple margins. The optimum temperature range for pathogen growth and disease development is 24 to 28°C (17). In Georgia, symptoms of Septoria leaf spot do not become widespread in the field until early

to late summer, after the crop has been harvested (19).

With the increasing acreage and intensity of blueberry production in the state (22), Septoria leaf spot is emerging as an important production constraint. In field studies on both rabbiteye and southern highbush blueberry cultivars, P. S. Ojiambo, H. Scherm, and P. M. Brannen (*unpublished*) showed that high levels of the disease in the summer and fall can reduce flower bud set and fruit yield in the following year. Thus, there is a need to devise management guidelines for Septoria leaf spot in order to minimize its yield-reducing effects. This requires knowledge of the epidemiology of the disease; however, such information presently is lacking in the *Septoria*-blueberry pathosystem. For example, very limited information is available on the temporal progress of the disease or how leaf attributes such as leaf age or leaf position in the canopy affect this process. Demaree and Wilcox (8) reported that young leaves that are still expanding are more susceptible to infection by *S. albopunctata* than fully expanded, mature leaves; however, this seems inconsistent with the rapid disease increase observed in the field in summer and early fall

(19), which is well past the period of leaf expansion for the spring flush of leaves. Milholland (17) reported that pycnidiospores of *S. albopunctata* are produced on new leaf lesions throughout the season, but the seasonal availability of inoculum and the influence of inoculum dynamics on disease progress have not been examined. As a result, current guidelines for Septoria leaf spot management are highly empirical and, where fungicides have been used for disease control, their application has been based on a calendar approach (3–5,7).

Based on the above considerations, the objectives of this study were to (i) characterize the temporal progress of Septoria leaf spot in the field and determine the effect of selected leaf attributes on disease progression, (ii) monitor the seasonal availability of pycnidiospore inoculum using spore samplers, and (iii) establish whether leaves are infected season-long or only during the period of leaf expansion.

MATERIALS AND METHODS

Field site. The study was carried out in an experimental blueberry planting at the University of Georgia Horticulture Farm near Athens from 2002 to 2004. The planting was established in 1988 and consisted of alternating rows of the rabbiteye blueberry cvs. Premier and Climax. Maintenance of the planting, including fertilization, pruning, and weed control, followed generally recommended practices (1). Supplemental overhead irrigation was applied when needed, primarily during the fruit maturation phase in the dry 2002 growing season. Plants remained untreated with fungicides throughout the 3-year period. Daily temperature and precipitation records were obtained from a Georgia Automated Environmental Monitoring Network weather station located about 500 m from the planting (13).

Evaluation of disease progress. On Premier, which is highly susceptible to Septoria leaf spot (21), 50 shoots were selected arbitrarily from 12 bushes (all located in the same row) during the period of leaf expansion (18) of the first (spring) flush of leaves in March or April each year. Each shoot was tagged at its base, and the distance from the base to the ground was measured to the nearest centimeter to provide a measure of leaf location in the canopy. At the time of tagging, shoots were about 4 cm long. Each leaf present or subsequently developing on the distal 20 cm of the selected shoots was monitored indi-

Corresponding author: H. Scherm
E-mail: scherm@uga.edu

Funded in part by MBG Marketing, the Southern Region Small Fruit Consortium, and the United States Department of Agriculture–CSREES Pest Management Alternatives Program (grant no. 01-34381-11181).

Accepted for publication 6 June 2005.

DOI: 10.1094/PD-89-1090
© 2005 The American Phytopathological Society

vidually during each year of the study; between 4 to 12 new leaves developed along individual shoots from the time when they were first tagged. Leaves were monitored by consistently numbering and assessing leaves on each shoot, starting with the proximal leaf to the distal leaf on each assessment date. Each leaf was assigned a number between 0 and 1 to indicate its position on the shoot, whereby the extreme values of 0 and 1 corresponded to the lowest and uppermost leaves, respectively. No new spring leaves emerged on selected shoots after mid- to late May, and a total of 410, 542, and 416 leaves were monitored in the 3 years.

Leaves were assessed for Septoria leaf spot severity beginning immediately after shoots had been tagged in early spring, expressing disease severity as number of spots per leaf. For the first 6 to 8 weeks, disease severity was assessed at 3- to 5-day intervals, after which assessments continued every 7 to 10 days for the remainder of the season. The last disease assessment was made in early to mid-November, after which leaf spot counts became impossible due to necrosis associated with natural leaf senescence. Throughout the study period, Septoria leaf spot was the only noticeable foliar disease on Premier.

To obtain an estimate of leaf developmental stage, the length of each leaf was measured on each disease assessment date for about 2 months after leaf emergence, by which time leaf expansion had ceased. Measurements of leaf length were made to the nearest millimeter using a ruler.

Inoculum dynamics. *S. albopunctata* does not have a known sexual stage (17). Seasonal availability of asexual pycnidiospores was monitored using funnel samplers similar to those described by Bertrand and English (2). Each year, six traps were installed in the planting to collect precipitation splash and runoff (from rain and sprinkler irrigation) from the shoots and branches. Funnels measuring 15 cm in diameter were attached to 1.0-liter plastic bottles containing 10 ml of 5% CuSO₄ solution. Each assembly was partially buried in the ground underneath a blueberry bush close to the crown, where it was firmly secured. The traps were positioned such that the height of the funnel above the ground was about 15 cm. After each precipitation event, the bottles were emptied by filtering the spore suspension through two layers of cheesecloth into a graduated cylinder to record the volume of water collected. A 50-ml subsample of the spore suspension was centrifuged at 3,000 min⁻¹ for 10 min, concentrated fivefold, and agitated for 5 s using a Vortex mixer. The number of pycnidiospores per milliliter in each sample was determined based on an average of four hemacytometer counts and converted to number per unit area (spore density) based on the volume of water collected and the area of the funnel.

Descriptive analyses. Disease severity values were used to calculate the area under the disease progress curve (AUDPC) for each leaf (6). Based on data from individual leaves, the PROC CORR procedure of SAS (v. 8.2; SAS Institute, Inc., Cary, NC) was used to assess whether significant ($\alpha = 0.05$) associations existed among disease variables (final disease severity and AUDPC) and leaf attributes (leaf position on the shoot and shoot height above the ground). Six correlation coefficients were assessed for significance simultaneously each year (Table 1); therefore, the Bonferroni correction (15) was used to obtain an overall significance level of $P = 0.008$ ($=\alpha/6$) for each test.

Disease progress curves. Disease progress curves were fitted based on disease data corrected for leaf abscission; that is, disease severity of a leaf that abscised midseason was carried along until the end of the season to calculate average disease severity at each subsequent assessment date. This correction was made because premature abscission of severely diseased leaves resulted in a drop in average disease severity toward the end of the season (Fig. 1).

Individual leaves were categorized into groups to fit disease progress curves for leaves with similar attributes. For leaf position, leaves were assigned to three categories depending on their location on the shoot, with position values (defined above) of 0 to 0.33, 0.34 to 0.66, and 0.67 to 1.0 assigned to lower, intermediate, and upper leaf position categories, respectively. Depending on the height of the shoot above the ground, three categories were constructed corresponding to distances from the ground to the base of the shoot of <70, 70 to 110, and >110 cm.

Separate disease progress curves were fitted for each category of leaf position,

shoot height, and leaf emergence date each year. A nonlinear logistic model of the form $y = K/[1 + \exp\{-r_L(t - m)\}]$ was fitted to the disease progress data using Genstat version 5.1 (20), where y = disease severity (number of spots per leaf), K = upper asymptote of the disease progress curve, r_L = logistic rate of disease increase, and m = parameter indicating the location of the inflection point of the curve in relation to time, t , in days. The appropriateness of the model in describing disease progress was assessed by correlation analysis of observed versus predicted y -values. The product $r_L K$, an overall measure of the absolute rate of disease increase (6), was calculated and used to compare disease progress among the different leaf categories.

Temporal infection windows. To determine empirically whether leaves become infected season-long or primarily during the period of leaf expansion when tissues are most susceptible (8), three potential infection windows were constructed for each leaf (Fig. 2): (i) a 2-week period centered on the date of full leaf expansion (referred to as ± 1 -week window henceforth), whereby the date of full leaf expansion is defined here as the assessment date when the leaf attained 95% of its final length; (ii) a 2-week period beginning at the date of full expansion; and (iii) the entire season from full leaf expansion to the last disease assessment. Cumulative spore numbers potentially available during the three windows were computed for each leaf based on its phenology of expansion in conjunction with the data obtained in the spore sampling study described above. For each year, correlation analyses were conducted in SAS to determine the association between final disease severity on individual leaves and cumulative spore numbers potentially available in each window.

Table 1. Pearson's correlation coefficients among Septoria leaf spot-related variables and leaf attributes on Premier rabbiteye blueberry

Year, variable 1 ^b	Variable 2 ^a		
	Final disease severity ^c	AUDPC	Shoot height ^d
2002			
AUDPC	0.802*	...	...
Shoot height	-0.315*	-0.344*	...
Leaf position	-0.170*	-0.184*	0.003
2003			
AUDPC	0.980*	...	...
Shoot height	-0.282*	-0.291*	...
Leaf position	-0.045	-0.004	0.012
2004			
AUDPC	0.986*	...	...
Shoot height	-0.210*	-0.185*	...
Leaf position	-0.162*	-0.173*	0.013

^a Asterisks indicate significant correlation coefficients at $P = 0.008$. Sample size (n) = 410, 542, and 416 in 2002, 2003, and 2004, respectively. Sample sizes were lower for shoot height ($n = 396, 531$, and 411 for the 3 years) due to loss of tags from some shoots before data on their height above the ground was recorded.

^b AUDPC = area under the disease progress curve (spot-days). Leaf position on the tagged shoot, where 0 = lowest (oldest) and 1 = highest (youngest) leaf.

^c Number of spots per leaf on the last disease assessment date.

^d Distance (cm) between the ground and the base of the tagged shoot segment.

Trap plants. Two- or three-year-old southern highbush blueberry plants of cultivar Star, which is highly susceptible to *Septoria* leaf spot (21), were used in a trap plant experiment to provide complemen-

tary data on the likelihood of infection in relation to leaf developmental stage. Plants were grown in a sheltered area on the Athens campus of the University of Georgia in 3.8-liter containers in a potting mix con-

taining sand and pine bark in a 1:3 vol/vol ratio. The potted plants continued to produce new leaves throughout the season and, shortly before exposure of the plants in the blueberry planting described above, nodes having leaves at three developmental stages were tagged. The stages were I = leaves recently emerged and not completely unfolded, II = young leaves completely unfolded but not waxy, and III = mature leaves with waxy cuticles. Trap plants were exposed to natural field inoculum on three to four occasions between April and September in 2003 and 2004, whereby each exposure period encompassed three to four plants with a total of 10 to 26 leaves per stage. Exposure was timed to coincide with predicted rainfall, and exposure periods ranged from 2 to 3 days with 11 to 50 mm of rain. Trap plants subsequently were removed from the field and placed in a greenhouse (approximately 25 and 18 ± 5°C average day and night temperature, respectively), where their foliage was kept dry. Each exposure period included one unexposed control plant transferred into the greenhouse at the time when the exposed plants were returned from the field. Symptom development was monitored on the tagged nodes for about 1 month after initial symptom appearance, and the incidence of infected leaves for each of the three developmental stages was determined for each exposure period.

RESULTS

Descriptive analyses. Significant correlations were observed among final disease severity, AUDPC, and leaf attributes (Table 1). In all 3 years, disease severity was negatively correlated with shoot height, indicating that leaves on shoots in the lower part of the canopy had higher levels of *Septoria* leaf spot. Disease severity also was negatively correlated with leaf position (i.e., lower leaves were more severely infected); however, this correlation was significant only in 2002 and 2004. AUDPC was highly correlated with disease severity; not surprisingly, therefore, correlations between AUDPC and leaf attributes were similar to those between disease severity and leaf attributes (Table 1).

Disease progress curves. Disease progress followed a logistic pattern in all 3 years, but the time of disease onset and final disease severity differed noticeably among years (Fig. 1). In 2002, symptoms first were observed at the end of April; this was followed by a rapid increase in disease severity up to late September, reaching a maximum of 60.6 spots per leaf on average (Fig. 1A). Thereafter, disease severity decreased toward the end of the disease assessment period due to abscission of severely infected leaves. In 2003 and 2004, disease onset occurred nearly 2 months later (Fig. 1B and C), reaching a maximum of 60.5 and 16.4 spots per leaf in 2003 and 2004, respectively. In the latter 2 years,

Fig. 1. Temporal progress of *Septoria* leaf spot on Premier rabbiteye blueberry in **A**, 2002, **B**, 2003, and **C**, 2004. Open circles (○) show disease progress as observed in the field, including a drop in disease severity toward the end of the season due to leaf abscission. Solid circles (●) show the same disease progress curves adjusted for defoliation (i.e., disease severity of a leaf that abscised midseason was carried along until the end of the season to calculate average disease severity at each subsequent assessment date). In 2003, the adjusted disease severity curve was below the actual disease severity curve due to midseason loss of leaves with very low or no disease as a result of non-disease-related factors. The arrows represent the time of peak fruit harvest.

disease severity increased rapidly between late July and late September compared with slower disease increase in 2002 during the same period. When disease progress curves were adjusted for defoliation, disease severity increased sigmoidally and reached an average maximum of 23.7 to 81.4 spots per leaf at the end of the season (Fig. 1).

The logistic model provided a good description of the adjusted disease progress curves within each class of leaf position

and shoot height (Table 2). In all years, $r_L K$ and K were consistently highest on leaves in the intermediate position on the shoot and for leaves on shoots located closest to the ground. $r_L K$ and K were lowest for leaves in the upper positions on a shoot in 2002 and 2004 and for leaves in lower position in 2003 (Table 2).

Inoculum dynamics. Pycnidiospores of *S. albopunctata* were present in splash and runoff from blueberry bushes in all 3 years throughout most of the period from April

through late October. However, relative spore numbers varied from year to year, being highest in 2003 and lowest in 2004 (Fig. 3). Further, no consistent seasonal pattern or trend in spore numbers was observed across the 3 years. Because funnel traps were used for spore monitoring, spore dispersal events were associated, by necessity, with precipitation events. However, only about half of all precipitation events resulted in the dissemination of spores across the 3 years, and there was no clear association between spore numbers and precipitation volume (Fig. 3).

Temporal infection windows. Final severity of Septoria leaf spot and cumulative numbers of *S. albopunctata* pycnidiospores within the three potential infection windows were positively associated, albeit with different levels of statistical significance (Table 3). Consistently across the 3 years, correlation coefficients were highest and statistically significant ($P \leq 0.05$) for the entire-season window. In 2003, the association involving cumulative spore numbers during the 2-week window after full leaf expansion also was statistically significant, but the level of significance was weaker and the correlation coefficient considerably smaller than that for the entire-season window.

Trap plants. Incidence of Septoria leaf spot on leaves of trap plants exposed to natural inoculum in the field was high, with values ranging from 70.0 to 100% (Table 4). Symptoms first appeared between 20 and 32 days after exposure and

Fig. 2. Schematic depiction of the temporal windows used to summarize the cumulative numbers of *Septoria albopunctata* pycnidiospores collected in funnel samplers based on relative times after full leaf expansion; leaves were considered fully expanded when they had attained 95% of their final length. The entire-season window refers to the cumulative spore numbers from the time of full leaf expansion until the end of the study period. Similarly, the 2-week window refers to spore numbers collected during the first 2 weeks after full leaf expansion. The ± 1 -week window represents spore numbers collected during the period from 7 days prior to 7 days after leaves were fully expanded.

Table 2. Results of nonlinear regression analysis of temporal progress of Septoria leaf spot on Premier rabbiteye blueberry obtained using the logistic model for different classes of leaf position and shoot height^a

Year, variable ^b	Rate (r_L)	SE for r_L	Upper asymptote (K)	SE for K	Absolute rate ($r_L K$)	r^c	Sample size (n)
2002							
Leaf position							
Lower	0.0374	0.0015	88.6	1.730	3.31	0.997	97
Intermediate	0.0415	0.0023	116.8	3.140	4.85	0.996	155
Upper	0.0515	0.0032	61.8	1.560	3.18	0.995	154
Shoot height							
<70 cm	0.0443	0.0019	137.7	2.570	6.10	0.996	89
70-110 cm	0.0407	0.0024	84.9	2.590	3.45	0.995	209
>110 cm	0.0361	0.0028	54.2	2.270	1.96	0.991	108
2003							
Leaf position							
Lower	0.0645	0.0029	39.6	0.485	2.55	0.994	146
Intermediate	0.0609	0.0017	81.5	0.667	4.96	0.997	197
Upper	0.0692	0.0027	51.2	0.519	3.54	0.996	199
Shoot height							
<70 cm	0.0598	0.0015	66.5	0.594	3.98	0.995	122
70-110 cm	0.0620	0.0022	55.0	0.560	3.41	0.993	305
>110 cm	0.0611	0.0027	48.3	0.463	2.95	0.991	115
2004							
Leaf position							
Lower	0.0900	0.0036	18.2	0.1640	1.64	0.995	125
Intermediate	0.0833	0.0013	44.8	0.1710	3.73	0.997	137
Upper	0.0671	0.0051	9.6	0.2170	0.64	0.995	154
Shoot height							
<70 cm	0.0807	0.0017	33.5	0.1740	2.70	0.992	139
70-110 cm	0.0818	0.0024	23.8	0.1700	1.95	0.997	133
>110 cm	0.0837	0.0041	14.1	0.1660	1.18	0.996	144

^a Leaf spot severity expressed as number of spots per leaf; SE = standard error.

^b Leaf position: leaves on shoot segments were assigned values between 0 and 1, with 0 to 0.33, 0.34 to 0.66, and 0.67 to 1.0 representing leaves in the lower, intermediate, and upper positions, respectively. Shoot height = distance between the ground and the base of the tagged shoot segment.

^c Linear correlation coefficient between observed and predicted disease severity values.

occurred on all leaves on the tagged nodes, irrespective of their developmental stage at the time of exposure. No symptoms were observed on control plants not exposed to inoculum in the field.

DISCUSSION

This report provides the first quantitative analysis of the temporal progress of *Septoria* leaf spot of blueberry and how leaf attributes such as position on the shoot

and location of shoots above the ground influence disease development. Disease severity increased logistically, suggesting a polycyclic epidemic. Leaves in intermediate positions on the shoot and leaves on

Fig. 3. A, B, and E, Numbers of pycnidiospores of *Septoria albobunctata* captured in funnel samplers and C, D, and F, daily precipitation at the experimental site in A and C, 2002, B and D, 2003, and E and F, 2004.

shoots in the lower part of the canopy were most severely infected. A drop in disease severity was observed toward the end of the season due to the abscission of severely diseased leaves (19). Splash-dispersed pycnidiospores were available throughout the season and, based on the analysis of potential infection windows combined with the results of the trap plant experiments, we conclude that leaves at all developmental stages can become infected by *S. albopunctata* season-long.

The earlier disease onset in 2002 (late April) compared with 2003 and 2004 (mid-June) may have been associated with warmer spring temperatures. For example, the monthly mean temperature for April was 18.1°C in 2002 but only 15.5°C in

2003 and 16.1°C in 2004. By contrast, the more rapid disease progression during 2003 likely was due to increased summer precipitation. The total amount of rain recorded between July and September was 482 mm in 2003 compared with 236 mm in 2002 and 130 mm in 2004. The low levels of disease observed in 2004 may have been due to low levels of disseminated inoculum. In addition, the 2004 season generally was dry, apart from four late peaks of rainfall associated with three hurricanes that struck the southeastern coast in the fall.

Relative to the effects of leaf position and shoot height above the ground on disease progression, the higher disease severity on leaves in intermediate positions on

the shoot compared with those in upper or lower position may have been due to the greater leaf area available for infection. Leaves in the former category typically were larger in size than those in the latter two groups (*data not shown*). Similarly, the higher disease severity in lower parts of the canopy could have been related to more favorable surface moisture retention and cooler temperatures due to this area's protection from direct sunlight, creating a microclimate more conducive for infection. *S. albopunctata* can overwinter in fallen leaves infected during the previous season (17); therefore, the proximity of the lower canopy to this inoculum source likely contributes further to the higher levels of disease severity observed in the lower canopy. Furthermore, studies in other *Septoria* pathosystems have documented the inhibition of spore germination in conditions of high light intensity (9,10,12); thus, it is possible that the lower disease levels observed in the upper canopy where radiation is greater may have been due to direct inhibition of *S. albopunctata*. In addition, upper leaves probably are not exposed to much of the secondary inoculum originating from leaf or stem lesions and carried downward by precipitation (11), similar to what has been documented for *Phomopsis amygdali* on peach (14) and *S. tritici* on wheat (16). Regardless of the mechanism, the higher disease levels on leaves in the lower canopy underscore the importance of adequate application of fungicides to lower parts of the bush.

The lack of a strong and significant association between final disease severity and cumulative spore numbers in the ± 1 -week and 2-week infection windows rela-

Table 3. Pearson's correlation coefficients between final *Septoria* leaf spot severity on leaves of Premier rabbiteye blueberry and the cumulative number of *Septoria albopunctata* pycnidiospores collected in funnel samplers during different potential infection windows^a

Temporal window ^b	Correlation coefficient (<i>r</i>)	Sample size (<i>n</i>)	<i>P</i> value
2002			
±1 week	0.22	43	0.1522
+2 weeks	0.29	43	0.0634
Entire season	0.36	43	0.0229
2003			
±1 week	0.06	301	0.3141
+2 weeks	0.19	509	0.0402
Entire season	0.31	509	0.0002
2004			
±1 week	0.09	181	0.1846
+2 weeks	0.11	243	0.0816
Entire season	0.21	243	0.0012

^a Leaf spot severity expressed as number of spots per leaf.

^b Relative to time of full leaf expansion; leaves were considered fully expanded when they had attained 95% of their final length. The entire-season window refers to the cumulative spore numbers from the time of full leaf expansion until the end of the study period. Similarly, the 2-week window refers to spores collected during the first 2 weeks after full leaf expansion. The ± 1 -week temporal window represents spores collected during the period from 7 days prior to 7 days after leaves were fully expanded.

Table 4. Incidence of *Septoria* leaf spot of blueberry on leaves of potted Star trap plants at different leaf developmental stages following exposure to natural inoculum of *Septoria albopunctata* in the field

Year, plant group	Date exposed	Date of first symptoms	Leaf stage ^a	Total no. of leaves ^b	No. of leaves infected	Disease incidence (%)
2003						
1	17 April	19 May	I	21	18	85.7
			II	24	22	91.6
			III	26	23	88.4
2	14 May	12 June	I	20	18	90.0
			II	24	24	100.0
			III	21	21	100.0
3	6 June	29 June	I	16	13	81.2
			II	18	17	94.4
			III	20	17	85.0
4	1 July	27 July	I	18	13	72.2
			II	19	16	84.2
			III	19	15	78.9
2004						
1	26 June	18 July	I	20	15	75.0
			II	23	17	73.9
			III	17	13	76.4
2	20 August	15 September	I	14	10	71.4
			II	12	9	75.0
			III	11	8	72.7
3	20 September	10 October	I	10	7	70.0
			II	11	8	72.7
			III	12	9	75.0

^a I = leaves recently emerged and not completely unfolded, II = young leaves completely unfolded but not waxy, and III = mature leaves with waxy cuticle.

^b Number of leaves on tagged nodes on three or four plants exposed on each date.

tive to the time of full leaf expansion suggests that infection by *S. albopunctata* is not restricted to young leaves in a relatively short period during leaf expansion. Instead, the consistent and significant association between disease severity and cumulative spore numbers in the entire-season window shows that leaves can become infected continuously throughout the season. This conclusion is supported by results of the trap plant experiments, in which leaves of all developmental stages became infected by *S. albopunctata* during all exposure periods. The sigmoidal shape of the disease progress curves observed in the field also suggests that multiple cycles of infection occur on leaves season-long.

Although inoculum of *S. albopunctata* was present season-long and infection was not restricted to young and emerging leaves, early-emerging leaves did develop higher disease severity levels. This could be due simply to the fact that these leaves were exposed to inoculum for a longer period and during more secondary cycles than later-emerging leaves. Our spore sampling data did not indicate the presence of large spore peaks early in the season, showing that later-emerging leaves did not simply escape inoculum exposure. Given a reported temperature optimum of 24 to 28°C for *S. albopunctata* (17) and the erratic distribution of rainfall during the season in our study, it also is unlikely that environmental conditions were consistently more favorable for infection on leaves that emerged early (when temperatures were considerably cooler than the reported optimum). Relative to disease management, the higher levels of Septoria leaf spot on early-emerging leaves indicate the need for implementing control tactics

prior to the rapid increase of the disease in the summer for these tactics to be effective; current recommendations for fungicidal control focus primarily on summer and fall applications after harvest of the crop (3–5).

ACKNOWLEDGMENTS

We thank H. Ngugi and A. Savelle for assistance with various aspects of this study.

LITERATURE CITED

1. Austin, M. E. 1994. Rabbit-eye Blueberries: Development, Production, and Marketing. Agscience, Auburndale, FL.
2. Bertrand, P. F., and English, H. 1976. Release and dispersal of conidia and ascospores of *Valsa leucostoma*. Phytopathology 66:987-991.
3. Brannen, P. M., Scherm, H., and Bruorton, M. D. 2001. Use of selected fungicides for control of Septoria leaf spot of blueberry, 2000. Fungic. Nematicide Tests 56:SMF1.
4. Brannen, P. M., Scherm, H., and Bruorton, M. D. 2002. Use of selected fungicides for control of Septoria leaf spot of blueberry, 2001. Fungic. Nematicide Tests 57:SMF46.
5. Brannen, P. M., Scherm, H., and Bruorton, M. D. 2003. Fungicidal control of Septoria leaf spot of blueberry, 2002. Fungic. Nematicide Tests 58:SMF019.
6. Campbell, C. L., and Madden, L. V. 1990. Introduction to Plant Disease Epidemiology. Wiley, New York.
7. Cline, W. O. 2002. Blueberry bud set and yield following the use of fungicides for leaf spot control in North Carolina. Acta Hort. 574:71-74.
8. Demaree, J. B., and Wilcox, M. S. 1947. Fungi pathogenic to blueberries in the eastern United States. Phytopathology 37:487-506.
9. Elmer, W. H., and Ferrandino, F. J. 1995. Influence of spore density, leaf age, temperature, and dew periods on Septoria leaf spot of tomato. Plant Dis. 79:287-290.
10. Ferrandino, F. J., and Elmer, W. H. 1996. Septoria leaf spot lesion density on trap plants exposed at varying distances from infected tomatoes. Plant Dis. 80:1059-1062.
11. Fitt, B. D. L., McCartney, H. A., and Walklate, P. J. 1989. The role of rain in dispersal of pathogen inoculum. Annu. Rev. Phytopathol. 27:241-270.
12. Hood, I. A., Chapman, S. J., Gardner, J. F., and Molony, K. 2002. Seasonal development of Septoria leaf blight in young *Eucalyptus nitens* plantations in New Zealand. Aust. For. 65:153-164.
13. Hoogenboom, G., and Gresham, D. D. 1997. Automated weather station network. Pages 483-486 in: Proc. Georgia Water Resources Conf. K. J. Hatcher, ed. Institute of Ecology, University of Georgia, Athens.
14. Lalancette, N., and Robison, D. M. 2001. Seasonal availability of inoculum for constriction canker of peach in New Jersey. Phytopathology 91:1109-1115.
15. Legendre, P., and Legendre, L. 1998. Numerical Ecology, 2nd ed. Elsevier, Amsterdam.
16. Lovell, D. J., Parker, S. R., Hunter, T., Welham, S. J., and Nichols, A. R. 2004. Position of inoculum in the canopy affects the risk of *Septoria tritici* blotch epidemics in winter wheat. Plant Pathol. 53:11-21.
17. Milholland, R. D. 1995. Septoria leaf spot and stem canker. Page 16 in: Compendium of Blueberry and Cranberry Diseases. F. L. Caruso and D. C. Ramsdell, eds. American Phytopathological Society, St. Paul, MN.
18. NeSmith, D. S., Krewer, G., and Williamson, J. G. 1998. A leaf bud developmental scale for rabbiteye blueberry (*Vaccinium ashei* Reade). HortScience 33:757.
19. Ojiambo, P. S., and Scherm, H. 2005. Survival analysis of time to abscission of blueberry leaves affected by Septoria leaf spot. Phytopathology 95:108-113.
20. Payne, R. D., Bird, D., Gilmour, A., Harding, S., Lane, P., Murray, D., Soutar D., Thompson, R., Todd, A., Wilson, G., Webster, R., and Welham, S. 2000. The Guide to Genstat Release 4.2. Lawes Agricultural Trust, Harpenden, England.
21. Scherm, H., Brannen, P. M., Ojiambo, P. S., Savelle, A. T., Krewer, G., and Bruorton, M. D. 2003. Blueberry leaf spots: Epidemiology, yield losses, and control. Pages 57-66 in: Proc. Southeast. Blueberry Conf. Savannah, GA.
22. Scherm, H., and Krewer, G. 2003. Blueberry production in Georgia: Historical overview and recent trends. Small Fruits Rev. 2:83-91.