A Bacterial Leaf Spot of Highbush Blueberry Hardwood Cuttings Caused by Pseudomonas andropogonis

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ABSTRACT

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A leaf spot has been observed for several years on nursery-grown blueberry cuttings throughout southern New Jersey. A bacterium that produced a white-pigmented colony on yeast extract-dextrose-calcium carbonate agar and was nonfluorescent on King's B agar was repeatedly isolated from lesions on diseased leaves collected from various locations. The bacterium was identified as Pseudomonas andropogonis using diagnostic tests, Biolog, and fatty acid analysis. Infiltration of bacterial suspensions at concentrations of 10⁶ and 10⁸ cells per ml into leaves of 3- to 5-year-old potted plants and 1-year-old hardwood cuttings resulted in the appearance of necrotic lesions similar to leaf spot symptoms observed on plants in the field. The bacterium was reisolated from the necrotic lesions produced by these inoculations. Inoculation of blueberry isolates into cranberry leaves also caused pathogenic responses. This is believed to be the first report of a bacterial leaf spot on Vaccinium species.

Blueberry (Vaccinium corymbosum L.) production in New Jersey spans two counties in the southern part of the state, and is valued at an average of 25 million dollars annually. Although a single plant may continue producing fruit for up to 50 years, individual plants are often replaced in the field on a yearly basis due to natural attrition. As a consequence, blueberry cultivation is a continuous process, and typically begins with the propagation of hardwood cuttings from mature plants. Cuttings are planted in early spring in raised beds and are irrigated by fixed spray or rotating input driven sprinklers (14). Cuttings remain in propagating beds for 1 year to establish good rooting, prior to transplanting into nursery locations for further sizing or directly to the field for production purposes. Hardy establishment of cuttings in propagation beds during the first year is critical to achieve successful transplantation in the field in subsequent years.

Sporadic occurrence of a leaf spot of rooted blueberry cuttings in propagation beds has been observed for several years throughout the blueberry-growing regions of southern New Jersey. In many cases, leaf spotting was observed to be most severe on cuttings planted nearest sprinkler

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heads. Disease has also been observed on occasion during the summer and fall after periods of heavy rainfall and hail storms. In severe cases, the disease was observed to affect growth of cuttings, contributing to poor establishment of plants during the first year of growth. This report describes the identification of the causal agent of the leaf spotting agent on blueberry cuttings as Pseudomonas andropogonis.

MATERIALS AND METHODS

Isolation and identification of bacterial pathogen. Leaves of blueberry hardwood cuttings grown in nurseries that displayed leaf spot symptoms were collected from various sites throughout the blueberry-growing region of Burlington and Atlantic counties in southern New Jersey. Leaves with disease symptoms were collected from several cultivars that included Berkeley, Bluecrop, Bluetta, Duke, Herbert, Northland, Spartan, and Weymouth. Bacterial streaming was detected by microscopic examination of lesions that had zones of water soaking around necrotic areas.

Isolations were conducted shortly after or within 24 h of collecting leaves. Diseased leaves were individually rinsed thoroughly in H2O and dried with paper towels before leaf tissue was excised at the margins of lesions. Excised material was ground with a glass rod in sterile distilled H₂O and streaked on yeast extract-dextrose-calcium carbonate agar (YDC) (22), King's B medium agar (KB) (10) and Miller Schroth medium agar (MS) (13). Predominant colony types appearing on YDC and KB after 2 to 3 days incubation at 28°C were re-streaked on YDC. Four isolates, recovered from different cultivars at different locations within two counties. were kept for further characterization. These included S94A10 (isolated from cv. Herbert in Chatsworth, N.J.), S94B2 (isolated from cv. Duke in Hammonton, N.J.), S94H1 (isolated from cv. Bluecrop in Hog Wallow, N.J.), and S94C1 (isolated from cv. Weymouth in Jenkins, N.J.).

Physiological and biochemical tests were performed essentially as described previously (12,15). Gram reactions were determined by the conventional staining method (15) and by using 3% potassium hydroxide (18). Ice nucleation was tested by adding drops of turbid bacterial suspensions to 10 ml of H₂O cooled between -5 and -10°C. Species identification tests included the use of the Biolog MicroStation System, GN data base release 3.50 (Hayward, Calif.), and fatty acid analysis, conducted by Microbial ID, Inc. (Newark, Del.). Characterized isolates were routinely maintained on YDC or KB agar, and stored at -80°C in liquid media supplemented with 10% dimethylsulfoxide.

Plants and pathogenicity tests. Inocula were prepared by streaking individual isolates on YDC and incubating plates at 28°C for 48 h. Cells were scraped from agar plates and suspended in sterile distilled H₂O to a final density of approximately 108 cfu per ml by adjusting the optical density of the suspension at A₅₉₅ to a value of 0.1. These suspensions were diluted to prepare other inocula concentrations of 10⁶ and 10⁴ cfu per ml.

Blueberry leaf inoculations were performed by two different methods. The first method involved spray inoculation using a hand-held aerosol sprayer. Prior to inoculation, whole plants or stems of plants were covered with plastic bags for 60 min to enhance stomatal opening on leaves. The second method involved pressure infiltration of the underside of leaves using a 1-ml syringe, similar to the principle described by Hagborg (8).

Blueberry plants used for pathogenicity tests included 3- to 5-year-old potted blueberry plants of cvs. Duke, Bluetta, Berkeley, and Bluecrop, and first-year cuttings of cv. Herbert. Potted plants and rooted cuttings were grown in a 1:1 mixture, vol/ vol, of coarse sand and peat moss. Cranberry (Vaccinium macrocarpon Aiton) plants (cv. Early Black) were grown similarly to blueberries. Soybean (cv. Merit), sweet corn (cv. Golden Cross Bantam), and bush bean (cv. Blue Lake 290) were grown in 4-inch pots using Promix (Red Hill, Pa.) as a soil medium. Most plants were grown on greenhouse benches maintained at 18 to 20°C for pathogenicity studies. Cranberry and blueberry plants were maintained in growth chambers under 14 h per day of 500 µE fluorescent light at 30°C and 70% humidity during pathogenicity studies. For all plant inoculations, Pseudomonas syringae pv. tomato PT23 (D. Cooksey, 2) and P. syringae pv. tabaci ATCC 11528 were used as pathogenic, avirulent controls for comparisons with P. andropogonis.

A minimum of three plants were used for each isolate for all inoculation studies. Plants were scored on a daily basis for the appearance of symptoms. Mean values for time of symptom appearance on *Vaccinium* spp. inoculated with *P. andropogonis* isolates at 10⁸ cfu per ml were compared by analysis of variance, and separated using Duncan's multiple range test using the Microstat-III statistical software system (Ecosoft, Inc., Indianapolis, Ind.).

RESULTS

Field symptoms. Leaf spot symptoms on rooted hardwood cuttings of blueberry grown in propagation beds were observed as irregularly shaped, reddish brown necrotic lesions. In severe cases, lesions coalesced and covered much of the leaf surface. Older lesions often appeared as dry, brittle, necrotic areas. In many cases, older lesions had a shot hole appearance. Zones of water soaking were often observed in younger lesions. Disease symptoms were observed on several different cultivars of blueberry, including Berkeley,

Bluecrop, Bluetta, Duke, Herbert, Northland, Spartan, and Weymouth. Diseased plants were observed at various grower locations throughout the blueberrygrowing region in Burlington and Atlantic counties in southern New Jersey. Symptoms were also observed on young leaves of potted blueberries grown in the open at The Blueberry and Cranberry Research Center of Rutgers University (Jenkins, N.J.).

In all cases where leaf spot symptoms were observed, plants had been irrigated by overhead watering using fixed spray or rotating sprinkler systems. Often, incidence of leaf spot was greater on plants in close proximity to sprinkler heads positioned around propagation beds. Exceptions to these observations involved blueberry cvs. Herbert, Berkeley, and Bluetta, in which leaf spotting was severe on all plants regardless of the position of individual plants in propagation beds (data not presented).

Bacterial isolation and identification. A slow-growing, gram-negative, rod-shaped bacterium, which produced a white-pigmented colony on YDC after 48 to 72 h incubation at 30°C, was repeatedly recovered from diseased tissue. The bacterium was nonfluorescent on KB agar, and was unable to grow on MS agar.

Four isolates, chosen for further characterization based on the geographical locations where they were recovered, did not differ in their reactions to basic biochemical and physiological tests used as presumptive identification for *P. andropogonis* (Table 1). A hypersensitive reaction (HR) on tobacco, often used as a diagnostic feature for certain plant pathogenic bacteria (15), was not observed within 24 h after tobacco leaves were infiltrated with 10^8 cfu per ml. However, a weak, bleached necrosis appeared in the infiltrated area 3

to 5 days later. Ice nucleation activity was not detected in any of the four isolates.

Strains S94A10, S94B2, S94H1 and S94C1 were tested using Biolog GN Microplates. A search within the Microlog GN database (release 3.50) resulted in similarity index values greater than 0.9 for species identification as *P. andropogonis* for all four strains (Table 1). Species identification was confirmed by fatty acid analysis (Table 1).

Pathogenicity tests. The four selected *P. andropogonis* blueberry isolates were individually inoculated onto blueberry plants for pathogenicity tests. Isolates were infiltrated at concentrations of 10⁸ cfu per ml into newly emerged leaves (1 week old) of 3- to 5-year-old potted plants of blueberry cvs. Berkeley, Bluecrop, Bluetta, and Duke. No plant reaction was observed within 24 h after leaf infiltration with bacteria. However, a reddish brown lesion similar to that observed on propagated hardwood cuttings appeared in the area of leaf infiltration of all isolates on all cultivars after 2 to 3 days (data not shown).

Since all isolates appeared similar in their pathogenic ability based on symptom production on leaves of potted plants, isolate S94A10 was selected for spray inoculation studies on blueberry. Both mature (1- to 3-month-old) leaves and newly emerged leaves were inoculated by the spray method. However, no symptoms appeared up to 14 days after inoculation of leaves with 10⁸ cfu per ml on either potted plants of Berkeley or cuttings of Herbert.

Lack of symptom production from spray inoculations may have been due to unfavorable conditions for infection, such as the lack of a moisture period following inoculation. Due to the failure to obtain symptoms by spray inoculations, pathogenicity tests were performed by infiltrating leaves with a series of diluted inoculum concentrations consisting of 108, 106, and 104 cfu per ml of bacteria. Plants of two different stages of growth were chosen for inoculation. These included 3- to 5year-old potted plants of Berkeley, and first-year rooted cuttings of Herbert. The leaves of 3- to 5-year-old potted plants chosen for inoculation included mature, hardened leaves. Leaves of rooted cuttings of cv. Herbert selected for inoculation included newly emerged, young leaves. A differential response based on the time that necrotic lesions appeared was observed between both the age of plants and the age of leaves that were inoculated (Table 2).

A reddish brown lesion similar to that observed for leaf spotting on nursery plants appeared within 2 days after infiltration of 10⁸ cfu per ml of bacteria in newly emerged leaves of hardwood cuttings. Necrotic lesions also appeared when *P. andropogonis* was inoculated at lower cell concentrations. In these cases, however, symptom appearance took longer and was inconsistent among isolates (data not

Table 1. Biochemical and physiological characteristics of bacterial isolates recovered from blueberry leaf spots

Characteristic	Isolate						
	Pseudomonas andropogonis ^w	S94A10	S94B1	S94H1	S94C1		
Gram stain reaction	_	-	_	_	_		
Arginine dihydrolase	_	-	_	_	_		
Oxidative (glucose)	+	+	+	+	+		
Fermentative (glucose)	_		_	_	_		
Nitrate reductase	_	_		_	_		
Motility	+	+	+	+	+		
Catalase	+	+	+	+	+		
Oxidase	_			_	_		
Poly-β-hydroxybutyrate accumulation	+	+	+	+	+		
Tobacco hypersensitive response		_x	_	_	_		
Ice nucleation activity		_	_	_	_		
Biolog similarity value ^y		0.998	0.998	0.931	0.921		
Fatty acid similarity value ^z		0.841	0.921	0.511	0.596		

^{*}Characteristics for presumptive diagnosis of P. andropogonis, according to Lelliott and Stead (12).

x Weak necrosis appeared 3 to 5 days after infiltrating 108 cells per ml into leaves of tobacco.

y Values reflect results from searching the ML2 database (release 3.50, Microlog, Inc.), where >0.7 similarity indicates species identification.

² Values reflect results from searching the MIDI Microbial Identification System database (MIDI, Newark, Del.), where >0.5 indicate species identification.

shown). Symptom production was also observed in leaves of 3- to 5-year-old potted plants infiltrated with high inoculum concentrations; however, symptom appearance on these plants was consistently delayed compared with that on hardwood cuttings. Symptom production at lower inoculum concentrations on mature leaves of potted plants was only observed in one case (data not shown). In all cases, P. andropogonis was consistently recovered from lesions that appeared upon inoculation on blueberry cuttings, even after extended incubation periods of greater than 1 month.

The necrotic lesions produced by infiltration of P. andropogonis into leaves were similar to leaf spot symptoms observed in the field; however, it was unclear if the necrosis was due to a pathogenic response or the result of the host defensive HR that is observed when high concentrations of plant pathogenic bacteria (>10⁶ cfu per ml) are infiltrated into tobacco or other nonhost plants (11). Therefore, isolates of P. syringae pv. tomato and pv. tabaci, pathogens of tomato and tobacco, respectively, were infiltrated into blueberry leaves and host responses were compared with those produced by P. andropogonis isolates. A differential response was observed between mature leaves of potted blueberries and leaves of propagated cuttings. No lesion formation or necrosis indicative of an HR was observed when leaves of 3- to 5year-old blueberry plants were infiltrated with 10⁸ cfu per ml of either *P. syringae* pathovar into leaves (Table 2). In contrast, a weak necrotic lesion was observed within 24 h that became more pronounced over time after infiltration of 108 cfu per ml into the newly emerged leaves of hardwood cuttings. No necrosis or other symptom was observed up to 14 days after leaves were infiltrated with the lower cell concentrations of 10⁶ and 10⁴ cfu per ml of either P. syringae pathovar (data not shown).

To examine the host range of the P. andropogonis blueberry isolates, leaves of various plant species that included cranberry and previously reported hosts for P. andropogonis were infiltrated with each of the four isolates at concentrations of 10⁸, 10⁶, and 10⁴ cfu per ml. Newly emerged, yellow leaves (approximately 1 week old) and mature, hardened, dark green leaves (approximately 1 month old) of cranberry were chosen for inoculation. No response at any inoculum concentration was observed 24 h after inoculation; however, reddish brown lesions appeared on leaves approximately 2 days after inoculation with the highest concentration of cells (10⁸ cfu per ml) for all four isolates on juvenile leaves and after 3 days on mature leaves (Table 2). Lesions also appeared on leaves infiltrated with 106 cfu per ml within 1 week after inoculation. Similar to responses on mature leaves of potted blueberry plants, the result of infiltration of P. syringae pathovars into cranberry leaves

was no necrosis that resembled an HR or any other response in leaf tissue at any inoculum concentration for up to 14 days after inoculation (Table 2).

Infiltration of P. andropogonis isolates at 108 cfu per ml into the leaves of bush bean and soybean resulted in the appearance of faint necrotic lesions, similar to HR necrosis, within 24 h. Although these necrotic lesions became more pronounced with time, no symptoms appeared within 14 days incubation at the lower inoculum concentrations of 10⁶ and 10⁴ cfu per ml (Table 2). Due to the rapid appearance of necrosis and lack of symptom production at lower inoculum concentrations, reactions on bush bean and soybean were regarded as nonhost HR necrosis.

In contrast to bush bean and soybean, a differential pathogenic response between the four isolates were observed when leaves of sweet corn were infiltrated with bacterial inocula. The appearance of necrotic, water-soaked leaf streaking was observed for S94A10 and S94B2 48 h after inoculation of the highest cell concentration of 108 cfu per ml (Table 2). After 1 week of incubation, similar symptoms were observed on leaves infiltrated with the lower cell concentrations of 106 and 10⁴ cfu per ml of both isolates (data not shown). In contrast, inoculum of the highest cell concentration of 108 cfu per ml of isolates S94C1 and S94H1 produced necrotic lesions but not water-soaked symptoms in the area where leaves were infiltrated. With the exception of one leaf inoculated with 10⁶ cfu per ml of S94C1, which showed a necrotic lesion appearing after 5 days, no reactions were observed in leaves infiltrated with lower cell concentrations of either isolate S94C1 or S94H1.

DISCUSSION

Few bacterial diseases have been reported on species of Vaccinium. A stem canker caused by Pseudomonas syringae was reported on blueberry in 1953 (16,20). Gall formations on blueberry, caused by Agrobacterium tumefaciens (5) and a Nocardia sp. (6), have also been reported. Frost damage, which has been problematic on leaves and blossoms of blueberry in New Jersey (A. W. Stretch, unpublished observations), may possibly be due to ice nucleating bacteria. However, identification of the presence of ice nucleating bacteria on blueberry has not been confirmed. In this study, P. andropogonis was consistently isolated and identified from leaf spots occurring on propagated hardwood cuttings of blueberry. Inoculations of these blueberry isolates into blueberry and cranberry leaves resulted in the formation of necrotic lesions. The same bacterium could be isolated from these lesions, fulfilling Koch's postulates. Based on the inoculum concentrations that induced lesion formation and the time required for lesion development, these responses were not regarded as nonhost HR necrosis. Therefore, we regard the reaction of P. andropogonis on blueberry and cranberry as a pathogenic response, and believe this to be the first report of a bacterium causing leaf spot on *Vaccinium* spp.

Leaf spot symptoms were found throughout the blueberry-growing region of southern New Jersey. At each site where leaf spot was observed, hardwood cuttings originated from mother plants grown at the same location; however, leaf spot symptoms were not observed on mother plants. Significant differences between isolates determined by Biolog similarity values and fatty acid analysis provide further supporting evidence that isolates obtained from different sites differ at the biochemical and physiological levels. Furthermore, differential pathogenic responses on sweet corn indicate that two of the four isolates characterized in this study differed at the

Table 2. Number of days for a response to appear in leaves of various plants inoculated with Pseudomonas andropogonis blueberry isolates and P. syringae pathovars²

	Pseudomonas andropogonis				Pseudomonas syringae pv.	
	S94A10	S94C10	S94H1	S94B1	tabaci	tomato
Vaccinium spp.						
Blueberry						
Young leaves on 1-year-old hard- wood cutting	1.3 b	2.3 ab	2 b	1.7 b	1	1
Mature leaves on 3- to 5-year-old potted plant	3.7 a	3.7 a	3.7 a	3.3 a	NS	NS
Cranberry						
Young leaves	2 a	2.3 ab	2 a	2.7 abc	NS	NS
Mature leaves	3.3 bcd	3.7 cd	3.3 bcd	4 d	NS	NS
Other hosts						
Bush bean	1	1	1	1	NT	NT
Soybean	1	1	1	1	NT	NT
Sweet corn	1 (ws)	1 (nc)	1 (nc)	1 (ws)	NT	NT

² Plant leaves were infiltrated with 10⁸ cells per ml, and were scored for the appearance of symptoms over a 14-day period. NS = no symptoms; NT = not tested; (ws) = water soaking; (nc) = necrotic lesion. Each value reflects the mean of three inoculations. Similar letters following values for Vaccinium spp. indicate no significant difference according to Duncan's multiple range test (P = 0.05).

pathogenic host range level. Based on the observed differences between isolates characterized in this study, it is unlikely that yearly infections originate from a single pathogen source; this may suggest that the bacterium is endemic to the region.

To date, disease has been observed only on leaves of propagated hardwood cuttings and juvenile leaves of potted plants grown in nurseries. It is possible that cultural practices contribute to environmental differences that lead to disease in nurserygrown plants. The apparent lack of disease observed on plants grown in the field may also be due in part to the physiological state of leaves at different stages of maturity. In pathogenicity studies, hardened mature leaves on potted plants were not completely resistant to symptom production by the pathogen when mechanically infiltrated with high densities of the pathogen. However, symptom appearance in these older leaves was significantly delayed compared with younger leaves infiltrated with the same concentration of bacteria. In most cases only the highest cell concentrations of the pathogen led to symptom production in mature leaves. At lower cell concentrations, growth of the pathogen in leaves was apparently unable to increase to population levels that resulted in visual symptoms.

At all sites where disease was observed, no cultivar appeared to be completely devoid of leaf spot symptoms. However, differences in intensity of leaf spot symptoms were observed between various cultivars in at least two different locations (A. W. Stretch, D. Y. Kobayashi, and P. V. Oudemans, unpublished observations). In these cases, some cultivars, such as Berkeley, Herbert and Bluetta, appeared to be more susceptible than others to disease.

Irrigation practices appear to be a major contributing factor to disease incidence. In all cases where disease was observed, overhead sprinklers were used for irrigation, and disease appeared to increase and intensify in individual plants around sprinkler heads (D. Y. Kobayashi, A. W. Stretch, and P. V. Oudemans, unpublished observations). Force infiltration, such as by wind-driven rain, is thought to enhance bacterial infections (17). and may be a significant factor in infection of blueberry by P. andropogonis.

Pseudomonas andropogonis has been reported as a leaf spotting pathogen of several host species, including maize and sorghum (19,21), statice (1), clover (3,7, 9), red kidney bean (3), velvet bean (3,23), Bougainvillea (12), and chickpeas (4). Symptoms are characterized as a reddish brown leaf streak on maize and sorghum, and as reddish brown, irregularly shaped leaf spots on other hosts. As a species, P. andropogonis appears to have a broad host range with the ability to infect plant species belonging to several different families. However, individual isolates of P. andropogonis have been reported to have limited host ranges (3,4). The blueberry isolates characterized in this study were pathogenic on both blueberry and cranberry, thus extending the host range for this bacterial species to include Vaccinium spp. However, differential responses on sweet corn indicate that host ranges between individual isolates differ, and that blueberry isolates are not limited to *Vaccinium* spp.

In cases in which leaf spot of blueberry hardwood cuttings reaches high severity levels, the disease can contribute to reduced vigor of the plant, which in turn leads to poor establishment and development of cuttings during the first year of growth. Furthermore, it is apparent that, under the appropriate conditions, this disease could be problematic with blueberries propagated by other methods. With the identification of the causal agent as P. andropogonis, management practices, including chemical control, can now be investigated to reduce incidence of the disease in nursery propagation beds.

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