Accepted for publication 17 May 2007. Published 17 September 2007.

Genetic Diversity of Lettuce for Resistance to Bacterial Leaf Spot Caused by *Xanthomonas campestris* pv. *vitians*

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Bull, C. T., Goldman, P. H., Hayes, R., Madden, L. V., Koike, S. T., and Ryder, E. 2007. Genetic diversity of lettuce for resistance to bacterial leaf spot caused by *Xanthomonas campestris* pv. *vitians*. Online. Plant Health Progress doi:10.1094/PHP-2007-0917-02-RS.

Abstract

Lettuce plants were artificially inoculated with three isolates of *Xanthomonas campestris* pv. *vitians* in field and greenhouse evaluations for genetic variation in resistance to bacterial leaf spot. The cultivar Little Gem had the least amount of disease, whether evaluated for disease severity or disease incidence. Disease severity levels for cultivar Batavia Reine des Glaces were not significantly different from those of Little Gem. Several cultivars including Vista Verde, Pybas 251, Pacific, Clemente, Salinas 88, and Sniper were highly susceptible. There was a strong correlation between results obtained in the greenhouse and those obtained in the field (r = 0.77, P = 0.009) indicating that greenhouse assays may be used to increase the number of cultivars evaluated and to speed breeding efforts.

Introduction

Bacterial leaf spot of lettuce, caused by *Xanthomonas campestris* pv. *vitians*, is an important disease of lettuce in California (2,3). The disease is sporadic but problematic throughout North America (4,7,8,10). The pathogen causes small angular leaf spots which are initially water-soaked and later become necrotic (brown to black) and papery. The leaf spots coalesce forming large necrotic regions [on rating system, see Fig. 1 in (3)]. The symptoms reduce the quality and yield of the lettuce and increase the potential for postharvest losses (4).

Chemical applications, including those suitable for certified organic production, may reduce bacterial leaf spot and fit into a comprehensive management strategy (3,4,6,8). However, the effectiveness of the chemicals depends on their application prior to symptom development. Occurrence of the disease is sporadic and unpredictable, and in most seasons these preemptive applications would be unnecessary. Therefore, host resistance remains one of the most efficient and desirable tools for the management of bacterial leaf spot of lettuce.

Bacterial leaf spot has been observed in field plantings on all major market types of lettuce including leaf, crisphead, butterhead, and romaine (4,7,10). Of these, relatively resistant crisphead, and green and red leaf cultivars adapted to Eastern North America have been identified from field (4) and greenhouse experiments (7,8).

The goal of this research was to identify resistant germplasm from lettuce cultivars useful in the coastal California production system, and as parents to breed new bacterial leaf spot resistant cultivars. Field and greenhouse assays were developed and compared in order to determine whether greenhouse assays could be productively used for cost efficient screening of resistant germplasm.

Field Evaluations for Resistance to Bacterial Leaf Spot Among Lettuce Cultivars

Seven field experiments were established at two locations during the spring or fall between 2002 and 2006, using previously described methods (3). Lettuce was direct seeded in two rows per 102 cm (40-inch) bed in either early April or late August and thinned three to four weeks later to 30 cm between plants. Treatment replicates were distributed among field plots that were 7.6 m long and one bed wide, with approximately 30 plants per plot and a minimum of a 0.6 m gap between plots.

A mixture of three *Xanthomonas campestris* pv. *vitians* strains Xav 98-12, BS339, and BS347 was used in all experiments. All three strains were originally isolated from diseased lettuce plants in the Salinas Valley, CA (1,3). Bacteria were stored at -80°C in a 50:50 solution of glycerol and nutrient broth until needed. For all experiments, the strains were grown in individual flasks of nutrient broth on a shaker at 200 rpm for 48 h. Cultures were centrifuged (7000 rpm for 10 min) to pellets and pellets were re-suspended in sterile distilled H_2O, and centrifuged again. The resultant bacterial pellets of each strain were adjusted spectrophotometrically to approximately 1×10^8 cfu/ml and then combined in equal parts. Bacterial concentrations were confirmed by dilution plating. Approximately 1 ml of inoculum was applied to each plant using a CO_2 pressurized handheld sprayer (Model D, R & D Sprayers, Opelousas, LA) at thinning and again 2 weeks later. To enhance disease development, 5 min of overhead irrigation was applied immediately prior to bacterial inoculations. All lettuce plantings were grown according to standard commercial practices. Overhead irrigation was used for the duration of the trial.

Two sets of cultivars were tested. The first set included 11 cultivars (Batavia Blonde de Paris, Batavia Reine des Glaces, Batavia Rossia, Holborn Standard, Iceberg, Little Gem, Prizehead, Pybas 251, Salad Bowl, Salad Crisp, and Vista Verde) evaluated in five experiments from 2002 until 2004. The second set included five additional cultivars (Grand Rapids, Red Line, Salinas 88, Sniper, and Waldmann's Green) that were compared to cultivars of interest from the first set (Batavia Reine des Glaces, Holborn Standard, Iceberg, Little Gem, Salad Crisp, and Vista Verde) in one experiment each in 2005 and 2006. Pacific and Clemente were evaluated in only one replicated field trial along with cultivars of the second set. Experiments had at least three replicates of each cultivar tested. Plants were rated for disease incidence and severity one week before harvest. Disease incidence was determined by calculating the proportion of diseased plants in each treatment replicate. Disease severity was evaluated on a per-plant basis. A rating of 0 was given for plants with no visible symptoms; 1 for plants with a few individual lesions; 2 for plants with many individual lesions; 3 for plants with small patches of coalesced lesions; 4 for plants with medium sized patches of coalesced lesions; and 5 for plants with large patches of coalesced lesions (3). Per-plant disease severity values were then averaged across all plants within each treatment replicate. Data were analyzed nonparametrically and relative treatment effects and their confidence intervals were calculated using Proc Mixed of SAS (SAS Institute Inc., Cary, NC) and macros (9). Relative treatment effects are nonparametric statistics (ranging from 0 to 1) that are used to compare the distribution of observations (and not just the central values of distributions, such as means) for different groups (9), and are valid for continuous, binary, and ordinal data (such as the severity ratings in our study). Additionally the Spearman's rank correlation was used to compare field and greenhouse results.

To ensure that we could distinguish symptoms caused by *X. campestris* pv. *vitians* from other spots on the various lettuce cultivars, we isolated and identified bacteria from at least one lesion in each plot in the early experiments. Leaf tissue (approximately 3 × 3 mm square) was excised and surface disinfested with bleach (0.5 % sodium hypochlorite) for 1 min followed by rinsing in sterile distilled water three times. The tissue was macerated in a drop of sterile, distilled water and spread onto maltose methyl green antibiotic medium (MMG) (11). Plates were incubated at 27°C for at least four days prior to counting colonies. Yellow-green colonies that formed a yellow halo in the media were tentatively identified as *X. campestris* pv. *vitians*. The identity of an individual from each plate was further verified using the polymerase chain reaction of repetitive bacterial sequences (rep-PCR) with the BOXA1R primer (5'-CTA-CGG-CAA-GGC-GAC-GCT-GAC-G-3'), using previously published methods (5). Fingerprints generated from different lesion isolates were consistently identical to fingerprints from strains of *X. campestris* pv. *vitians*.

Cultivars Vista Verde and Pybas 251 consistently had the highest disease severity ratings and 100 % disease incidence in the experiments in which they were tested (Tables 1 and 2). In the five experiments in which they were compared, disease severity levels for Vista Verde and Pybas 251 did not differ from each other (Table 1). Pacific, Clemente, Salinas 88, and Sniper were highly susceptible to bacterial leaf spot. Disease incidence for these cultivars did not differ from Vista Verde ($P = 0.05$) (Table 2). Additionally, disease severity did not differ from Vista Verde for Pacific and Clemente in both experiments in which they were tested and for Sniper in one out of two experiments (*data not shown*).

The cultivar Little Gem was the most resistant cultivar evaluated (Tables 1 and 2). The disease incidence and severity ratings for Little Gem were significantly ($P = 0.05$) lower than all other cultivars in four of seven experiments (*data not shown*). In those experiments in which Little Gem did not have the numerically lowest levels of disease, disease levels were not significantly different from the cultivars (Batavia Reine des Glaces and Prizehead) with the lowest numeric levels (*data not shown*). When data from experiments were pooled, Little Gem had disease incidence significantly lower than all other cultivars and had disease severity significantly lower than the levels for all cultivars except Batavia Reine des Glaces (Tables 1 and 2). The relative susceptibility of the other cultivars that were tested varied somewhat among experiments, but all consistently ranked between the most susceptible (Vista Verde and Pybas 251) and the least susceptible cultivars (Little Gem and Batavia Reine des Glace).

Waldmann's Green and Grand Rapids were the least susceptible of the nine cultivars evaluated in field trials in Canada (4). In field trials in California, Waldmann's Green and Grand Rapids were significantly more susceptible than four cultivars (Little Gem, Batavia Reine des Glace, Iceberg, and Holborn Standard) based on disease incidence and severity levels (Table 2). These more resistant cultivars were not tested in the experiments conducted in Canada.

Table 1. Severity and incidence of bacterial leaf spot on field grown lettuce cultivars[v].

Cultivar	Market type	Disease severity[w]				Disease incidence[x]
		Median disease severity	RTE[y]	95% CI[z]		
				Lower limit	Upper limit	
Vista Verde	Crisphead (iceberg)	3.74	0.890 a	0.849	0.915	100 a
Pybas 251	Crisphead (iceberg)	3.62	0.871 a	0.811	0.907	100 a
Batavia Rossia	Crisphead (Batavia)	2.41	0.566 b	0.417	0.700	85 b
Holborn Standard	Crisphead (Batavia)	1.48	0.477 bc	0.382	0.573	73 bc
Batavia Blonde de Paris	Crisphead (Batavia)	1.54	0.474 abcde	0.376	0.572	82 b
Salad Crisp	Crisphead (iceberg)	1.57	0.460 bcde	0.332	0.594	78 b
Iceberg	Crisphead (Batavia)	1.57	0.453 b	0.349	0.561	77 b
Salad Bowl	Green leaf	1.28	0.378 cd	0.279	0.491	73 bc
Prizehead	Red leaf	1.47	0.363 cd	0.260	0.483	55 cd
Batavia Reine des Glaces	Crisphead (Batavia)	1.06	0.302 de	0.208	0.423	56 cd
Little Gem	Latin	1.00	0.266 e	0.186	0.372	44 d

[v] Data presented are pooled from five field experiments in which each cultivar was replicated three times.

[w] Disease severity was evaluated (1 = a few individual lesions; 2 = many individual lesions; 3 = small patches of coalesced lesions; 4 = medium sized patches of coalesced lesions; and 5 = large patches of coalesced lesions), then per-plant disease severity values were averaged across all plants within each treatment replicate.

[x] Statistical analysis done on arcsine transformed values but untransformed data are presented. Mean incidences followed by the same letter are not significantly different at $P = 0.05$ according to the LSDs for the mixed model.

[y] Relative Treatment Effect for disease severity. Values followed by the same letter are not significantly different at $P = 0.05$ according to the LSDs for the mixed model.

[z] 95% confidence interval for the relative treatment effect.

Table 2. Severity and incidence of bacterial leaf spot on additional field grown lettuce cultivars.

Cultivar	Market type	n[v]	Disease severity[u]					Disease incidence[y]
			Median disease severity by trial		RTE[w]	95% CI[x]		
			1	2		Lower limit	Upper limit	
Vista Verde	Crisphead (iceberg)	10	3.81	4.81	0.898 a	0.833	0.927	100 a
Pacific	Crisphead (iceberg)	3[z]	NT	4.4	0.899 ab	0.824	0.941	100 a
Clemente	Romaine	3[z]	NT	4.05	0.810 abcd	0.658	0.901	100 a
Sniper	Crisphead (iceberg)	6	3.47	4.26	0.762 bc	0.662	0.837	100 a
Salinas88	Crisphead (iceberg)	6	2.94	4.31	0.755 bc	0.647	0.835	100 a
Wald-mann's Green	Green leaf	9	2.74	3.95	0.640 cde	0.561	0.711	100 a
Grand Rapids	Green leaf	6	2.10	3.07	0.544 de	0.471	0.616	100 a
Salad Crisp	Crisphead (iceberg)	10	1.28	2.92	0.511 d	0.404	0.616	99 a
Red Line	Red leaf	6	1.87	1.76	0.442 f	0.395	0.491	99 a
Holborn Standard	Crisphead (Batavia)	11	0.89	1.29	0.249 g	0.200	0.310	70 b
Iceberg	Crisphead (Batavia)	9	1.09	1.17	0.241 g	0.180	0.320	69 bc
Batavia Reine des Glaces	Crisphead (Batavia)	6	0.43	1.33	0.185 gh	0.103	0.331	59 c
Little Gem	Latin	9	0.25	1.04	0.109 h	0.076	0.174	46 d

[u] Disease severity was evaluated (1 = a few individual lesions; 2 = many individual lesions; 3 = small patches of coalesced lesions; 4 = medium sized patches of coalesced lesions; and 5 = large patches of coalesced lesions), then per-plant disease severity values were averaged across all plants within each treatment replicate.

[v] Total number of replicates in two experiments.

[w] Relative Treatment Effect for disease severity. Values followed by the same letter are not significantly different at $P = 0.05$ according to the LSDs for the mixed model.

[x] 95% confidence interval for the relative treatment effect.

[y] Statistical analysis done on arcsine transformed values but untransformed data are presented. Mean incidences followed by the same letter are not significantly different at $P = 0.05$ according to the LSDs for the mixed model.

[z] These cultivars were only tested in one of these two experiments.

Greenhouse Evaluation of Resistance of Lettuce Cultivars to Bacterial Leaf Spot

Eleven cultivars of lettuce (Batavia Reine de Glace, Grand Rapids, Holborn Standard, Iceberg, Little Gem, Pybas 251, Red Line, Salad Crisp, Sniper, Vista Verde, and Waldmann's Green) were planted in 2 × 2 cm square cells in potting mix (SuperSoil, Rod Mclellan Co., San Mateo, CA) in 11 by 15 cell flats. For each replication a row of 9 cells was planted to a single cultivar and lettuce was planted around the borders of each flat to insure uniform microclimatic conditions. Flats were incubated at 10°C for 2 days in the dark followed by incubation at 20°C at 16:8 L:D until 50% of the cells had germinated seedlings. The plants were acclimated to the greenhouse for one week prior to inoculation with *X. campestris* pv. *vitians*. Inoculum was prepared as described for field experiments and was adjusted to approximately 1×10^9 CFU/ml prior to combining individual strains. The inoculum was sprayed onto the leaves of three-week-old plants until run-off, with each plant receiving approximately 1 ml, using a hand held spray bottle. Plants were incubated in the greenhouse on a misting table for a total of 21 days. The top three leaves of each plant were evaluated for disease severity and incidence 7, 14, and 21 days after the initial inoculation and were inoculated again at 7 and 14 days. A rating of 0 was given for plants with no disease; 1 for plants with few lesions of < 3 mm; 2 for plants with lesions > 3 mm; and 3 for plants with coalesced lesions. Experiments were designed and analyzed as randomized complete blocks with 6 replications per treatment. Data and analyses from two of three experiments are shown, because not all cultivars were used in the preliminary experiment. Area under the disease progress curve (AUDPC) of disease severity ratings were analyzed nonparametrically as described above.

As in the field experiments, Little Gem was the most resistant cultivar in greenhouse experiments (Table 3). Disease severity levels for Little Gem were not different from those of Batavia Reine des Glaces. Similar to results from the field experiments, Pybas 251 was the most susceptible cultivar in greenhouse assays. Disease severity of the susceptible cultivar Vista Verde was not significantly different from Pybas 251 in one greenhouse experiment but was slightly lower than Pybas 251 in a second experiment (*data not shown*), resulting in significant differences between these cultivars in analysis of data pooled from the two experiments. Also reflecting field trial findings, Waldmann's Green and Grand Rapids were significantly more susceptible than Little Gem in greenhouse evaluations.

Although there were some minor differences in the ranking of cultivars both among and between greenhouse trials and field trials, in general there was a strong correlation between results obtained in the greenhouse and those obtained in the field (r = 0.77, $P = 0.009$), as determined by Spearman's correlation coefficient.

Table 3. Severity of bacterial leaf spot on greenhouse grown lettuce cultivars[w].

Cultivar	Median disease severity[x]	RTE[y]	95% CI[z]	
			Lower limit	Upper limit
Pybas 251	6.04	0.765 a	0.610	0.861
Grand Rapids	5.49	0.723 ab	0.593	0.818
Red Line	5.03	0.618 abc	0.449	0.759
Vista Verde	5.05	0.626 bc	0.498	0.735
Waldmanns Green	5.12	0.639 b	0.532	0.731
Sniper	4.27	0.495 cd	0.366	0.624
Holborn Standard	4.17	0.413 de	0.261	0.589
Salad Crisp	3.67	0.362 e	0.256	0.489
Iceberg	3.86	0.351 e	0.248	0.474
Batavia Reine des Glaces	3.16	0.271 ef	0.177	0.401
Little Gem	3.35	0.238 f	0.147	0.375

[w] Data presented are pooled from two experiments, each with four replications per cultivar.

[x] Disease severity was evaluated on the top three leaves (0 = no disease; 1 = few lesions < 3< mm; 2 = lesions > 3 mm; 3 = coalesced lesions), then per-plant disease severity values were averaged across all plants within each treatment replicate.

[y] Relative Treatment Effect for disease severity. Values followed by the same letter are not significantly different at $P = 0.05$ according to the LSDs for the mixed model.

[z] 95% confidence interval for the relative treatment effect.

Conclusions

Here we demonstrate a high level of resistance to bacterial leaf spot in the cultivars Little Gem and Batavia Reine des Glaces. The data represent the first report of differences in the levels of bacterial leaf spot severity among cultivars in field trials and were supported by disease incidence data when the incidence was less than 100%. Carisse et al (4) reported differences in susceptibility based on the percent diseased leaves per plant but not from severity data. In those trials, cultivars Waldmann's Green and Grand Rapids were the least susceptible of the nine cultivars evaluated. The relatively weak performance of Waldmann's Green and Grand Rapids in the experiments reported here, compared to those reported in Canada, may be due to genotype by environment interactions, genetic differences between seed lots of these cultivars or the methods by which resistance was assessed. Regardless, this report further substantiates the existence of genetic variation for resistance to bacterial leaf spot in lettuce, and indicates the potential to identify high levels of resistance by screening larger portions of the available germplasm. To date, we have screened 49 genotypes (46 commercially available cultivars, 3 PI lines) in non-replicated field trials (see Appendix). Those identified as relatively resistant have then been evaluated in replicated field and/or greenhouse trials (*data not shown*). Still, this is a small proportion of the 2258 *L. sativa* accessions and 1245 WRPIS Plant Introductions available in the Salinas working germplasm collection.

For the 36 named cultivars that have been evaluated in replicated experiments, no generalization about market types and resistance can be made. Previous studies reported susceptible cultivars from butterhead, romaine, and leaf lettuce (4,8,7), and in this study the crisphead cultivars Pybas 251, Vista Verde, Pacific, and Sniper, were the most or among the most susceptible cultivars. It is interesting to note that during the severe bacterial leaf spot outbreaks in California in the early to mid-1990s, cultivar Pybas 251 was commonly and severely diseased in the Salinas and Santa Maria valleys (Koike, *personal communication*). Likewise, resistance has been identified in butterhead, leaf, and crisphead cultivars (4,7) and the Latin type cultivar Little Gem (reported here). Market categories of lettuce (romaine, crisphead, green or red leaf, latin, butterhead, etc.) consist of individuals of varying degrees of relatedness. Genetic relationships but not market types may be appropriate for developing inferences about the potential for susceptibility or resistance of cultivars.

There was a strong correlation between the greenhouse assay and field evaluations. This relationship has allowed us to successfully use the greenhouse assays to more quickly advance breeding goals. This is significant because although resistance has been reported, there are no reports describing the nature of resistance in these cultivars. We are currently using the greenhouse assay to evaluate the genetic basis of resistance conferred by Little Gem and Batavia Reine des Glaces (Hayes and Bull, *unpublished*).

Acknowledgments

The authors thank Denis Shah for helpful discussion of non-parametric statistical analysis methods. Special thanks to Sharon Benzen, Nicole Morris, Alison Pepper, Ruby Renteria, Bert Robinson, Freddy Rosales, and E. J. Rowland for technical support on this project. We appreciate the comments provided by Drs. Rebbeca Grube and William Pfender on this work. Funding for this work was provided in part by the California Lettuce Research Board.

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Appendix: Evaluation of Cultivars in Trials with No Replication

Spring 2002

Cultivar	Number of plants	Proportion diseased	Disease severity rating[x] (avg. of per plant rating)
Salinas	29	1.00	3.1
Pacific	26	1.00	2.5
Darkland	29	0.07	2.6
Great Lakes	25	0.96	1.7
Calmar	17	0.77	1.9
Lobjoits	34	0.56	1.2

[x] 1 = a few individual lesions; 2 = many individual lesions; 3 = small patches of coalesced lesions; 4 = medium sized patches of coalesced lesions; and 5 = large patches of coalesced lesions.

Fall 2002

Cultivar	Number of plants	Proportion diseased	Disease severity rating[x] (avg. of per plant rating)
Calmar	32	1.00	1.9
Darkland	29	1.00	2.3
Great Lakes	38	1.00	2.4
Lobjoits	46	1.00	1.8
Pacific	33	1.00	2.8
Parris Island	35	1.00	2.6
Salinas	30	1.00	1.5

[x] 1 = a few individual lesions; 2 = many individual lesions; 3 = small patches of coalesced lesions; 4 = medium sized patches of coalesced lesions; and 5 = large patches of coalesced lesions.

1 Spring 2003

Cultivar	Number of Plants	Proportion diseased	Disease severity rating[x] (avg. of per plant rating)
Midas		1.00	2.5
PI 226514		1.00	4.4
PI 491224		1.00	2.3
Balady Aswan		1.00	4.0
Deer's Tongue		1.00	3.3
La Brilliante		0.84	1.8
Salinas		1.00	4.3
Salinas 88		0.96	2.5

[x] 1 = a few individual lesions; 2 = many individual lesions; 3 = small patches of coalesced lesions; 4 = medium sized patches of coalesced lesions; and 5 = large patches of coalesced lesions.

Spring 2004

Cultivar	Size of plot	Disease severity rating[x] for whole plot	
		First rating	Harvest rating
Bayview	50 ft	1	1
Big Ben	50 ft	1	1
Early Bird	50 ft	1	1
Corona	50 ft	1	1
Cochise 47	50 ft	2	2
Red Fox	50 ft	4	2
Durango	50 ft	1	1
El Dorado	50 ft	2	1
Green Beauty	50 ft	1	1
Hallmark W	50 ft	2	1
Jupiter	50 ft	1	3
Laguna Fresca	50 ft	1	2
Legacy	50 ft	3	2
Silverado	50 ft	2	1
Sniper	50 ft	1	1
Spanish Bay	50 ft	1	1
Spreckels	50 ft	1	1
Sure Shot	50 ft	2	3
Terlluride	50 ft	2	1
Tiber	50 ft	2	3
Titan	50 ft	3	2
Trojan	50 ft	2	2
Big Hoss	50 ft	1	1
Venus	50 ft	1	1
Wallaby	50 ft	3	2
Mohawk	50 ft	3	2
Little Gem	50 ft	4	4
Bat RenDG	50 ft	--	3
Horlborn Standard	50 ft	3	3
Vista Verde	50 ft	1	1
PI251246	50 ft	2	3
Salinas	50 ft	1	1
Iceberg	50 ft	3	3
Batavia Blonde Paris	50 ft	3	3
Salad Bowl	50 ft	4	4

[x] Severity rating (1 = severe disease - 4 = no disease).

Spring 2005

Line	Number of plants	Proportion diseased
Bay View	34	0.47
Big Ben	43	0.91
Block Buster	32	0.25
Cannery Row	42	0.50
Colossus	39	0.00
Del Rey	46	0.48
El Toro	52	0.27
H.S	107	0.00
Jupiter	39	0.00
Legend	51	0.14
Pacific	45	0.44
Batavia Reine des Glacies	92	0.00
Salinas	44	1.00
Salinas 88	128	0.30
Sniper	51	0.10
Spreckles	45	0.20
Sureshot	43	0.12
Tiber	31	0.48
Titan	50	0.00
Triple Crown	45	0.20
Trojan	47	0.02
Vista Verde	88	0.72
Vandenberg	36	0.00