Wind Speed Effects on the Quantity of *Xanthomonas citri* subsp. *citri* Dispersed Downwind from Canopies of Grapefruit Trees Infected with Citrus Canker

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ABSTRACT

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The epidemic of citrus canker (*Xanthomonas citri* subsp. c*itri*) in Florida continues to expand since termination of the eradication program in 2006. Storms are known to be associated with disease spread, but little information exists on the interaction of fundamental physical and biological processes involved in dispersal of this bacterium. To investigate the role of wind speed in dispersal, wind/rain events were simulated using a fan to generate wind up to 19 $m \cdot s^{-1}$ and spray nozzles to simulate rain. Funnels at ground level and panels at 1.3 m height and distances up to 5 m downwind collected wind-driven splash. Greater wind speeds consistently dispersed more bacteria, measured by concentration (colony forming units [CFU] ml^{-1}) or number sampled (bacteria flux density [BFD] = bacteria cm^{-2} min^{-1}), from the canopy in the splash. The CFU ml^{-1} of *X. citri* subsp. c*itri* collected by panels 1 m downwind at the highest wind speed was up to 41-fold greater than that collected at the lowest wind speed. BFD at the highest wind speed was up to 884-fold higher than that collected at the lowest wind speed. Both panels at distances >1 m and funnels at distances >0 m collected many-fold more *X. citri* subsp. *citri* at higher wind speeds compared to no wind (up to 1.4×10^3-fold greater CFU ml^{-1} and 1.8×10^5-fold the BFD). The resulting relationship between wind speed up to 19 $m \cdot s^{-1}$ and the mean CFU ml^{-1} collected by panel collectors downwind was linear and highly significant. Likewise, the mean CFU ml^{-1} collected from the funnel collectors had a linear relationship with wind speed. The relationship between wind speed and BFD collected by panels was generally similar to that described for CFU ml^{-1} of *X. citri* subsp. *citri* collected. However, BFD collected by funnels was too inconsistent to determine a meaningful relationship with increasing wind speed. The quantity of bacteria collected by panels declined with distance, and the relationship was described by an inverse power model (R^2 = 0.94 to 1.00). At higher wind speeds, more bacteria were dispersed to all distances. Windborne inoculum in splash in subtropical wet environments is likely to be epidemiologically significant, as both rain intensity and high wind speed can interact to provide conditions conducive for dispersing large quantities of bacteria from canker-infected citrus trees. Disease and crop management aimed at reducing sources of inoculum and wind speeds in a grove should help minimize disease spread by windborne inoculum.

Citrus canker (caused by *Xanthomonas citri* subsp. *citri* (ex Hasse) Gabriel et al.) is a disease that affects several citrus species and causes erumpent, necrotic lesions on leaves, shoots, branches, and fruit. Yield loss due to fruit and leaf drop can be substantial, and on fruit the unsightly blemishes leads to reduced marketability (14,15,34). The disease is widespread in citrus growing regions where humid-wet tropical and subtropical conditions conducive for spread prevail. Citrus canker is endemic in Florida and continues to spread among groves (18,19, 21,25,34).

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Lesions of citrus canker exude bacteria the moment water is present, and the quantity produced can be substantial. The bacteria are expressed from lesions for a prolonged period (>52 h) when conditions are suitable for their reproduction and dispersal (4,33). After the initial burst of production from the lesion, the quantity of bacteria slowly declines as the population is depleted (4,33). With time the quantity produced levels off, becoming more consistent after the initial population of *X. citri* subsp. *citri* in the lesion is depleted and regeneration of the population occurs. Throughout this time, these bacteria are available for dispersal from the vicinity of the lesion, although several other factors might influence the quantity produced, including lesion age (33,40) and ambient temperature (4,26,39).

Wind and rain are dispersal agents, either singly or in combination, for many plant pathogens (1,11,13,24,27,30), including various bacterial diseases (5,9,11,13, 42,43). The initial pattern of citrus canker in groves suggests a combined effect of wind and splash in dispersing *X. citri* subsp. *citri* (7,20,21). Furthermore, powerful storms, including tropical storms and hurricanes, have been implicated in disease development up to 56.3 km distance (19,25). Even in regular thunderstorms that occur on a frequent basis in Florida during the summer, the rain can be intense for short periods with locally strong winds. The effect of wind speed in combination with splash as agents dispersing *X. citri* subsp. *citri* has not been characterized, but if it can be demonstrated that reducing wind speeds reduces inoculum dispersal, both windbreaks and planting strategies can be optimized to minimize the incident wind. Furthermore, although wind can disperse droplets of spray containing *X. citri* subsp. *citri* (4), the relationship between wind speed and dispersal of the pathogen has not been quantified or characterized.

In one report, in a simulated rainfall experiment in calm conditions, splash dispersal of *X. citri* subsp. *citri* was demonstrated to be 60 cm (33). *X. citri* subsp. *citri* has reportedly been collected up to 32 m from infected plants after storms (6,39), and some earlier studies found that wind could disperse bacteria-laden droplets from infected plants (37). The concentration of *X. citri* subsp. *citri* was reported to increase with wind speed in these droplets from both upper and lower surfaces of the leaves (35). Using simulated wind and rain, bacteria were not only dispersed for long periods of time but were collected up to 12 m (the maximum distance sampled) from an inoculum source with winds of 19 $m \cdot s^{-1}$ applied to an infected canopy (4), but very few *X. citri* subsp. *citri* were collected downwind from cull piles of mature harvested fruit (15). Not only is the relationship between wind speed and dispersal of *X. citri* subsp. *citri* uncharacterized, there is little information available on the relationship among wind speed, quantity of inoculum dispersed, and distance from the source of inoculum.

Typically, raindrop diameters range from 0.2 to 5.0 mm (13,27). Larger droplets are more efficient for dispersing fungal pathogens, but bacteria are much smaller and could be dispersed in aerosol-sized droplets (42). Rainfall rates are highly

variable, but most studies (27) suggest the relationship between rainfall rate and dispersal is not straightforward. Although dispersal in still conditions might be sensitive to droplet size, in high-speed winds even small rain drops impacting and swirling in a tree canopy may become impregnated with bacteria, or broken apart on impact. The resulting droplets and aerosol-sized particles (~1.0 to 7.0 µm) can carry numerous bacteria (42). Such aerosols would only be viable when humidity was high, as evaporation would inevitably render them short-lived, but along with larger droplets, they could be a vehicle for transporting bacteria.

Establishing the effects of wind speed on the quantity of *X. citri* subsp. *citri* dispersed from canopies, the relationship between wind speed and bacteria collected, and the resulting dispersal gradients is useful for applying disease management strategies, particularly windbreaks (2,22). In most rain storms, windbreaks can be used to reduce the speed of wind striking the canopies and disrupt or deflect windblown rain, thereby reducing windborne splash. If slowing down wind reduces the amount of inoculum dispersed, and/or the distance it is dispersed, the incidence of infection will be reduced, slowing down the progress of the disease and reducing the severity of the epidemic. Furthermore, knowledge of the relationship between wind speed and dispersal is useful for assessing a storm's risk for spreading disease. The objectives of these experiments were to (i) determine the quantities of *X. citri* subsp. *citri* dispersed in rain splash at different wind speeds, and (ii) identify the relationship between wind speed and the quantity of bacteria dispersed from canker-infected trees.

MATERIALS AND METHODS

Experimental design. All experiments were done at a contained USDA field site in Broward Co., FL. Two experimental designs were used. In each design, three young, canker-infected trees in 38-liter containers acted as the source of inoculum and were placed in a triangular formation with each pot situated at a point of the triangle, such that the third one was situated to the front of the group. Trees were similar in stature and pruned to be approximately 1.5 m tall with a crown approximately 0.8 × 0.8 m, although there was inevitably some variability in canopy structure. An axial fan (Model AM22 2HP, Air Max Fans, Florence, SC) was used for the source of wind, and different wind speeds at the canopy face were achieved by situating the fan at various fixed distances from the trees. The fan generates wind of approximately 18 $m \cdot s^{-1}$ at 1 m and

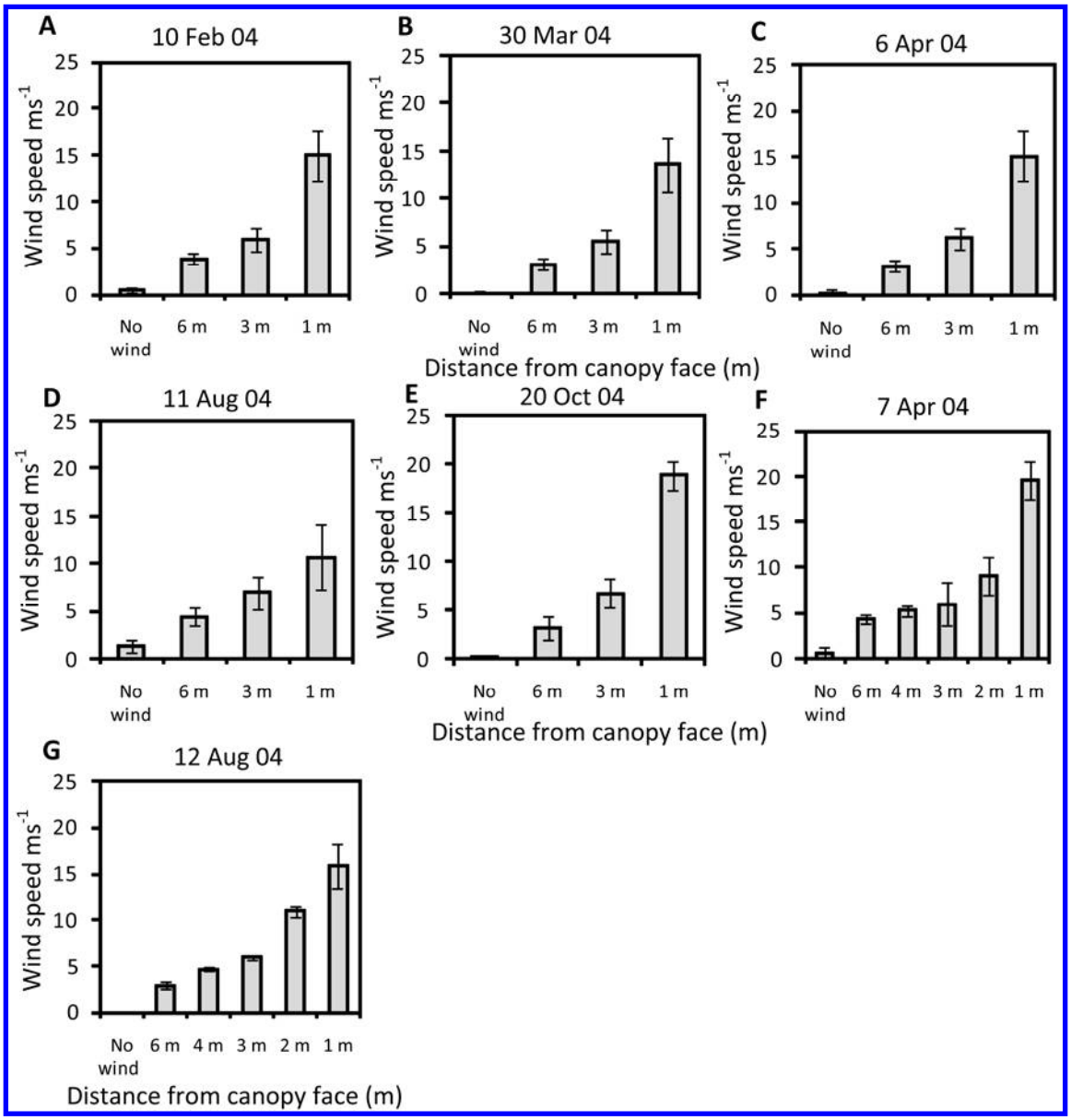

Fig. 1. Mean wind speed at the canopy face (indicated by vertical bars) when the fan was positioned at different distances upwind of the canopy of canker-infected grapefruit trees in seven experiments **(A to G)** in 2004. Standard deviations of wind speeds are indicated by whiskers. Sampling periods were 5 min.

4 m·s^{-1} at 6 m, as specified by the manufacturer. To simulate rain, spray was applied through a series of four overhead garden sprayers (Orbit/Sunmate 7 Pattern Zinc Pistol Nozzles, Orbit Irrigation Products, Inc., Bountiful, UT) set on the "cone" setting. Firstly, four wind speeds were tested and samples were collected at three or four distances downwind from the infected canopy. This experiment was repeated four times. Secondly, six different wind speeds were tested against the dispersal of bacteria from the infected canopies. This experiment was repeated once. Each experiment had two or three replicate samples collected from which data were averaged for each day. Each wind speed treatment (fan and spray) was run for periods of 5 min. Plants were pretreated to simulated rain for at least 1.5 h to allow initial dispersal of bacteria to occur (4). Initially, large quantities of bacteria are released from lesions, and if this is not allowed to stabilize, early treatments would have disproportionately large quantities of bacteria related to the initial lesion population, and not necessarily related to the applied treatments.

Two sampling methods were used: one set to collect airborne splash and spray traveling downwind at canopy height (panel samplers), and a second set to collect spray and splash at ground level (funnel samplers) under and downwind of the canopy (4,31). The panels were placed vertically in the line of the windblown splash with a height of 1.5 m. Panels (36 × 36 cm, 1,296 cm^2) were 144-fold larger in surface area compared to the funnels (9 cm^2). The funnels were placed with the outlet through a hole drilled in the lid of a conical collection flask, which was set directly on the ground at set distances from the source of inoculum, depending on the experiment. The panel sample was directed into a collection vessel at the base of the panel. The panels were rinsed with 50 ml of water after each sample run to ensure any remaining bacteria on the panel surface were collected. Each panel was thor-

Table 1. Range in volume (ml) of splash collected, concentration of bacteria (CFU ml^{-1}), and bacteria flux density (BFD, bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected for each wind speed and distance experiment by both panel and funnel collectors positioned downwind from canker-infected canopies of grapefruit trees

Collection device	Month	Range of volume collected (ml)	Range of concentration (CFU ml^{-1})	Range of BFD (bacteria cm^{-2} min^{-1})
Panels	10 Feb 04	0-925	0-413	0-50
	30 Mar 04	0-817	0-2,810	0-356
	6 Apr 04	0-1,138	0-6,761	0-1,173
	7 Apr 04	490-725	278-4,317	16-428
	11 Aug 04	94-613	211-3,622	<1-93
	12 Aug 04	27-233	4-1,100	<1-15
	20 Oct 04	0-130	0-2,167	0-13
Funnels	10 Feb 04	3-188	15-1,130	4-2,617
	30 Mar 04	6-74	1,237-14,967	51-16,999
	6 Apr 04	15-80	3,556-19,222	56-82,368
	12 Aug 04	3-153	50-5,533	5-1,2919
	20 Oct 04	0-219	0-3,543	0-8,745

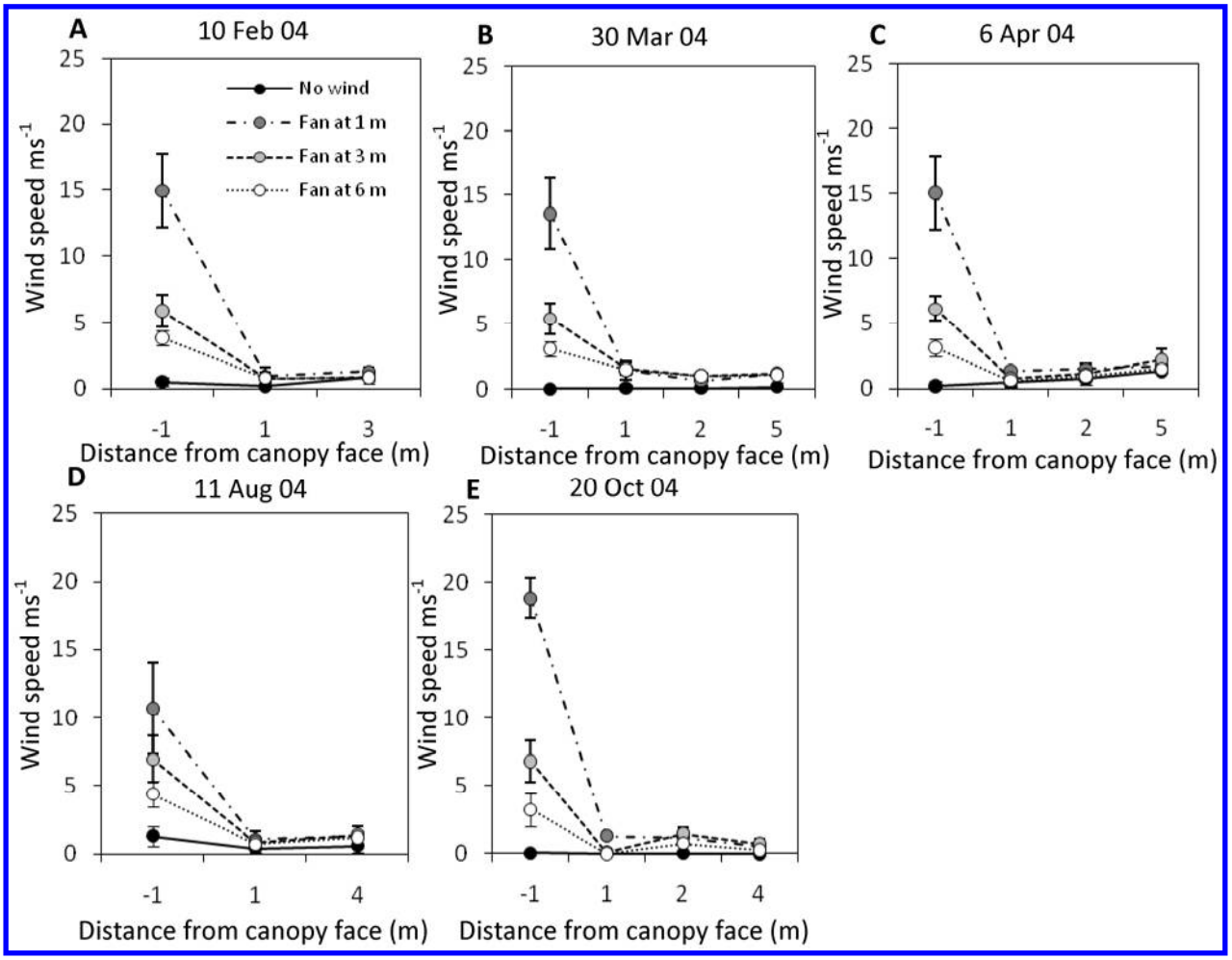

Fig. 2. Mean wind speed at the canopy face (indicated by data points) and at different distances downwind from the canopy when the fan was positioned at different distances upwind of the canopy of canker-infected grapefruit trees in five experiments **(A to E)** in 2004. Standard deviations of wind speeds are indicated by whiskers. Sampling periods were 5 min.

oughly washed and allowed to drain dry between samples. All collection vessels were thoroughly cleaned between samples.

In the first series of experiments, the fan was operated at 1, 3, and 6 m from the tree canopy. Zero wind speed was obtained with the fan switched off. Panel collectors were situated at 1, 2, 3, and 5 m, or at 1, 2, and 4 m from the plant canopy. Funnels were situated at 0 (under the canopy), 1, 2, and 3 m or at 0, 1, and 2 m, respectively. There were five experiments run at various times during the year to ensure that a range of conditions were experienced (10 February, 30 March, 5 April, 10 August, and 30 October 2004). In the second series of experiments, the fan was operated at 1, 2, 3, 4, and 6 m from the canopy with zero wind speed obtained with the fan switched off. Three replicate panels were placed 1 m downwind from the canopy. The experiment was repeated twice (7 April and 11 August 2004). The lesions on individual plants generally ranged in age from a few weeks old to several months, depending on the timing of flush relative to the experiment. The same group of three plants was used for experiments on 10 February and 30 March, a second group on 5 and 6 April, a third group on 10 and 11 August, and a fourth group on 30 October. Disease symptoms were estimated on these plants as described previously (4). Plant height and canopy size were similar for all plants, and mean numbers of lesions on the groups of three plants ranged from 9 to 30 lesions per infected leaf. The mean percent leaves infected ranged from 87.5 to 99.1%.

The volume of the sample collected over the 5-min period was measured, and the CFU of *X. citri* subsp. *citri* were counted using dilution plating, from which the bacteria concentration (CFU ml^{-1}) and bacteria flux density (BFD, bacteria cm^{-2} min^{-1}, 32) were calculated. CFU ml^{-1} provides a measure of the average concentration of bacteria in the collected splash, which is of interest as a major factor in infection, while BFD provides a standardized measure for valid comparisons among samplers, or to other studies (32). The samples were immediately plated out on KCB semiselective media composed of nutrient agar (NA) amended with kasugamycin (16 mg $liter^{-1}$), cephalexin (35 mg $liter^{-1}$), and chlorothalonil (12 mg $liter^{-1}$ tetrachloroisophthalonitrile). In addition to the samples of splash, well water used for spray was also plated out to act as a control. The plates were incubated at 27°C for

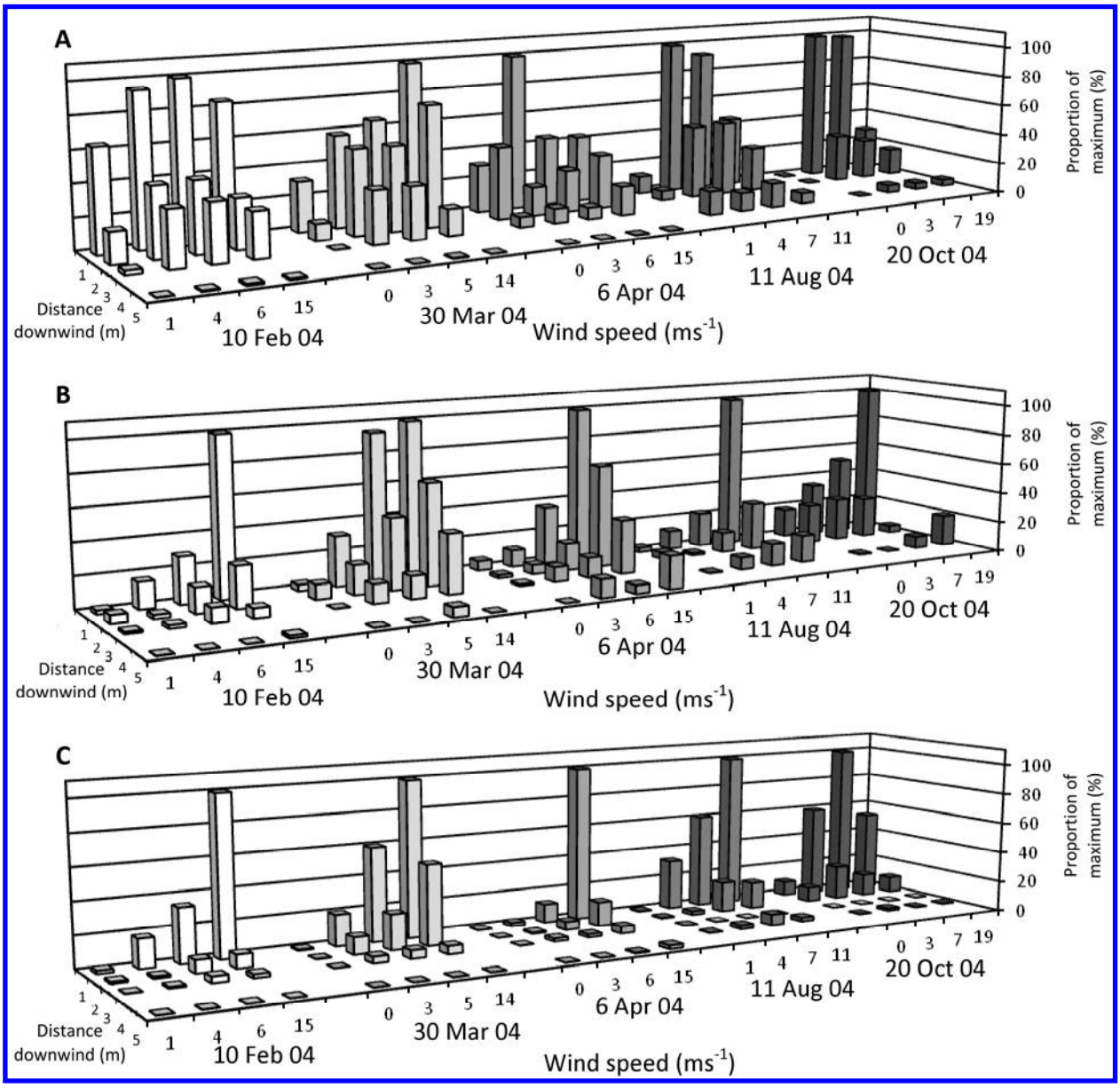

Fig. 3. A, Volume of water (ml), **B,** concentration (CFU ml^{-1}), and **C,** quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected in panel samplers downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in five separate experiments (10 Feb to 20 Oct) in 2004. Data in each experiment are normalized as a percentage of the maximum collected in any treatment in that experiment (% = [Quantity collected in sample ÷ maximum collected in experiment] × 100).

5 to 7 days prior to counting colonies typical of reference cultures of *X. citri* subsp. *citri*.

Meteorological variables. Weather data were recorded using Davis Weather instruments (Weather Wizard III, Davis Instruments, Hayward, CA). Wind speed sensors were cup anemometers, and measurements were taken every 60 s. Standard deviations were calculated for mean wind speeds. Temperature was recorded using a temperature probe, and simulated rainfall rate was recorded using a tipping bucket rain gauge. The rainfall rate was 235 $mm \cdot h^{-1}$.

Typical rainfall in rain showers can range from <1 $mm \cdot h^{-1}$ to 100 $mm \cdot h^{-1}$, but in thunderstorms, tropical storms, or hurricanes typical of Florida, it can easily be >100 $mm \cdot h^{-1}$ for short periods of time (even >400 $mm \cdot h^{-1}$ is possible, with a maximum of 1,872 $mm \cdot h^{-1}$ being the world record; 29,38,41). A high-speed camera (Phantom V, Vision Research, NJ) operated at 1,000 frames per second was used to record droplets produced by the nozzles for subsequent size measurement. Droplet size ranged from <1 mm to 4.3 mm, with 30% of them being larger than 2 mm. Larger droplets are more efficient for splash dispersal (12,13,27).

Data analysis. Data for each of the seven experiments were analyzed individually (after averaging sample replicates for each day) using regression analysis with SAS (SAS Systems, Cary, NC). Linear regression ($y = a + bx$) was used to explore the relationship between wind speed and quantity of bacteria collected (PROC REG). This was done for each sampling distance and for the mean for both panel and funnel collection devices. Model fit was ascertained based on the coefficient of determination (R^2) and the significance of the model (based on F and P values). Similarly, the relationship between quantity of bacteria collected and distance from the plants was tested, but using a nonlinear regression model (PROC NLIN). An inverse power law model ($y = ax^b$) was fit to these data, and the appropriateness judged using the R^2, F, and P values as for the linear model.

RESULTS

Wind speed. The mean wind speed at the canopy face depended on distance of the fan from the tree (Fig. 1). The standard deviations of these mean wind speeds show that the variability of the mean wind speed tended to increase with the speed,

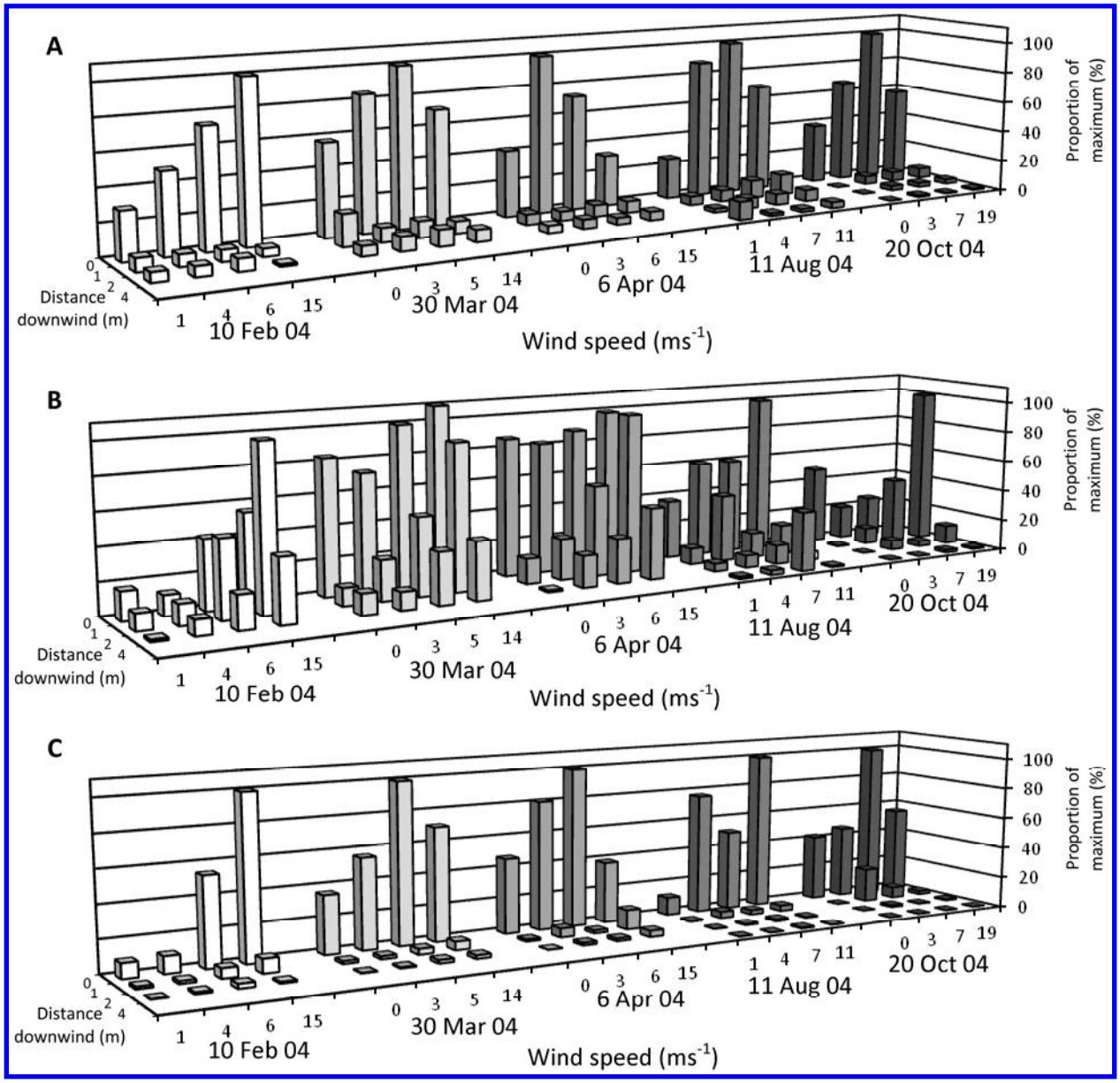

Fig. 4. A, Volume of water (ml), **B,** concentration (CFU ml^{-1}), and **C,** quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected in funnel samplers downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in five separate experiments (10 Feb to 20 Oct) in 2004. Data in each experiment are normalized as a percentage of the maximum collected in any treatment in that experiment (% = [Quantity collected in sample ÷ maximum collected in experiment] × 100).

reflecting increasing gustiness. Fans produce a turbulent flow of air, and thus wind speeds are expected to be somewhat variable. Mean wind speed declined rapidly with distance downwind of the canopy, with mean wind speeds being similar at all distances downwind of the canopy regardless of the speed at the canopy face (Fig. 2). That is, at 1 m downwind, there was little effect of precanopy mean wind speeds due to a "wind shadow" effect. Mean temperature in the foliage of the plants during the experiments ranged from 20.5°C (st dev = 0.8) on 10 February to 26.6°C (st dev 1.3) on 12 August.

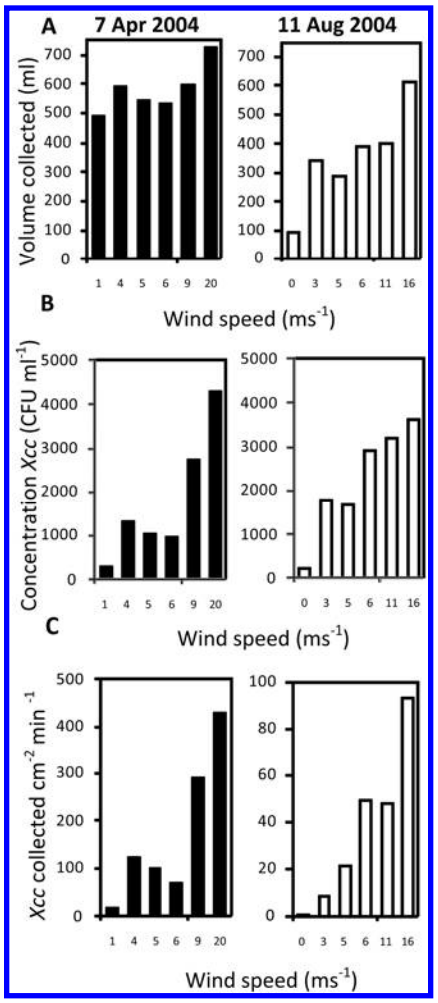

Fig. 5. A, Volume of water (ml), **B,** concentration (CFU ml^{-1}), and **C,** quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected in panel samplers downwind from canker-infected grapefruit canopies subject to six different wind speeds in simulated wind-rain events in two separate experiments in 2004.

Volumes collected, CFU and BFD. Among experiments and between treatments there was a wide range in volume of water, CFU ml^{-1}, and BFD by both panels and funnels (Table 1, Figs. 3, 4, 5, and 6). These parameters generally increased with wind speed and decreased with distance, although the volume collected with respect to wind speed and distance was not always entirely consistent (Figs. 5 and 6). With both panels and funnels, the least volume was generally collected at the lowest wind speed, but the greatest volume was not necessarily collected at the highest wind speed. The amount of splash getting through a canopy is presumably in part dependent on characteristics of canopy density and architecture of individual trees. Nonetheless, there were consistent effects of wind speed increasing the quantity of bacteria (both CFU ml^{-1} and BFD) dispersed from the canopy in the splash. The highest CFU ml^{-1} collected in panels was 6.8×10^3 bacteria ml^{-1} (6 April), and in funnels was 1.9×10^4 (11 August). The highest BFD collected in panels was 1,173 bacteria cm^{-2} min^{-1} (6 April), and in funnels was 8.2×10^4 (11 August).

The quantities of bacteria escaping the canopy and collected in panels at 1 m increased many-fold (Fig. 3). In the five wind speed by distance experiments, the CFU ml^{-1} of bacteria dispersed 1 m downwind at the highest wind speed was up to 41-fold that at the lowest wind speed. The BFD at the highest wind speed was up to 884-fold that collected at the lowest wind speed, and in the two additional experiments on 6 April and 11 August, the increase in CFU ml^{-1} was 16- and 17-fold, respectively, and in the BFD 27- and 263-fold, respectively. In the funnel collectors, under the canopy, CFU ml^{-1} collected at the highest wind speeds was up to threefold that at the lowest wind speed, and BFD at the highest wind speed was up to 11-fold that with no wind. Thus, although higher wind speeds invariably lead to large increases in bacteria collected downwind, the quantity collected immediately under the canopy did not increase as dramatically. Both panels at distances >1 m and funnels at distances >0 m collected many more bacteria at higher wind speeds compared to no wind (up to 1.4×10^3-fold greater CFU ml^{-1} and 1.8×10^5-fold greater BFD, respectively).

Relationship between test wind speed and quantity of *X. citri* subsp. *citri*. As wind speed increased, the number of CFU ml^{-1} of *X. citri* subsp. *citri* dispersed downwind increased. The resulting relationship between wind speed up to 19 $m \cdot s^{-1}$ and the mean CFU ml^{-1} collected by panel collectors downwind was linear (Fig. 7A and B, Table 2). The linear model displayed acceptable to good coefficients of determination (>0.87) with *F* values of 14 to 177 and *P* values ≤0.06. However, at specific distances, the quantity of bacteria collected with wind speed was not always consistent, resulting in a poor linear relationship for some distances (*F* values = 1 to 1,047, *P* values = 0.001 to 0.4). Similar results were observed for the funnel collectors (Fig. 7C and Table 3), where the mean CFU ml^{-1} collected also had a linear relationship with wind speed (coefficients of determination 0.70 to 0.98, *F* values 5 to 126, *P* values 0.008 to 0.17). Similar to the panel data, at specific distances the quantity of bacteria collected with wind speed was not completely consistent, and sometimes poor relationships resulted.

The relationship between wind speed and BFD on the panels was generally similar to that described for CFU ml^{-1} of *X.*

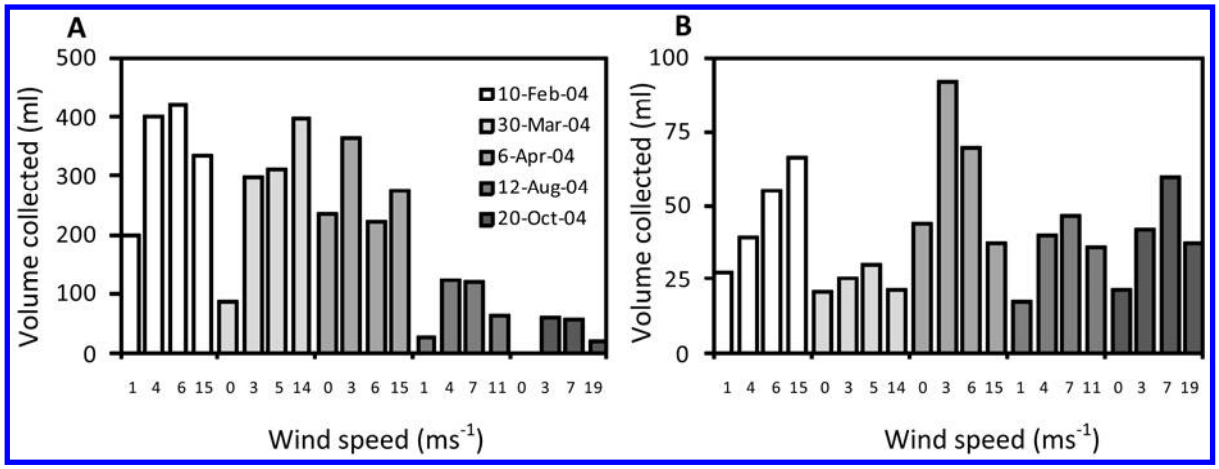

Fig. 6. Mean volume (average of all replicates and distances for that wind speed) collected in **A,** panel, and **B,** funnel samplers at different wind speeds downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in seven separate experiments in 2004.

citri subsp. *citri* collected. The relationships between wind speed and mean BFD were linear (Table 4 and Fig. 8), with statistics of the regression lines suggesting a good fit, except for data collected on 20 October. For the other dates, coefficients of determination ranged from 0.94 to 0.99, (F values = 89 to 4,494, and P values = 0.011 to 0.0002). As with the data for CFU ml^{-1}, there were individual distances on each date when the BFD did not increase consistently with wind speed, precluding a meaningful fit. Similarly, the BFD from the funnels was analyzed using regression analysis, and although all applied wind speeds caused greater dispersal, in most cases these data were too inconsistent between experiments to determine a meaningful relationship with wind speed (Fig. 9).

The effect of distance. The quantity of bacteria collected at different distances under simulated conditions was reported previously (4). The effect of distance from the source at all canopy-face wind speeds for both panels (Fig. 10 and Table 5) and funnels (Fig. 11 and Table 5) confirms those observations. The volume collected and quantity of bacteria dispersed declined with distance, and this relationship was described by an inverse power law model. Model fit was good (R^2 = 0.86 to 1.00) for all parameters on all dates except for CFU ml^{-1} with funnel samples on 10 February (R^2 = 0.08). At higher wind speeds, more bacteria were dispersed to all distances,

Table 2. Linear regression analysis[a] of relationship between wind speed and concentration (CFU ml^{-1}) of bacteria of *Xanthomonas citri* subsp. *citri* collected by panels positioned at 1.5 m height collecting wind-driven splash dispersed downwind different distances from canker-infected canopies of grapefruit trees

Date[b]	Dist (m)[c]	Intercept (a)	Slope (b)	R^{2d}	F^e	P^f
10 Feb 04	1	–27.8	28.7	0.99	147	0.007
	2	9.9	6.5	0.84	10	0.09
	3	10.9	1.3	0.28	0.8	0.4
	5	–1.5	0.5	0.87	14	0.07
	Mean	–2.1	9.2	0.98	106	0.009
30 Mar 04	1	546.3	193.4	0.72	5	0.2
	2	323.0	116.7	0.91	21	0.045
	3	66.4	72.3	0.98	50	0.09
	5	…	…	…	…	…
	Mean	254.2	125.4	0.97	72	0.01
6 Apr 04	1	–142.1	448.2	0.98	98	0.01
	2	–322.7	305.7	0.97	64	0.015
	3	73.4	149.3	0.99	260	0.004
	5	137.9	83.6	0.76	6	0.1
	Mean	–63.4	246.7	0.99	177	0.006
12 Aug 04	1	–269.4	110.6	0.81	9	0.1
	2	–55.9	33.0	0.81	9	0.1
	4	–9.2	20.6	0.95	38	0.03
	Mean	–111.5	54.7	0.87	14	0.06
20 Oct 04	1	425.9	93.0	0.99	1,047	0.001
	2	648.5	–26.8	0.87	13	0.07
	4	–22.2	24.1	0.96	52	0.02
	Mean	350.7	30.1	0.98	80	0.01
7 Apr 04	1	138.8	219.3	0.93	55	0.0017
11 Aug 04	1	915.8	196.2	0.81	17	0.014

[a] Linear regression model $y = a + bx$ (a = intercept, b = slope).
[b] For experiments on 10 Feb, 30 Mar, 5 Apr, 10 Aug, and 30 Oct 2004, the fan was operated at 1, 3, and 6 m from the plant canopy. On 6 Apr and 11 Aug 2004 the fan was operated at 1, 2, 3, 4, and 6 m from the canopy. Calm conditions were obtained with the fan switched off.
[c] Distance of panel sampler from the fan in meters. Mean data based on all distances for that date, except 6 Apr and 11 Aug 2004 when there was only a single distance.
[d] R^2 = Coefficient of determination (proportion of variability accounted for by model).
[e] F = F distribution value that tests goodness of fit for the model.
[f] P = Probability the F value is significant.

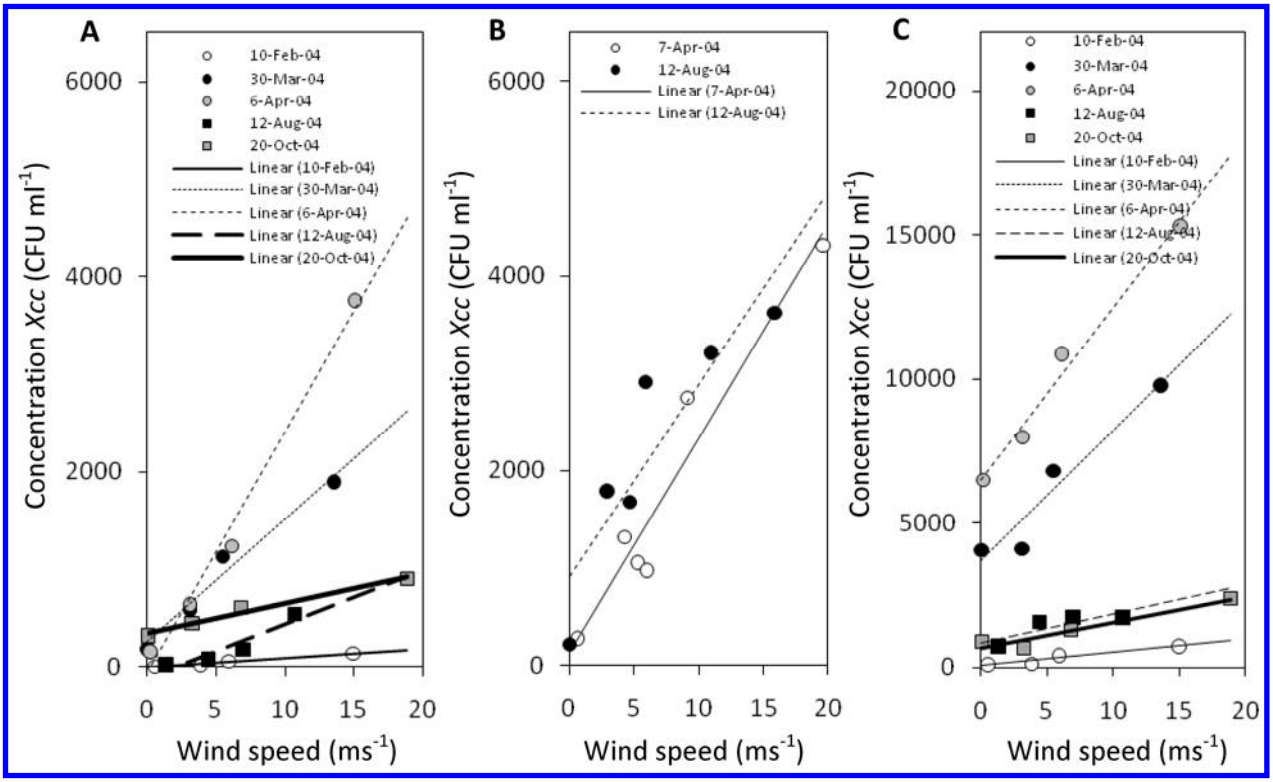

Fig. 7. Relationship between wind speed and concentration (CFU ml^{-1}) of bacteria of *Xanthomonas citri* subsp. *citri* collected downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in seven separate experiments. Samples collected from panels at 1.3 m height are shown in **A,** five experiments, and **B,** two experiments. **C,** Samples collected in funnels at ground level. Regression solutions are shown in Tables 2 and 3 for panel and funnel collectors, respectively.

Table 3. Linear regression analysis[a] of relationship between wind speed and concentration (CFU ml^{-1}) of bacteria of *Xanthomonas citri* subsp. *citri* collected by funnels positioned at ground level collecting wind-driven splash dispersed downwind at increasing distance from canker-infected canopies of grapefruit trees

Date[b]	Dist (m)[c]	Intercept (a)	Slope (b)	R^{2d}	F^e	P^f
10 Feb 04	0	154	32.5	0.77	7	0.1
	1	12	74.3	0.95	38	0.026
	2	14	29.1	0.97	73	0.01
	Mean	60	45.3	0.93	25	0.037
30 Mar 04	0	8,414	465.5	0.84	11	0.08
	1	1,191	678.4	0.99	173	0.006
	2	1,424	210.8	0.71	5	0.2
	Mean	3,676	451.6	0.93	27	0.035
6 Apr 04	0	15,600	190.0	0.81	9	0.01
	1	2,626	1,094	0.98	89	0.01
	3	1,335	502.0	0.91	20	0.047
	Mean	6,520	595.2	0.98	126	0.008
12 Aug 04	0	1,525	347.1	0.91	20.4	0.045
	1	1,199	0.6	0	0	0.99
	2	385	5.2	0	0	0.89
	4	346	42.5	0	0	0.8
	Mean	868.8	98.9	0.70	5	0.17
20 Oct 04	0	2,628	–76.6	0.40	1	0.4
	1	–100	391.1	0.99	168	0.006
	2	89	39.0	0.83	10	0.09
	4	24	4.0	0.29	1	0.5
	Mean	660	89.4	0.92	24	0.039

[a] Linear regression model $y = a + bx$ (a = intercept, b = slope).
[b] For experiments on 10 Feb, 30 Mar, 5 Apr, 10 Aug, and 30 Oct 2004, the fan was operated at 1, 3, and 6 m from the plant canopy. Calm conditions were obtained with the fan switched off.
[c] Distance of panel sampler from the fan in meters. Mean data based on all distances for that date.
[d] R^2 = Coefficient of determination (proportion of variability accounted for by model).
[e] F = F distribution value that tests goodness of fit for the model.
[f] P = Probability the F value is significant.

Table 4. Linear regression analysis[a] of relationship between wind speed and quantity of bacteria (bacteria flux density, BFD, bacteria cm^2 min^{-1}) of *Xanthomonas citri* subsp. *citri* collected by panels positioned at a height of 1.5 m collecting wind-driven splash dispersed downwind different distances from canker infected canopies of grapefruit trees

Date[b]	Dist (m)[c]	Intercept (a)	Slope (b)	R^{2d}	F^e	P^f
10 Feb 04	1	–2.47	3.42	>0.99	420	0.0024
	2	0.70	0.26	0.64	4	0.2
	3	0.45	0.07	0.24	1	0.5
	5	–0.003	0.0009	0.87	14	0.07
	Mean	–0.33	0.94	>0.99	242	0.0041
30 Mar 04	1	14.73	26.23	0.95	36	0.027
	2	0.99	13.33	>0.99	790	0.0013
	3	6.75	1.09	0.44	1	0.5
	5	0.05	–0.0001	0	0	0.99
	Mean	1.26	13.53	>0.99	4,494	0.0002
6 Apr 04	1	–177.5	83.60	0.92	24	0.04
	2	–15.64	12.82	0.98	104	0.0095
	3	5.38	3.13	0.93	28	0.034
	5	–3.21	1.91	0.96	47	0.02
	Mean	–47.7	25.38	0.94	31	0.03
	1	–2.06	1.61	>0.99	16,791	<0.0001
12 Aug 04	2	–0.37	0.32	0.72	5	0.2
	4	0.16	0.05	0.22	1	0.5
	Mean	–0.76	0.66	0.98	89	0.011
	1	11.84	0.32	0.08	1	0.7
20 Oct 04	2	4.01	-0.05	0.09	0	0.7
	4	0.18	-0.005	0.06	0	0.7
	Mean	5.35	0.09	0.05	0	0.8
7 Apr 04	1	1.54	22.61	0.90	34	0.0043
11 Aug 04	1	–1.24	5.65	0.91	40	0.0033

[a] Linear regression model $y = a + bx$ (a = intercept, b = slope).
[b] For experiments on 10 Feb, 30 Mar, 5 Apr, 10 Aug, and 30 Oct 2004, the fan was operated at 1, 3, and 6 m from the plant canopy. On 6 Apr and 11 Aug 2004, the fan was operated at 1, 2, 3, 4, and 6 m from the canopy. Calm conditions were obtained with the fan switched off.
[c] Distance of panel sampler from fan in meters. Mean data based on all distances for that date, except 6 Apr and 11 Aug 2004 when there was only a single distance.
[d] R^2 = Coefficient of determination (proportion of variability accounted for by model).
[e] F = F distribution value that tests goodness of fit for the model.
[f] P = Probability the F value is significant.

but the relationships with distance remained the same (data by wind speed not shown).

DISCUSSION

Several studies have dealt with the spatiotemporal spread of citrus canker (16,17,20,21,23), providing a detailed and important understanding of epidemic development. The spread is a result of the pathogen dispersal processes, and these fundamental aspects are only partially characterized for citrus canker where both wind and rain play a role in pathogen dispersal (4,33,35,37,39). These results demonstrate that with increasing wind speed, more *X. citri* subsp. *citri* were dispersed downwind in rain splash from lesions in a canker-infected citrus canopy. This is the first time the quantity of *X. citri* subsp. *citri* dispersed downwind from an infected canopy at different wind speeds and distances has been characterized, and that a linear relationship with wind speed (up to 19 $m \cdot s^{-1}$) has been demonstrated. These data corroborate results from previous studies of splash dispersal of *X. citri* subsp. *citri* (4,33), and observations that at higher wind speeds greater numbers of bacteria in water droplets were collected (35). The linear relationship between wind speed and the quantity (both CFU ml^{-1} and total) of bacteria of *X. citri* subsp. *citri* collected downwind from a canker-infected canopy was evident up to 19 $m \cdot s^{-1}$. But intuitively, a wind speed must be reached where the quantity of bacteria dispersed is limited by that available from the lesions in the canopy; at this point an asymptote would be reached. Apparently that wind speed was not reached in this study, and it remains to be established.

The rain drop size in the simulated rain was sufficient for splash dispersal in calm conditions, and larger rain drops cause more dispersal (12,13,27). The rainfall rate was high but not unusual for heavy rainstorms common in Florida for short periods (235 $mm \cdot h^{-1}$; 29,38,41), and plants were exposed for only brief periods (5 min), so these data relate to field conditions that are experienced within citrus groves. Previously, a rainfall rate of 35 $mm \cdot h^{-1}$ was used to study dispersal of *X. citri* subsp. *citri* in calm conditions with limited dispersal (33), and few bacteria were collected more than 0.6 m from the infected plant. However, our data show substantial dispersal is possible from tree canopies subject to wind and rain. The effect of rain drop size and rate at various wind speeds has not been studied in a tree canopy infected with *X. citri* subsp. *citri*, but the relationship between rainfall rate and dispersal is complex in other systems (27,28,44).

Production of *X. citri* subsp. *citri* from canker lesions is not constant with time, and after an initial steep decline during the first few minutes of a dispersal stimulus,

the subsequent quantity released becomes more consistent over many hours (4,33,40). These experiments were all performed on plants that had been exposed to dispersal stimuli for at least 1.5 h to ensure earlier treatments did not have disproportionately large quantities of bacteria related to the initial lesion population. This temporal gradient in dispersal allows the pathogen to capitalize on short, turbulent storms that characterize many locations where citrus canker is important, particularly Florida, but also other subtropical countries (18,23,34). It also ensures the pathogen will be available for dispersal during more prolonged dispersal events.

In this study, foliar lesions were the source of inoculum, while in a previous study (15), harvested, infected grapefruit cull piles were the source of inoculum to study the effect of wind speed on dispersal of *X. citri* subsp. *citri*. Very little dispersal from infected fruit was detected even at wind speeds of 25 $m \cdot s^{-1}$ (15). Differences in the activity of lesions on leaves, and how wind flows over or around surfaces, compared to lesions on mature, harvested fruit might explain the huge difference in bacteria caught downwind in this study compared to that on fruit. This also accentuates the relatively low risk that mature, harvested, canker fruit pose as a source of inoculum, compared to foliage.

The sample collected by panel collectors (1.5 m aboveground) and funnels (ground level) reflected a linear increase in the concentration (CFU ml^{-1}) for both collector types and locations (regardless of volume). CFU ml^{-1} provides a measure of any change in concentration of bacteria in the splash collected, and the concentration of bacteria per se is an important factor in infection. Thus, when a canopy infected with canker was exposed to wind, there was an increase in the quantity of bacteria dispersed. Presumably the surfaces of leaves (and lesions thereon) are more exposed to the splash in windy conditions, resulting in greater quantities of bacteria becoming suspended in the splash. Inoculum concentration is related to infection (3). Evidence suggests that greater wind speed causes more infection, so when wind speed causes greater dispersal of bacteria from a canopy, more infection results (3,35,36). The BFD (bacteria cm^{-2} min^{-1}) was linearly related with wind speed for panel samples, but the quantities collected by the funnels were not always greatest at the highest wind speed. Nevertheless, wind invariably increased the quantity of *X. citri* subsp. *citri* dispersed compared to calm conditions. The measure of BFD provides a standardized measure of change in the quantity of bacteria dispersed regardless of sampler surface area or volume collected, and funnels had a smaller surface area for collection compared to panels. The resulting smaller volume collected, perhaps combined with the characteristics of canopy density, architecture, wind speed, and host disease status and distribution, may have resulted in somewhat variable BFD over the 5-min sample periods in the funnels compared to the larger panels. The panel samplers collected a larger, more representative sample of the downwind splash (both volume and CFU ml^{-1}). Furthermore, as wind speed increased, more spray and splash was blown through the canopy downwind, and this may also have resulted in smaller volumes (and BFD) being collected immediately under the canopy in the funnels. Regardless, higher quantities of *X. citri* subsp. *citri* were dispersed downwind with potential to cause disease either locally (20) or at distances in excess of 50 km during hurricane conditions (19,25).

Conversely, reducing wind speed can reduce pathogen dispersal, disease spread, and consequently epidemic development. Windbreaks and planting strategies may be used to lower wind speeds in groves and reduce disease severity (2,22). By minimizing splash dispersal and wind-assisted

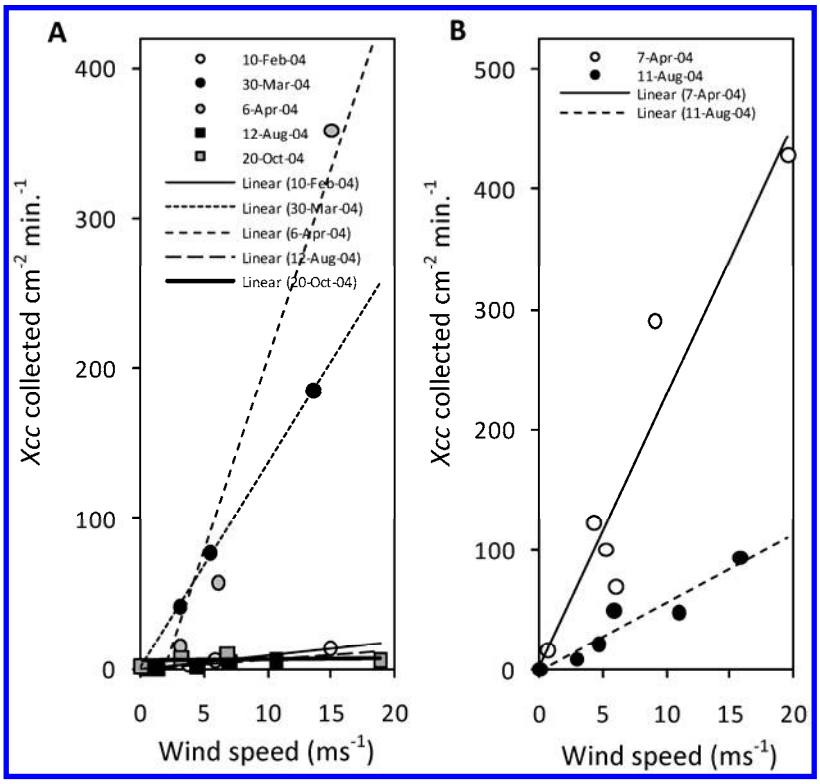

Fig. 8. Relationship between wind speed and the quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected by panels downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in seven separate experiments. Samples collected from panels at 1.3 m height are shown in **A,** five experiments, and **B,** two experiments. Regression solutions are shown in Table 4.

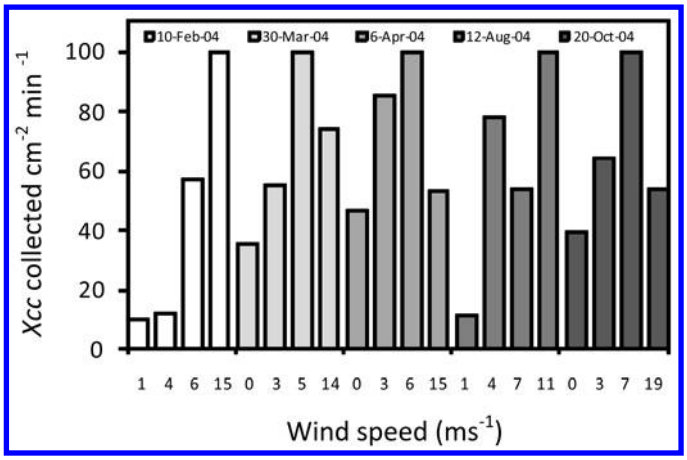

Fig. 9. Quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected at different wind speeds by funnels at ground level from canker-infected grapefruit canopies subject to simulated wind-rain events in five separate experiments. Data in each experiment are normalized as a percentage of the maximum collected in any treatment in that experiment (% = [Quantity collected in sample ÷ maximum collected in experiment] × 100).

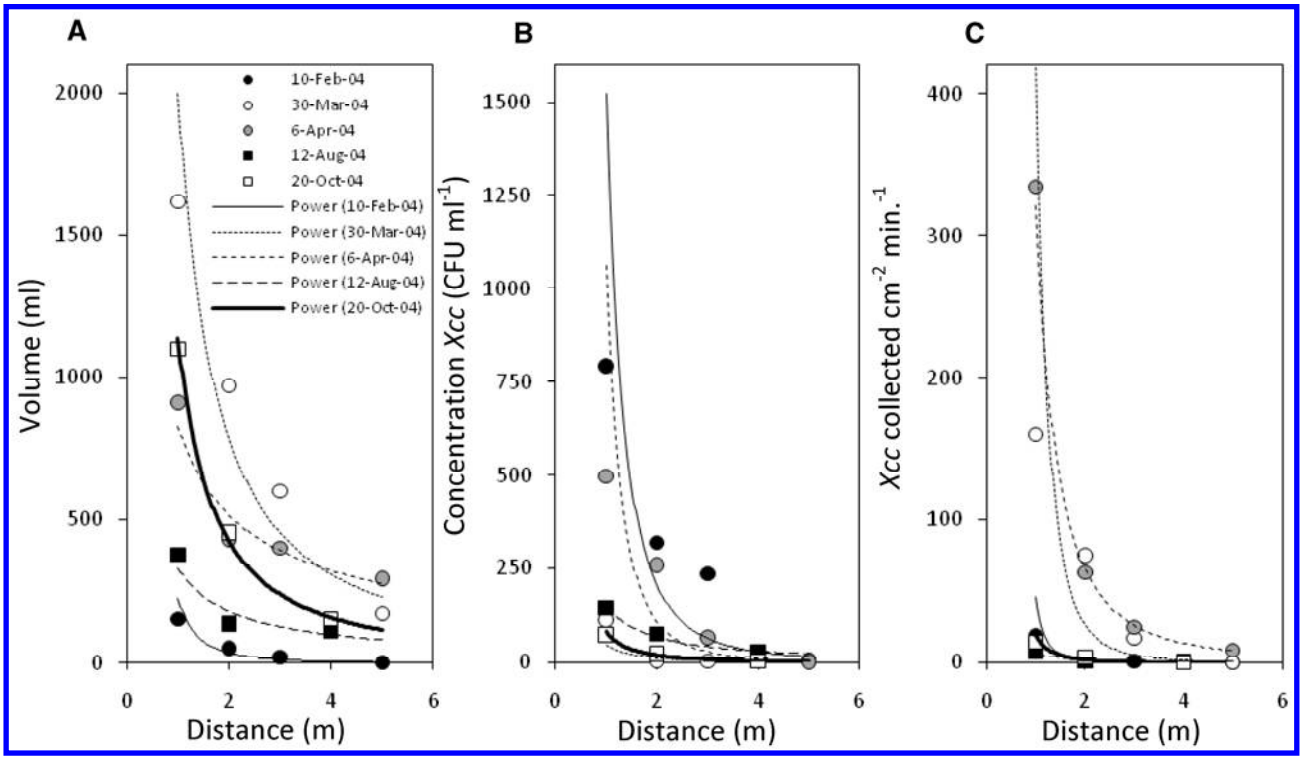

Fig. 10. Relationship between distance and **A,** volume of water (ml), **B,** concentration (CFU ml^{-1}), and **C,** quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected by panels downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in five separate experiments. Regression solutions can be found in Table 5.

Table 5. Inverse power law relationship[a] between distance from canker-infected canopies of grapefruit trees and volume of splash collected, concentration (CFU ml^{-1}), and bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected by both panel and funnel collectors

Collection device	Variable	Month[b]	Intercept (a)	Slope (b)	R^{2c}	F^{d}	P^{e}
Panel	Volume (ml)	10 Feb 04	153.7	–1.77	0.99	278	0.0036
		30 Mar 04	1,660.2	–0.98	0.96	80	0.012
		11 Aug 04[a]	889.4	–0.79	0.96	124	0.008
		12 Aug 04	370.7	–1.14	0.95	38.7	0.113
		20 Oct 04	1,103.3	–1.33	0.99	987	0.0225
	CFU ml^{-1}	10 Feb 04	797.9	–1.35	0.97	74	0.013
		30 Mar 04	113.9	–4.74	0.99	425	0.0024
		11 Aug 04[a]	508.3	–1.41	0.94	35	0.0282
		12 Aug 04	146.1	–1.05	0.99	230	0.0466
		20 Oct 04	73.9	–1.71	0.99	314	0.0399
	BFD (bacteria cm^{-2} min^{-1})	10 Feb 04	19.1	–3.01	<0.99	7,319	0.0001
		30 Mar 04	163.2	–1.54	0.96	43	0.0226
		11 Aug 04[a]	335.0	–2.40	0.99	41,989	<0.0001
		12 Aug 04	7.3	–2.23	0.99	1515	0.0182
		20 Oct 04	14.2	–2.10	0.99	218	0.0478
Funnel	Volume (ml)	10 Feb 04	14.2	–0.92	0.99	907	0.0235
		30 Mar 04	9.1	–0.81	0.99	1,767	0.0168
		11 Aug 04[a]	19.4	–0.90	0.99	355	0.0375
		12 Aug 04	11.4	–0.86	0.99	468	0.0021
		20 Oct 04	6.9	–1.21	0.99	10,100	<0.0001
	CFU ml^{-1}	10 Feb 04	332	–0.07	0.08	5	0.3
		30 Mar 04	4,314	–0.41	0.98	89	0.075
		11 Aug 04[a]	8,050	–0.32	0.96	60	0.09
		12 Aug 04	813	–0.43	0.95	58	0.0169
		20 Oct 04	544	–0.51	0.86	14	0.0664
	Bacteria (bacteria cm^{-2} min^{-1})	10 Feb 04	104.0	–1.04	0.99	1,310	0.0195
		30 Mar 04	741.3	–1.33	1.00	2,420,205	0.0005
		11 Aug 04[a]	4,438.1	–1.09	0.99	47,820	0.0032
		12 Aug 04	228.9	–1.29	0.99	24,970	<0.0001
		20 Oct 04	443.0	–0.97	0.99	213	0.0047

[a] Inverse power law model, $y = ax^b$ (a = intercept, b = slope).
[b] Data for each date are averaged across wind speeds.
[c] R^2 = Coefficient of determination (proportion of variability accounted for by model).
[d] F = F distribution value that tests goodness of fit for the model.
[e] P = Probability the F value is significant.

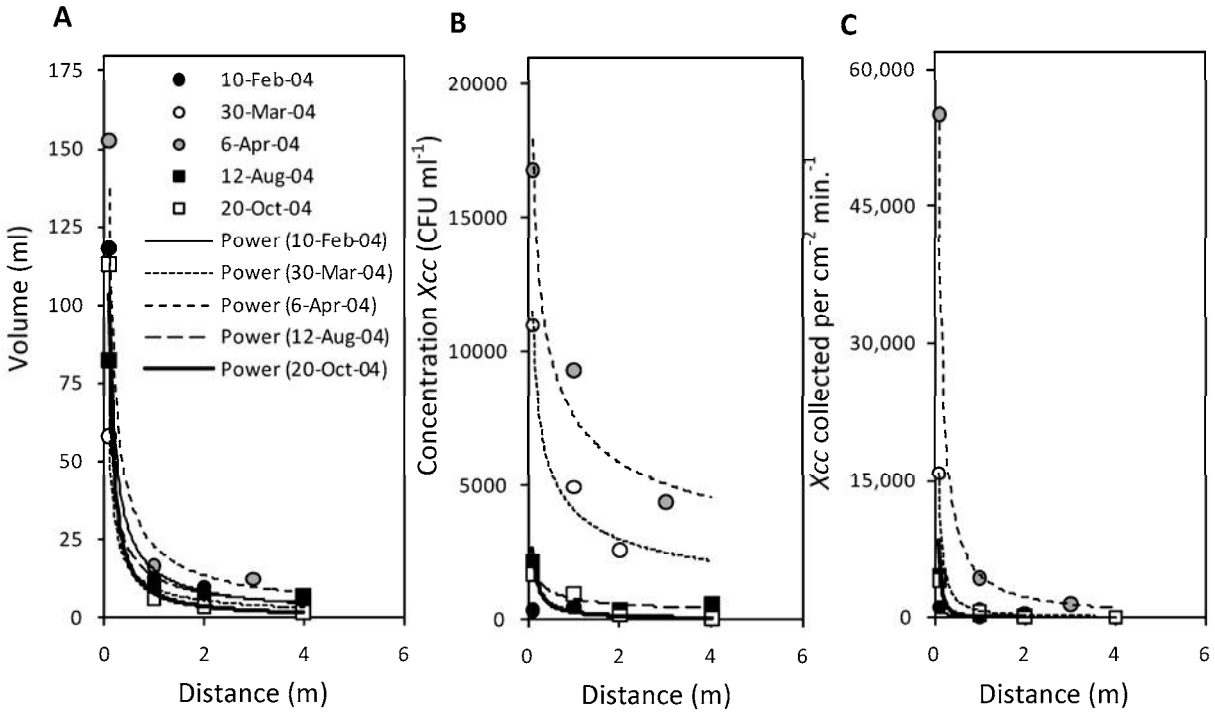

Fig. 11. Relationship between distance and **A,** volume of water (ml), **B,** concentration (CFU ml^{-1}), and **C,** quantity of bacteria (bacteria flux density [BFD] bacteria cm^{-2} min^{-1}) of *Xanthomonas citri* subsp. *citri* collected by funnels underneath and downwind from canker-infected grapefruit canopies subject to simulated wind-rain events in five separate experiments. Regression solutions can be found in Table 5.

infection, the rate of epidemic development can be reduced. Furthermore, avoiding other management practices, such as overhead irrigation, will also reduce spread (33), and integrating various approaches (2,22) should reduce the amount of disease further.

Samplers greater distances downwind of the canopy collected less *X. citri* subsp. *citri*, and the relationship between the quantity of bacteria collected and distance was described by an inverse power law model (10,24). *X. citri* subsp. *citri* have been sampled at various distances downwind from infected citrus plants (4,6,39). These experiments relied on wind/rain simulation, and inevitably there was a decline in wind speed with distance. Why there was no decline in CFU ml^{-1} with distance for the funnel samples on 10 February is not known, but it might be due to the somewhat variable nature of canopies in relation to windblown spray, and the small size of the funnel sampler, which could also lead to a less representative sample. Nonetheless, the rapid decline in quantity collected on other dates was likely due, in part, to declining wind speeds with distance, allowing droplets to be deposited close to the source. *X. citri* subsp. *citri* is effectively dispersed from the canopy in wind-driven rain splash, so it is not surprising that the parameters of CFU ml^{-1}, volume, and BFD collected all have similar relationships with distance. Larger droplets often contain a greater number of propagules (8,12,13), and these splash droplets would be the first to fall as wind speed declines. Smaller droplets carrying fewer propagules might travel further, resulting in a lower concentration (CFU ml^{-1}) further downwind, as observed in this study. In a real rainstorm, the wind shadow effect is likely to be less pronounced. In rainstorms, air masses travel across the landscape; whereas in these simulated experiments we were pushing generated wind against highly resistant still air, resulting in a rapid decline in wind speed with distance. Thus, considering the inevitable loss in wind speed with distance in these simulated conditions, the results are likely to be conservative and more bacteria would be dispersed further in an equivalent field situation.

Increased wind speed causes an increase in dispersal of *X. citri* subsp. *citri* in wind-driven splash downwind of a canker-infected canopy. The epidemiological significance of this windborne inoculum in tropical wet environments is likely to be considerable. Both rain intensity and high wind speed can interact to produce conditions for dispersing large quantities of bacteria out of a canker-infected citrus canopy, although very local dispersal might also occur in calm conditions (33). Disease and crop management aimed at reducing sources of inoculum and wind speeds in a grove should help minimize disease spread through windborne inoculum.

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