Phytopathol. Mediterr. (2010) 49, 42–50

Infection and dispersal processes of *Pseudomonas syringae* pv. *coriandricola* on coriander

Stephen J. REFSHAUGE [a], Murali NAYUDU[b], John VRANJIC[c] and Clive H. BOCK[d]

[a]CSIRO Division of Plant Industry, Clunies Ross Street, Black Mountain, ACT 2601, Australia
[b]School of Botany and Zoology, Australian National University, Canberra, ACT 0200, Australia
[c]Australian Government - Department of the Environment, Water, Heritage and the Arts, GPO Box 787, Canberra ACT 2601, Australia
[d]USDA-ARS-SEFNTRL, 21 Dunbar Road, Byron, Georgia 31008, USA

Summary. An Australian isolate of *Pseudomonas syringae* pv. c*oriandricola* (*Psc*) was used to study aspects of dispersal of the pathogen and infection of coriander. Needle inoculation of *Psc* in the stem of coriander resulted in up to 94% plant mortality. The total biomass of inoculated plants decreased significantly four weeks after inoculation as compared to the control plants. Systemic infection was rapid and one week after inoculation a bacterial population of about 10^4 to 10^8 cfu g^{-1} was isolated from different parts of the stems and roots. Surface contamination of coriander seed with *Psc* prior to planting resulted in low disease incidence (8%). However, spray inoculation of healthy coriander plants with *Psc* at concentrations equal to or greater than 10^3 CFU mL^{-1} caused disease on the leaves, suggesting infection was common through the stomata. Splash dispersal of *Psc* was demonstrated, with disease being observed on surrounding coriander seedlings. *Psc* bacteria were dispersed up to 70 cm from the inoculum source.

Key words: Coriander blight, *Coriandrum sativum*, epidemiology, disease spread.

Introduction

Pseudomonas syringae pv. c*oriandricola* (*Psc*) causes bacterial blight of coriander (*Coriandrum sativum*), and is a severe disease of the coriander crop in America (Cooksey *et al.*, 1991; Pernezy *et al.*, 1997), Australia (Gooden *et al.* 1995; Dennis and Wilson, 1997; Refshauge and Nayudu, 2001) and Europe (Taylor and Dudley, 1980; Toben and Rudolph, 1996; Cazorla *et al.*, 2005). Until 1993, coriander was a lucrative alternative crop in Australia, with average yields of 1.5 t ha^{-1} worth up to AU$1000 t^{-1} (Benson, 1997; Dennis and Wilson, 1997). However, epidemics of bacterial blight of coriander have subsequently reduced yield significantly, which has resulted in reduced planting of coriander in Australia to approximately one fifth of peak levels (Dennis and Wilson, 1997).

The disease appears in the field during flowering (Toben and Rudolph, 1996) and causes brown lesions on the shoots and inflorescences, which result in wilting and, in severe cases, plant death (Mavridis *et al.*, 1989; Toben *et al.*, 1991; Toben and Rudolph, 1996). The disease is seed-borne and the pathogen has a short survival period in crop trash and soil (Toben and Rudolph, 1996; Dennis and Wilson, 1997; Toben and Rudolph, 1997). Infected seeds may become shrivelled and discoloured, reducing the quality of the coriander seed.

Previous studies of *P. syringae* pathovars indicate that stomata and wounds are important sites of entry for various plant hosts (Crosse, 1966; Panopoulos and Schroth, 1974; Hattingh *et al.*, 1989; Surico, 1993a,b). Once entry is gained, infection becomes systemic via the host's vascular system (Walker, 1969; Hattingh *et al.*, 1989; Sigee, 1993; Surico, 1993b; Hallmann *et al.*, 1997).

Corresponding author: C.H. Bock
Fax: +1 478 956 2929
E-mail: clive.bock@ars.usda.gov

An examination of infected coriander tissues revealed an accumulation of *Psc* in leaf veins, xylem vessels and adjacent pith cells, indicating that the pathogen uses the hosts' vascular system for multiplication and transport (Refshauge and Nayudu, 2001). While it is clear that *Psc* systemically infects coriander, the processes of dispersal and infection have not been studied in detail. A better knowledge of these processes can provide valuable information for insight into disease spread and serve as a basis for disease management. With splash-dispersed pathogens, such as *Phytophthora cactorum*, the use of various different ground covers (hay or artificial mulches) was shown to affect dispersal of the pathogen from strawberry fruits (Madden *et al.*, 1993). Resistance has been detected in several coriander breeding lines; however all currently available varieties exhibit susceptibility ranging from small isolated, local lesions to systemic infection (Hooper and Dennis, 2002).

The objective of this study was to gain information on infection processes of *Psc* on coriander, its effect on the host plant, and to study the dispersal of the pathogen.

Materials and methods

Bacterial strain

Strain 1088b of *Psc* (obtained from J. Dennis and J. Goodan, South Australian Research and Development Institute, Adelaide, Australia) was used in these studies. Young cultures were grown on King's B medium (King *et al.*, 1954) at 25°C for 24 h. In addition, affiliation of the strain was checked with carbon source utilisation using an Oxoid BIOLOG™ GN2-Microplates™ system (Oxoid Australia Pty. Ltd., West Heidelberg, Australia).

Coriander plants

Coriander seeds used in this study were surface-sterilised in 0.5% HCl for 24 h and germinated at 20°C on Herridges medium (Delves *et al.*, 1986) in Petri dishes. Except where stated otherwise, coriander plants were grown in 150 mm pots containing a standard potting mix (AMGROW, Sydney, Australia) and maintained in a controlled environment greenhouse with a natural photoperiod at 25°C/15°C (day/night), and were watered daily.

Effects of coriander blight on survival and plant biomass

To assess survival, fifty plants were inoculated by dipping a sterile 25 gauge needle into a 24-h-old-culture of *Psc* grown on King's B medium, and inserting the needle through the crown region of a two-week-old plant, thus ensuring transfer of a similar inoculum quantity to each crown. Five control plants were wounded with a sterile needle previously dipped in sterile distilled water (SDW). The inoculated plants and the control plants were kept in a greenhouse and checked regularly. The number of dead plants was counted after 6 weeks (Refshauge and Nayudu, 2001), and the percent mortality calculated.

To investigate the effect of the disease on the plant biomass, two-week-old coriander seedlings were wound-inoculated as described above with two strains of *Psc*, a wild-type strain 1088b, and a rifampicin-resistant strain (*Psc* rif) which was a spontaneous mutant resistant to 200 μg mL^{-1} rifampicin on nutrient agar. The rif mutant was included to determine whether antibiotic resistance to rifampicin caused a change in pathogenicity compared to the wild type, which would preclude its use in the experiment on plant colonisation, or other studies (Refshauge, 2000; Refshauge and Nayudu, 2001). Control plants were inoculated with a sterile needle previously dipped in SDW (effecting the same damage, but adding no *Psc* inoculum). Plants were arranged in a randomised complete block design and samples were harvested weekly over 5 weeks. Five replicates (individual plants) of each treatment (wild type *Psc*, *Psc* rif, control) were randomly sampled at each harvest and roots and shoots were separated at the crown, gently cleaned of soil and oven-dried for 3 days at 70°C. The dry weights of roots and shoots were recorded and the root:shoot ratios (RSR) calculated.

Colonisation of coriander by *Psc*

The location and movement of the pathogen within the host was investigated by inoculating two-week-old plants with the *Psc* rif mutant in the crown region; this was done by inserting a needle with inoculum through the crown region as described above. One-cm-long sections of roots, stems, petioles and leaves were sampled weekly for four weeks. Two replicate samples were collected for each tissue type, weighed, surface-sterilised in

70% ethanol for 10 s, rinsed in SDW and macerated with a glass rod in 1 mL of nutrient broth. Samples of the suspension were 10-fold diluted in nutrient broth, vortexed, and 100 μL samples were spread onto nutrient agar medium supplemented with 200 μg L^{-1} rifampicin. The number of colonies on each plate was counted after 24 h incubation at 25°C.

Seed infection and plant wounding

External seed inoculation was achieved by coating coriander seeds with a bacterial population made from the wild-type *Psc* strain (1088b). A culture of *Psc* was grown in nutrient broth (Oxoid nutrient broth CM1, 25 g L^{-1}, Difco yeast extract 5 g L^{-1}) for 24 h at 25°C. Ten mL of the bacterial culture was concentrated by centrifugation at 1300 *g*. The pellet was resuspended in SDW and this was repeated twice before resuspending the pellet in 2 mL of the supernatant solution. The suspension was then added to 50 mL of 15% methylcellulose (w:v) and thoroughly mixed. Coriander seeds were mixed into the solution, removed and coated in potter's clay. Inoculum-free seed was obtained by surface-disinfecting seeds in 0.5% HCl for 24 h, then rinsing in SDW before mixing in uninoculated methylcellulose (15% w:v) and coating in potter's clay. Seeds were sowed in potting mix and thirty days after emergence half of the plants in each treatment were selected randomly and wounded by inserting a sterile needle through the crown region to check if any *Psc* on the surface might cause infection. There were 12 plants in each treatment, with all plants being arranged in a randomised block design in a greenhouse (Refshauge and Nayudu, 2001). Disease scores (Table 1), plant and meristem heights were recorded weekly for up to 40 days after wounding. Seed number and the dry weights of seeds and shoots were determined for each plant.

Concentration of inoculum, splash dispersal

i) Concentration of inoculum: to determine the effect of inoculum quantity, one-month-old coriander plants were spray-inoculated to run-off with 0, 10^1, 10^3, 10^5, 10^7 and 10^9 CFU mL^{-1} wild-type *Psc*, prepared by dilution from a suspension at 10^9 CFU mL^{-1} (determined photometrically). Plastic bags were placed over each plant for 24 h after inoculation to maintain humidity. Pots were irrigated from below and maintained in the greenhouse. Disease incidence and severity were recorded every 4 days for 40 days (Refshauge and Nayudu, 2001).

Table 1. Disease scoring system used to assess the progress of coriander blight.

Disease score	Symptoms
0	No visible symptoms of disease
1	Lesions or blackening of veins on leaves
2	Localised spread within leaf veins
3	Dehydration and death of leaves
4	Dehydration and death of entire branches
5	Dehydration of whole plant
6	Death of whole plant

ii) Splash dispersal: four seedling trays (each 30×40 cm) containing coriander seedlings were arranged in a rectangle (60×80 cm) with a small upturned pot in the centre of the square. A 9-cm diameter Petri dish containing a 3-mm-deep suspension of a wild-type *Psc* strain of about 3×10^8 CFU mL^{-1} was suspended on the upturned pot. Splash was generated by drops of SDW falling from a height of 2 m into the Petri dish containing the suspension of *Psc*. Water drops from a hypodermic needle inserted into the base of a container holding 500 mL water fell at a rate of 30 drops min^{-1} for 4 min. To simulate natural conditions after splash treatment, seedlings were left uncovered and were bottom irrigated in the greenhouse (Refshauge and Nayudu, 2001), and assessed 28 days after splash inoculation. The incidence of diseased plants was determined in each consecutive 10 cm block from the source in 100 cm^2 (10×10 cm) blocks. The distance travelled by *Psc*-containing droplets was obtained by repeating the experiment with two rows of 9 cm Petri dishes side-by-side containing King's B medium with dishes placed at 10, 20, 30, 40, 50, 60, 70, 80 and 90 cm from the inoculum source. The number of drops on each plate was counted in one row, and in the second row spread, to obtain CFUs.

Statistical analysis

Analysis of variance (ANOVA) was used to determine treatment effects in the inoculation

experiments with the two strains (*Psc* rif mutant and wild-type *Psc*) and to investigate the effect of seed infection and wounding. Differences were considered significant at $P \leq 0.05$. Relationships between disease incidence, number of CFUs and distance from the inoculum source were analysed by regression, and an exponential model ($y=ae^{-bx}$) was fitted to the data. Correlation analysis was used to investigate associations between droplet number, CFU and disease incidence. All analyses were done with SAS V9.1 (SAS, Cary, NC, USA).

Results

Effects of coriander blight on survival and plant biomass

Of the 50 inoculated plants, 47 died (94%). Plants in the control treatment did not develop any disease symptoms. The total plant biomass of *Psc*-inoculated plants was lower compared to the control plants (Figure 1a-d). ANOVA demonstrated that total dry weight, shoot and root dry weights and the root-to-shoot ratios were significantly reduced ($P<0.05$) at the 4th and 5th weeks after inoculation. No significant difference was detected between plants inoculated with the wild-type and the rif mutant strains of *Psc* (Figure 1a–d).

Colonisation of coriander by *Psc*

Plant colonisation was rapid, and the *Psc* rif-mutant was widespread at the time of the first sampling. Depending on the time of sampling, concentration varied from zero to 10^8 CFU g^{-1}. There were no consistent trends (Figure 2). Despite data transformations, there was large variation among replicates in this experiment.

Seed infection and plant wounding

No uninoculated plants developed disease symptoms, and only five of the inoculated seeds produced infected plants (Table 2). Disease incidence was higher on seed inoculated on December 1st and 13th. Only maximum plant height and meristem height early in plant growth appeared to be reduced by seed inoculation. There was no effect of seed inoculation after December 13th in disease

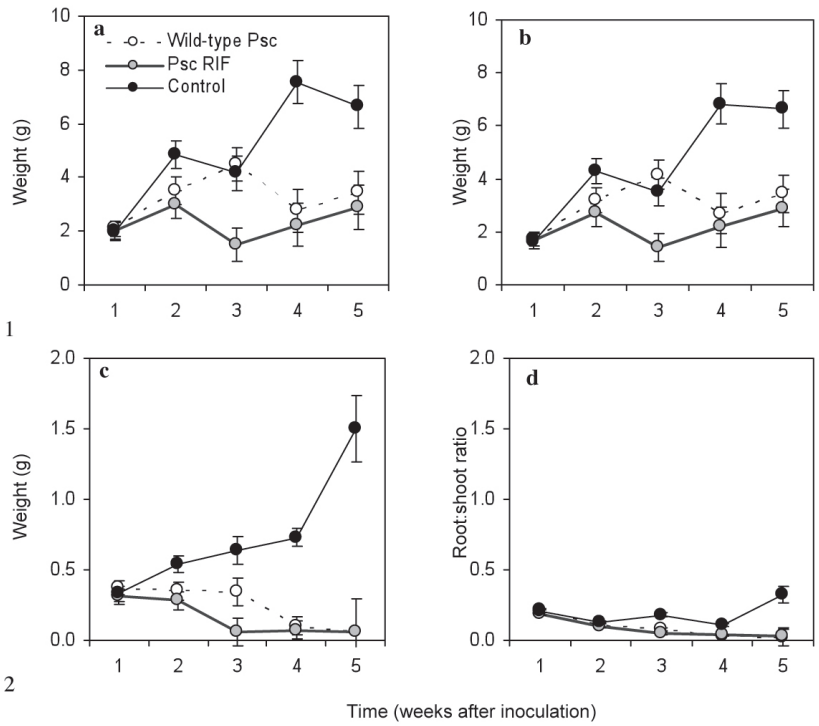

Figure 1. Effect of coriander blight on a) total plant dry weight, b) shoot dry weight, c) root dry weight, and d) root-shoot ratios of fortnight-old seedlings inoculated with wild-type *Pseudomonas syringae* pv. c*oriandricola (Psc)*, *Psc* rif and an uninoculated control. Standard errors of the means are indicated.

Table 2. Effect of seed contamination with *Pseudomonas syringae* pv. c*oriandricola* and subsequent wounding of the plant crown in inducing bacterial blight of coriander.

Category	Days after emergence	Seed infected [a]		Plant wounded [b]	
		No	Yes	No	Yes
Disease score [c]	14	0 a [d]	0 a	0 z	0 z
	23	0 a	0.3 b	0.13 z	0.17 z
	28	0 a	0.33 a	0.17 z	0.17 z
	35	0.04 a	0.46 b	0.21 z	0.29 z
	42	0 a	0.5 a	0.21 z	0.29 z
	49	0.04 a	0.6 a	0.21 z	0.38 z
	56	0.08 a	0.63 a	0.25 z	0.46 z
	63	0.13 a	0.71 a	0.38 z	0.46 z
	70	0.13 a	0.75 a	0.38 z	0.5 z
Maximum plant height (mm)	14	14.2 a	9. b	12.2 z	11. z
	23	11.5 a	10.3 a	10.5 z	11.3 z
	28	64.2 a	53.1 a	50. z	58.2 z
	35	104.6 a	91.5 a	97.6 z	98.5 z
	42	241.8 a	216.3 a	233.4 z	224.7 z
	49	355.8 a	357.5 a	357.5 z	355.8 z
	56	465. a	450.2 a	451.9 z	463.3 z
	63	474.4 a	461.5 a	460.2 z	475.6 z
	70	483.1 a	499.8 a	474. z	508. z
Meristem height (mm)	14	8.1 a	4.2 b	6.2 z	6.1 z
	28	12.9 a	11.5 a	12.5 z	11.9 z
	35	53.3 a	38.7 a	46.1 z	45.9 z
	42	211.5 a	176.8 a	202.1 z	186.3 z
	49	344.4 a	326. a	331. z	339.4 z
	56	446.9 a	422.9 a	433.1 z	436.7 z
	63	493.9 a	480.6 a	477.1 z	497.5 z
	70	500.6 a	519. a	593.3 z	526.3 z
Harvest data	Umbel wt (g)	2.88 a	2.28 a	2.57 z	2.59 z
	Seed No.	111.3 a	76.7 a	102.7 z	85.3 z
	Shoot wt (g)	3.6 a	3.5 a	3.3 z	3.8 z
	Root wt (g)	0.62 a	0.61 a	0.63 z	0.6 z

[a] Inoculated seeds were coated with *Pseudomonas syringae* pv. c*oriandricola* (*Psc*) in methylcellulose and covered in potter's clay. Inoculum-free seed was treated the same way but no *Psc* was added. Numbers with the same letter are not significantly different by means separation analysis.

[b] Thirty days after emergence, half the plants in each treatment were selected at random and wounded by inserting a sterile needle through the crown region. Numbers with the same letter are not significantly different by means separation analysis.

[c] Twelve replicates of each treatment with all plants being arranged in a randomised block design. Disease scores and plant heights were recorded weekly for up to 40 days after wounding, when the numbers of seeds and the dry weights of seeds and shoots were measured for each plant.

[d] Based on analysis of variance. Treatment means separation was achieved using Tukey's HSD test.

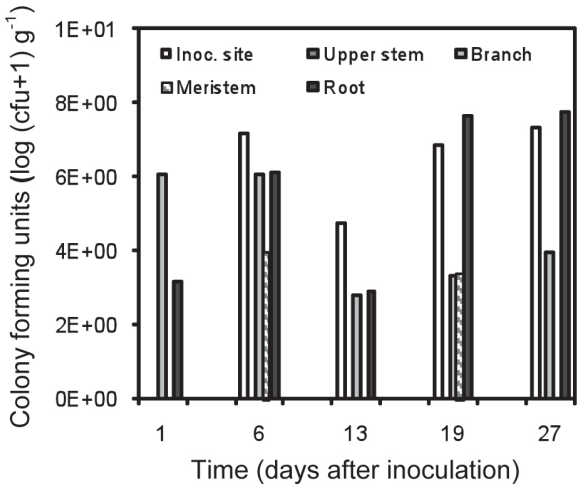

Figure 2. Location and movement of *Pseudomonas syringae* pv. c*oriandricola* (*Psc*) within coriander plants. Two-week-old plants were inoculated with a normal growth-rate rif mutant of *Psc* in the crown, and 1-cm sections of roots, stems, petioles and leaves were taken at weekly intervals and the bacteria extracted and dilution-plated to estimate CFUs g^{-1}. On day 1 the quantity of bacteria at the inoculation site were too numerous to count.

incidence, plant or meristem height, or any yield variable. Wounding of the crown had no effect on disease incidence, plant height, seed mass, seed number or plant biomass (Table 2).

Concentration of inoculum, splash dispersal

Disease symptoms developed with concentrations ≥10^3 CFU mL^{-1}. At concentrations of 10^7 and 10^9 CFU mL^{-1}, symptoms developed in 8 days (Figure 3a and b), resulting in the mortality of some plants. Disease developed faster at the higher concentrations, but final disease incidence was not greater above 10^3 CFU mL^{-1}. Lower concentrations of inoculum developed less severe disease at any given time. No symptoms appeared on plants sprayed with 10^1 CFU mL^{-1} or the control solution.

Splash dispersal of *Psc* resulted in infection of surrounding coriander seedlings. The incidence of

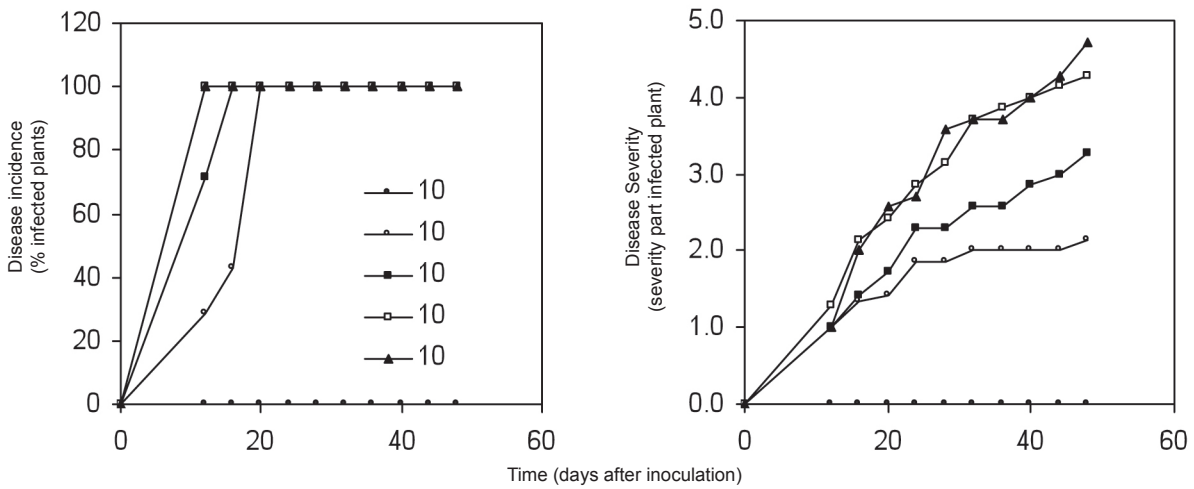

Figure 3. Incidence (a) and severity (b) of coriander blight on coriander plants spray-inoculated with *Pseudomonas syringae* pv. c*oriandricola* in nutrient broth at concentrations of 0 (control), 10^1, 10^3, 10^5, and 10^7 CFU mL^{-1}.

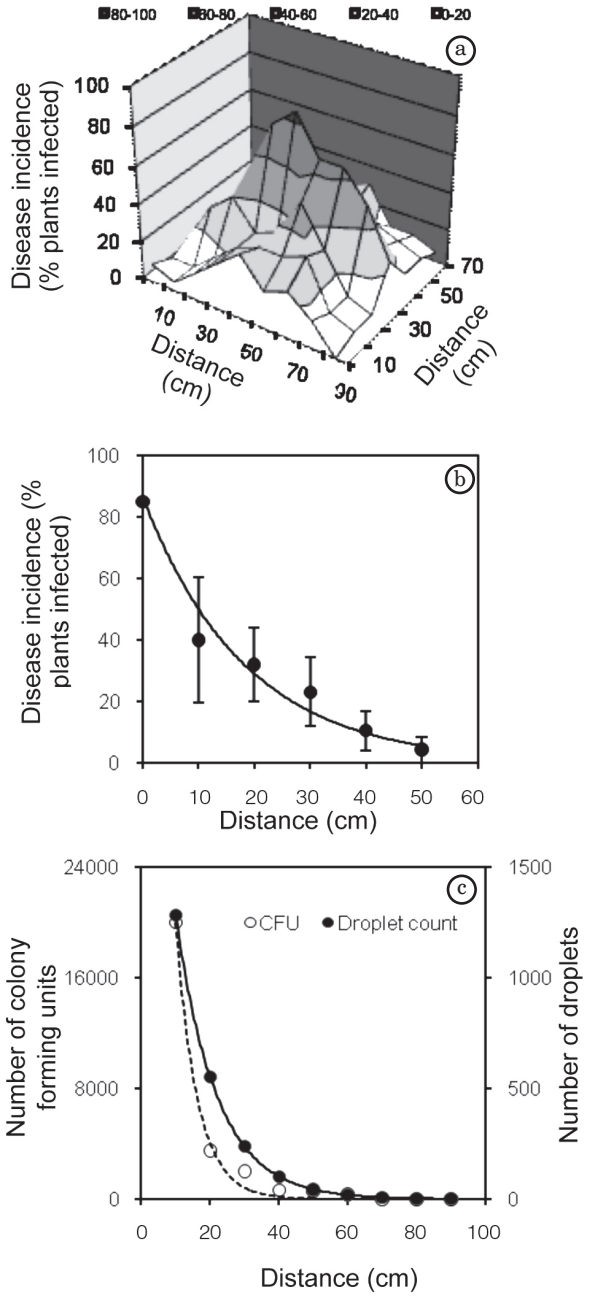

Figure 4. (a) Incidence of coriander blight (% plants infected in each 100 cm^2) in a stand of coriander seedlings 28 days after splash dispersal of *Pseudomonas syringae* pv. *coriandricola* (*Psc*) from a central inoculum source; (b) relationship between incidence of coriander blight and distance from inoculum source ($y=86.832e^{-0.0055x}$, $R^2=0.96$); (c) Number of droplets and colony forming units (CFUs) of *Psc* splash dispersed on King's B medium at different distances from a point source (droplets, $y=97981e^{-0.1592x}$, $R^2=0.99$, CFUs $y=2983e^{-0.0843x}$, $R^2=0.99$).

Table 3. Percentage of droplets and CFUs of *Pseudomonas syringae* pv. *coriandricola* collected on King's B medium at different distances from the source of splash inoculum.

Distance from inoculum source (cm)	Total droplets (%)	Total CFU (%)
10	-	74.0
20	58.4	13.0
30	27.1	7.4
40	10.5	2.4
50	3.5	2.0
60	0.5	1.3
70	0	0
80	0	0
90	0	0

infection in the coriander seedlings was highest when close to the source of inoculum and decreased with distance (Figure 4a), showing a significant negative exponential decrease in incidence of disease with increasing distance from the inoculum source ($R^2=0.96$; $F=156$; $P<0.001$, Figure 4b) with plants developing disease up to 45 cm from the source of splash. The dispersal of bacteria on King's B medium showed a similar pattern of distribution (Figure 4c). Over 95% of droplets fell within 40 cm of the inoculum source (Table 3), and no colonies were found beyond 70 cm from the inoculum source. There was a positive correlation between the incidence of disease and both droplet number ($r=0.9215$, df=8, $P<0.05$) and CFUs dispersed ($r=0.9639$, df=8, $P<0.05$). There was also a correlation between CFUs and droplet number ($r=0.9901$, df=14, $P<0.05$).

Discussion

Wound inoculation of coriander seedlings with *Psc* caused high mortality, and illustrates the damage caused by this disease. Bacterial blight diseases generally reduce plant host biomass (Müller *et al.*, 1997; Garry *et al.*, 1998), and the obtained results confirmed that the dry weight of coriander was reduced by infection with *Psc*. The decreasing root-shoot ratio observed in infected plants indicates that resource allocation was altered to favour shoot growth. This effect has previously been seen in *Ascochyta* blight of peas (Garry *et al.*, 1998). The population dynamics of

bacterial pathogens within their host plants has been reviewed by Hirano and Upper (1990), who reported that numerous bacterial plant pathogens rapidly achieve large *in planta* populations, and the results of the present study are in agreement with that study, showing that *Psc* populates its host rapidly and is readily transmissible within the host. This supports previous visual observations of *Psc* in different cell types of coriander (Refshauge and Nayudu, 2001).

Seed infection is considered to be essential for the occurrence of many seed-borne diseases, including pea and coriander bacterial blights (Taylor and Dudley, 1980; Roberts, 1992; Rennie, 1998). Our results confirm that external contamination can lead to disease (though internal infection of the seed might cause greater disease severity). Even though a relatively low incidence of seed infection was found in this study, Dennis and Wilson (1997) reported that a very low frequency (0.5%) of seed contamination can lead to a very high (>25%) disease incidence in the field. Apart from seed-borne inoculum, wounding the host plant has been implicated in higher rates of infection (Walker, 1969; Hallmann *et al.*, 1997); although no effect of wounding on coriander plants grown from inoculated seed was recorded, this might be because older tissue is more resistant to infection. Infection from the inoculum-rich seed coating may have occurred through the emerging cotyledons or through subsequent leaves, but further trials are required to determine the true impact of seed infection and subsequent wounding on disease incidence.

Various methods of pathogen dispersal have been described and demonstrated (Walker, 1969; Al-Mousawi *et al.*, 1982; Hattingh *et al.*, 1989; Mansvelt and Hattingh, 1989; Rudolph, 1995; Hallmann *et al.*, 1997). Bacteria commonly enter the host tissues through the stomata. The results of the spray inoculation and splash dispersal studies suggest that stomata are entry sites exploited by *Psc*. Roberts (1993) recognised rain splash as a means of dispersing the pea blight pathogen, *P. s.* pv. *pisi*. In the present study, splash was sufficient to disperse *Psc* over short distances, with disease developing up to 45 cm from the splash source. Using the agar-based splash assay, viable bacteria were collected up to 70 cm from the inoculum source. This is typical for splash dispersed pathogens (Fitt *et al.*, 1989). Importantly, disease developed on plants throughout this range, showing that low quantities of bacteria were sufficient to cause disease. A useful and practical consideration is that splash dispersal of pathogens in some crops might be reduced by the use of straw or various ground cover mulches that reduce rain drop impact (Madden *et al.*, 1993).

The rapid colonisation of coriander by *Psc* explains, in part, the considerable virulence of this pathogen. Further, the apparent ease with which inoculum can be transferred between plants may account for the severe crop losses observed despite low levels of seed infection (Dennis and Wilson, 1997). Sowing clean seed is an important way to minimise inoculum in the developing crop, and the results demonstrating splash dispersal suggest ground covers might be used to reduce the risk of an abrupt epidemic (Madden *et al.*, 1993), and that overhead irrigation should be avoided.

Acknowledgments

This research was made possible through a research grant issued by D. Jacobs (AgSearch Australia Pty. Ltd., Harden, Australia). J. Gooden and J. Dennis (South Australian Research and Development Institute, Adelaide, Australia) are thanked for supplying *P. s.* pv. *coriandricola* strain 1088b, and Jan Gooden for her advice and help with culturing *Psc*.

Literature cited

Al-Mousawi A.H., P.E. Richardson, M. Essenberg and W.M. Johnson, 1982. Cotyledon and leaf ultrastructure of a bacterial blight-immune cotton line inoculated with a low-level of *Xanthomonas campestris* pv. *malvacearum*. *Phytopathology* 72, 1230–1234.

Benson D. 1997. Specialist crop reveals considerable potential. *Farming Ahead* 67, 7–8.

Cazorla F.M., M.A.Vázquez, J. Rosales, E. Arrebola, J. Navarro, A. Pérez-García and A. de Vicente, 2005. First report of bacterial leaf spot (*Pseudomonas syringae* pv. *coriandricola*) of coriander in Spain. *Journal of Phytopathology* 153, 181–184.

Cooksey D.A., H.R. Azad and A.O. Paulus, 1991. Leaf spot of cilantro in California caused by a nonfluorescent *Pseudomonas syringae*. *Plant Disease* 75, 101.

Crosse J.E. 1966. Epidemiological relations of the Pseudomonad pathogens of deciduous fruit trees. *Annual Review of Phytopathology* 4, 291–310.

Delves A.C., A. Matthews, D.A. Day, A.S. Carter, B.J. Carroll and P.M. Gresshoff, 1986. Regulation of the soybean-

Rhizobium nodule symbiosis by shoot and root factors. *Plant Physiology* 82, 588–590.

Dennis J.I. and J. Wilson, 1997. *Disease Control in Coriander and Other Spice Seeds*. Published by Rural Industries Research and Development Corporation (RIRDC) Research Paper No. 97, Barton, ACT2600, Australia, 41 pp.

Fitt B.D.L., H.A. McCartney and P.J. Walklate, 1989. The role of rain in dispersal of pathogen inoculum. *Annual Review of Phytopathology* 27, 241–270.

Garry G., M.H. Jeffrey and B. Tivoli, 1998. Effects of ascochyta blight (*Mycosphaerella pinodes* Berk. and Blox.) on biomass production, seed number and seed weight of dried-pea (*Pisum sativum* L.) as affected by plant growth stage and disease intensity. *Annals of Applied Biology* 132, 49–59.

Gooden D.J., M. Ramsey and C. Hayward, 1995. Bacterial blight in coriander. In: *Proceedings of the 10th Australasian Plant Pathology Society Conference,* Lincoln University, Christchurch, New Zealand, 44 (abstract).

Hallmann J., A. Quadt-Hallmann, W.F. Mahaffe and J.W. Kloepper, 1997 Bacterial endophytes in agricultural crops. *Journal of Microbiology* 43, 895–914.

Hattingh M.J., I.M.M. Roos and E.L. Mansvelt, 1989. Infection and systemic invasion of deciduous fruit trees by *Pseudomonas syringae* in South Africa. *Plant Disease* 73, 784–789.

Hirano S.S. and C.D. Upper, 1990. Population biology and epidemiology of *Pseudomonas syringae*. *Annual Review of Phytopathology* 28, 155–177.

Hooper P. and J. Dennis, 2002. *Coriander - Overcoming Production Limitations*. *Rural Industries Research and Development Corporation (RIRDC)* Publication No. 02/147, Barton, ACT 2600, Australia, 24 pp.

King E.O., M.K. Ward and D.E. Raney, 1954. Two simple media for the demonstration of pyocyanin and fluorescin. *Journal of Laboratory and Clinical Medicine* 44, 301–307.

Madden L.V., M.A. Ellis and L.L. Wilson, 1993. Field spread of anthracnose fruit rot of strawberry in relation to ground cover and Ambient Weather Conditions. *Plant Disease* 77, 861–867.

Mansvelt E.L. and M.J. Hattingh, 1989. Scanning electron microscopy of invasion of apple leaves and blossoms by *Pseudomonas syringae* pv. *syringae*. *Applied and Environmental Microbiology* 55, 533–538.

Mavridis A., H. Meier zu Beerentrup and K. Rudolph, 1989. Bacterial umbel blight of coriander in West Germany. In: *Proceedings of the 7th International Conference on Plant Pathology and Bacteriology*, Budapest, Hungary, 635–640.

Müller J., B. Völksch and W. Fritsche, 1997. Interactions between phytopathogenic *Pseudomonas* and plant cell cultures. In: *Developments in Plant Pathology Vol. 9: Pseudomonas syringae Pathovars and Related Pathogens*. (K. Rudolph, T.J. Burr, J.W. Mansfield, D. Stead, A. Vivian and J. Von Kietzell, ed.), Kluwer Academic Publishers, Boston, MS, USA, 305–310.

Panopoulos N.J. and M.N. Schroth, 1974. Role of flagellar motility in the invasion of bean leaves by *Pseudomonas phaseolicola*. *Phytopathology* 64, 1389–1397.

Pernezy K., R.N. Raid and J.B. Jones, 1997. Bacterial leaf spot of cilantro in Florida. *Plant Disease* 81, 232.

Refshauge S., 2000. *Bacterial Blight of Coriander*. Honors Thesis, School of Botany and Zoology, Australian National University, Canberra, Australia.

Refshauge S. and M. Nayudu, 2001. Infection by *Pseudomonas syringae* pv. *coriandricola* is responsible for bacterial blight of coriander. *Plant Science* 161, 635–639.

Rennie W.J., 1998. Seedborne Diseases. In: *The Epidemiology of Plant Diseases*. (D.G. Jones, ed.), Kluwer Academic Publishers, London, UK, 295–305.

Roberts S.J., 1992. Effect of soil moisture on the transmission of pea bacterial blight (*Pseudomonas syringae* pv. *pisi*) from seed to seedling. *Plant Pathology* 41, 136–140.

Roberts S.J., 1993. Effect of bacterial blight (*Pseudomonas syringae* pv. *pisi*) on the growth and yield of single pea (*Pisum sativum*) plants under glasshouse conditions. *Plant Pathology* 42, 568–576.

Rudolph K.W.E., 1995. *Pseudomonas syringae* pathovars. In: *Pathogenesis and Host Specificity in Plant Diseases*. (U.S. Singh, R.P. Singh, K. Kohmoto, ed.), Elsevier Science Ltd, Oxford, UK, 321 pp.

Sigee D.C., 1993. *Bacterial Plant Pathology: Cell and Molecular Aspects*. Cambridge University Press, London, UK, 337 pp.

Surico G., 1993a. Scanning electron microscopy of olive and oleander leaves colonized by *Pseudomonas syringae* subsp. *savastonoi*. *Journal of Phytopathology* 138, 31–40.

Surico G., 1993b. Symptom development in olive and oleander leaves inoculated with *Pseudomonas syringae* subsp. *savastanoi* and scanning electron microscopy of infections. *Petria* 3, 117–127.

Taylor J.D. and C.L. Dudley, 1980. Bacterial disease of coriander. *Plant Pathology* 29, 117–121.

Toben H., A. Mavridis and K. Rudolph, 1991. Bacterial umbel blight and seed decay of coriander caused by a nonfluorescent type of *Pseudomonas syringae*. In: *Proceedings of the 4th International Working Group on* Pseudomonas syringae *Pathovars*, Florence, Italy, 96–102.

Toben H. and K. Rudolph, 1996. *Pseudomonas syringae* pv. *coriandricola*, incitant of bacterial umbel blight and seed decay of coriander (*Coriandrum sativum* L.) in Germany. *Journal of Phytopathology* 144, 169–178.

Toben H. and K. Rudolph, 1997. Control of umbel blight and seed decay of coriander (*Pseudomonas syringae* pv. *coriandricola*). In: *Developments in Plant Pathology Vol. 9: Pseudomonas syringae Pathovars and Related Pathogens*. (K. Rudolph, T.J. Burr, J.W. Mansfield, D. Stead, A. Vivian, J. Von Kietzell, ed.), Kluwer Academic Publishers, Boston, MS, USA, 611–616.

Walker J.C. 1969. *Plant Pathology*. McGraw Hill Inc., Sydney, Australia, 819 pp.

Accepted for publication: January 4, 2010