Field dispersal of *Pseudomonas syringae* pv. *tomato*, *Xanthomonas campestris* pv. *vesicatoria*, and *Alternaria macrospora* by animals, people, birds, insects, mites, agricultural tools, aircraft, soil particles, and water sources

YOAV BASHAN

Department of Plant Genetics, The Weizmann Institute of Science, Rehovot 76 100, Israel

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Viable disseminating units of *Pseudomonas syringae* pv. *tomato* (Okabe) Young, Dye and Wilkie and *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye, the bacterial leaf pathogens of tomato and pepper, respectively, and *Alternaria macrospora* Zimm, the causal agent of *Alternaria* blight in cotton, were found to be carried by a wide variety of agents including animals, people, insects, mites, agricultural tools, aircraft, soil particles, and water sources. Of these, specific insects and tools commonly used for crop cultivation were the most heavily contaminated. Soil adhering to agricultural tools or carried by various water sources can also serve as a disseminating agent. It was concluded that nearly all accidental agents passing through the infested field may act as vectors of these pathogens.

BASHAN, Y. 1986. Field dispersal of *Pseudomonas syringae* pv. *tomato*, *Xanthomonas campestris* pv. *vesicatoria*, and *Alternaria macrospora* by animals, people, birds, insects, mites, agricultural tools, aircraft, soil particles, and water sources. Can. J. Bot. **64**: 276–281.

Les auteurs démontrent que plusieurs agents peuvent transporter les propagules du *Pseudomonas syringae* pv. *tomato* (Okabe) Young, Dye et Wilkie, du *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye, les pathogènes bactériens foliaires de la tomate et du piment respectivement, ainsi que *l'Alternaria macrospora* Zimm, l'agent causal de la flétrissure alternarienne du coton; ces propagules peuvent être transportées par plusieurs agents incluant les animaux, les gens, les insectes, les acariens, les outils agricoles, les avions, les particules de sol et les sources d'eau. Parmi ceux-ci, certaines espèces d'insectes ainsi que les outils communément utilisés pour la culture se sont avérés les plus contaminés. Le sol adhérant aux outils agricoles ou transporté par diverses sources d'eau contribue également à la dissémination des propagules. L'auteur conclut qu'à peu près n'importe lequel agent passant accidentellement à travers un champ infesté peut agir comme vecteur de ces organismes pathogènes.

[Traduit par le journal]

Introduction

Inoculum dispersal is of the utmost importance for the biology of any plant disease agent. Many phytopathogenic bacteria and fungi are remarkably well adapted to passive dispersal by wind, seeds, insects, vegetatively propagated plants, irrigation water, agricultural tools, and other means (18,19,27,35).

The dispersal mechanisms, highly dependent on environmental conditions, are not equally efficient (10). The importance of each means of transmission varies according to the conditions prevailing in the field, i.e., differences in plant cultivation techniques, sanitary conditions, weed control, monoculture, and growing season (29), and therefore several means acting simultaneously may be necessary to ensure dispersal.

The transmission of pathogenic agents is inefficient if their compatible hosts are long distances apart. Therefore, since many pathogenic agents usually find their host by accidental encounter, they must produce a large number of cell dispersal units.

Pseudomonas syringae pv. *tomato* (PST), *Xanthomonas campestris* pv. *vesicatoria* (XCV), and *Alternaria macrospora* (AM) are known to be transmitted by seeds, transplants, soil, nonhost plants, dry leaves, or plant debris (3,5,6,7,8,11,12,14,15,17,20,23,24,25,26,28,30,31,33,37).

The aim of this study was to find and evaluate the contribution of less conventional means of dispersal of these three leaf-disease agents in the field.

Materials and methods

Organisms

Pseudomonas syringae pv. *tomato* (Okabe) Young, Dye and Wilkie, *Xanthomonas campestris* pv. *vesicatoria* (Doidge) Dye, and *Alternaria macrospora* Zimm were isolated from infected host plants during 1983–1984. Isolation of these pathogens was also attempted from several other organisms or substrates, which are summarized in Table 1.

Tomato plants (*Lycopersicon esculentum*) cv. M-82 and cv. VF-314, pepper plants (*Capiscum annuum*) cv. Ma'or, and cotton plants (*Gossypium barbadense*) cv. Pima were commercially grown in open fields in the Sharon region, Yavne'el valley, Jordan Valley, and Bet She'an Valley.

Agricultural tools

Attempts were made to isolate bacteria and fungi from several cultivating tools, which are summarized in Table 2. Samples were taken from both metal or plastic tool coverings and from the mud adhering to them. Additionally, samples were taken from farmers' hammers, wrenches, and metal wires obtained from storage or from agricultural spray airplanes and ultralight sport airplanes, stationed in the Ein-Shemmer agricultural airfield.

Isolation procedures

(*a*) Mammals: Animals, trapped by box-bait traps in the fields, were washed with 0.5 L sterile tap water, dried, and set free. (*b*) Reptiles: Animals were caught by a rough plastic net (agamas) or picked by hand (chamaeleons) and washed as above. (*c*) Human hand skin and clothes: Skin and clothes were washed with 0.5 and 2 L sterile tap water, respectively. (*d*) Birds: Feathers (5 ± 1), plucked randomly from each bird (trapped as were the mammals and then set free), were all washed together in 100 mL sterile tap water. (*e*) Insects and mites: These organisms were collected by one of the following tools: flame-sterilized forceps (larvae of cotton leafworm, ants, red mites); pheromone traps (butterflies of cotton leafworm and spiny bollworm); a very delicate plastic net (tobacco whitefly); and a thin metal net (oriental hornet). The captured insects and mites were divided into groups (for details see Table 1), anaesthesized by chloro-

TABLE 1. Possible dispersal of disease agents by different organisms

Common name	Scientific name	Plant type in field sampled*	Total no. of samples taken	No. of contaminated samples	Mean no. of cells or propagules/sample: Before enrichment	Mean no. of cells or propagules/sample: After enrichment
Mammals						
Mouse	*Mus musculus*	C	8	8	4.3×10^1	ND
		P	10	6	4.8×10^2	ND
Rat	*Rattus* sp.	C	6	6	7.8×10^1	ND
Rabbit	*Lepus syriacus*	C	3	3	2.5×10^1	ND
Humans (skin of hand)	*Homo sapiens*	C	4	4	2.4×10^2	ND
		T	3	3	5.3×10^4	ND
		P	5	5	7.4×10^3	4.8×10^6
Reptiles						
Agama	*Agama stillio*	C	3	3	6	ND
		T	4	1	NDT	5.4×10^6
Chamaeleon	*Chamaeleo chamaeleo*	C	3	1	1.3×10^1	ND
		T	2	0	NDT	NDT
Birds						
House sparrow	*Passer domesticus biblicus*	C	6	6	8	ND
		T	6	5	NDT	7.8×10^6
		P	5	5	NDT	6.3×10^6
Common bulbul	*Pycnonotus capensis vallembrosa*	C	3	3	1.9×10^1	ND
Starling	*Sturnus vulgaris*	C	2	2	10^1	ND
		T	4	3	1.1×10^3	ND
Hooded crow	*Corvus corone*	C	1	0	NDT	ND
		T	3	1	NDT	7.1×10^6
		P	2	2	NDT	2.1×10^5
Insects						
Cotton leafworm (larvae)	*Spodoptera littoralis*	C	250	250†	4.25×10^2	ND
		T	250	250	6×10^4	ND
		P	250	250	4×10^3	ND
Cotton leafworm (butterflies)	*Spodoptera littoralis*	C	60	60‡	1.46×10^2	ND
		T	60	60	4×10^3	ND
		P	60	60	3.8×10^4	ND
Tobacco whitefly	*Bemisia tabaci*	C	200	200§	2.23×10^2	ND
		T	200	200	6.1×10^4	ND
		P	200	200	3.6×10^3	ND
Ants	*Acantholepis frauenfeldi bipartita*	C	200	200§	2.7×10^1	ND
		P	200	200§	4.4×10^4	ND
Oriental hornet	*Vespa orientalis*	C	6	2	1.3×10^1	ND
Spiny bollworm	*Earias insulana*	C	60	60‡	3.6×10^2	ND
Mite						
Red mite	*Tetranychus telarius*	C	250	250†	7.1×10^2	ND
		T	250	250	6.1×10^4	ND
		P	250	250	4.4×10^3	ND

NOTE: ND, not determined; NDT, not detected.
*C, cotton; T, tomato; P, pepper.
†Divided into five replicates (tested separately) of 50 insects or mites each.
‡Divided into five replicates (tested separately) of 12 butterflies each.
§Divided into five replicates (tested separately) of 40 insects each.

form vapor, washed under gentle stirring for 1 h in 0.5 L sterile tape water, and then filtered out using Whatman No. 42 filter paper in a funnel. All the water from each of treatments *a*–*e* was collected (separately) and after 10-fold serial dilutions, 0.1-mL aliquots of the suspension were streaked in triplicate on solid agar media. (*f*) Agricultural tools and airplanes: The metal or plastic body of the tool or aircraft was washed with 0.5–5 L sterile tap water (depending on tool size). The water was collected and treated as described under treatment *h*. (*g*) Soil particles adhering to tools: Mud adhering to various agricultural tools was collected, by a flame-sterilized spatula, in the farmers' yards. Approximately 200 g of soil was scratched from each tool, put in sealed, gamma-sterilized, polyethylene bags, and immediately transferred to cold storage (2°C). The following day, triplicates (2 g each) from each sample were suspended in 50 mL sterile 0.06 *M* potassium phosphate buffer (pH 7.0) and vigorously shaken (250 strokes/min) for 2 h at 4°C. The soil particles were

TABLE 2. Possible dispersal of disease agents by agricultural tools and light aircraft

Tool	Plant type in fields sampled*	Total no. of samples taken	No. of contaminated samples	Mean no. of cells or propagules/sample: Before enrichment	Mean no. of cells or propagules/sample: After enrichment
Plow	T	2	1	NDT	2.8×10^5
	P	2	2	NDT	4.1×10^5
Cultivator	C	3	3	2.23×10^2	ND
	T	2	2	NDT	6.4×10^3
	P	2	2	NDT	6.9×10^4
Towed motor sprayer	T	1	1	2.7×10^4	ND
	P	1	1	NDT	4.9×10^5
Motor duster	P	1	1	NDT	6.8×10^5
Tractor wheels (rubber)	C	6	5	7.12×10^2	ND
	T	3	3	4.6×10^5	ND
	P	4	4	6.4×10^5	ND
Labor shoes or boots	C	7	7	3.37×10^2	ND
	T	4	2	4.3×10^5	ND
	P	2	2	6.7×10^5	ND
Labor clothes	C	4	4	6.03×10^2	ND
	T	3	3	1.8×10^6	ND
Automatic cotton harvester	C	3	3	3.6×10^2	ND
Tomato harvester	T	2	2	4.9×10^4	ND
Hammer	T	2	2	NDT	6.6×10^5
	P	1	1	NDT	9.7×10^4
Wrenches	C	2	2	9	ND
	T	3	3	NDT	3.4×10^4
	P	1	1	NDT	9.1×10^4
Metal wires	T	10	10	4.1×10^3	ND
Agricultural spray aircraft	C	8	8	2.73×10^2	ND
Sport aircraft	C	4	3	1.02×10^2	ND

NOTE: ND, not determined; NDT, not detected.
*C, cotton; T, tomato; P, pepper.

allowed to precipitate for 30 min before the supernatants were diluted and streaked as described above. (*h*) Water sources: Two litres of drainage water was collected from access irrigation or rain, and 5 L of water from each of the other water sources was collected in each sampling. Following overnight storage at 2°C, the water was centrifuged in sterilized bottles in an industrial centrifuge at 6000 × *g* for 20 min. The pellets obtained were redissolved in phosphate buffer, diluted, and streaked as described above.

The following media were used for growing pathogens from all sources: King-B medium supplemented (per litre) with 9 mg basic fuchsin and 1.4 mg 3,4-triphenyltetrazolium chloride (for the detection of PST) (33); nutrient agar (Difco) supplemented with 10 g sucrose, 1.5 g $CaCl_2$, and 200 mg sodium deoxycholate (added after autoclaving) (for XCV determination) (13); Czapek medium supplemented with 200 mg chloramphenicol (for AM determination) (2). The cultures were incubated for 72 h at 22 ± 2°C (PST) or 30 ± 2°C (XCV and AM) before observation of colony morphology. "Suspect" colonies were tentatively identified by their typical colony formation (4,15,33), PST physiological characterization (39), typical yellow carotenoid (5,34), or by typical spore formation (3).

When not detected on their respective media, the bacterial pathogen sources were grown on enriched liquid medium and spread on solid agar plates (4).

Isolates from all sources were kept on agar slants (nutrient agar for bacteria, Czapek medium for the fungus) at 4°C. Pathogenicity tests were carried out on three isolates from each sample as follows: bacterial pathogens, grown for 48 h in nutrient broth (Difco) in a rotary shaker at 22 ± 2°C (PST) or 30 ± 2°C (XCV), were harvested by centrifugation, diluted to 10^9 colony-forming units (CFU)/mL (0.3 and 0.1 absorbance units at 540 and 420 nm, respectively), further diluted to 10^7 CFU/mL, and sprayed, until runoff occurred, with a hand sprayer on two tomato or pepper plants (four to six true leaves). These plants were then incubated at 22 ± 2°C and 30 ± 2°C, respectively, in a humidity chamber for 8 days, at which time typical symptoms were recorded. Cotton plants, sprayed with *A. macrospora* propagules at a concentration of 10 000 spores/mL, were incubated in a dark humidity chamber at 28 ± 2°C for 16 h and then transferred to an air-conditioned greenhouse, at the same temperature, for 7 days until the appearance of symptoms.

Results

Dispersal of disease agents by different organisms

Five groups of organisms, found in tomato, pepper, and cotton fields, were examined for their possible contribution to field dispersal of the three pathogens. Insects and mites were found to carry the highest plant pathogen population (more than 200 propagules/sample for AM and $10^3 - 10^4$ CFU/sample for the bacterial pathogens) (Table 1). Even the carnivorous insect (oriental hornet) carried AM propagules. All

TABLE 3. Possible dispersal of disease agents by soil particles adhering to tools

Soil source*	Plant type in sampling fields†	Total no. of samples taken‡	No. of contaminated samples	Mean no. of cells or propagules/sample
Tractor wheels	C	10	10	$4.7(\pm0.84)$§ $\times 10^2$
	T	10	10	$7.46(\pm0.17) \times 10^5$
	P	10	10	$1.84(\pm0.19) \times 10^5$
Wheels of the sampling car	C	5	4	$8.76(\pm0.36) \times 10^2$
	T	7	5	$4.55(\pm0.41) \times 10^5$
	P	6	2	$6.14(\pm0.73) \times 10^4$
Labor boots	C	6	6	$8.86(\pm0.27) \times 10^2$
	T	10	10	$5.65(\pm0.68) \times 10^5$
	P	8	8	$9.86(\pm0.41) \times 10^5$
Plow	C	5	2	$2.8\ (\pm0.6\ ) \times 10^1$
	T	10	4	$6.84(\pm0.16) \times 10^5$
	P	7	5	$7.08(\pm0.96) \times 10^4$
Cultivator	C	4	4	$3.76(\pm0.66) \times 10^2$
	T	6	6	$8.46(\pm0.21) \times 10^5$
	P	5	5	$7.76(\pm0.84) \times 10^5$

*Collected from the mechanical tools at the parking area at 10- to 14-day intervals.
†C, cotton; T, tomato; P, pepper.
‡Different tools.
§Standard deviation given in parentheses.

mammals trapped in the fields were capable of transmitting pathogenic cells, though less efficiently than insects. Birds were found to have a lower capability for transmission of pathogenic populations (bacterial pathogens were detected only after liquid enrichment, indicating the presence of only a few pathogenic cells). Two reptile species were found to have the lowest transmission capability (only several cells or propagules).

Dispersal of disease agents through agricultural tools and light aircraft

Pathogenic cells, at a high population level, were found to adhere to the plastic, rubber, or metal body of almost every tool that passed through plant foliage. Digging tools, plows, cultivators, and small hand tools had small populations of the bacterial leaf pathogens, detectable only after enrichment of the culture medium (Table 2). Agricultural spray aircraft and ultralight sport aircraft, which flew regularly at a low level above the fields, also carried AM propagules on their surfaces. People working in the fields were also good vectors for the three pathogenic organisms (Tables 1, 2, and 3).

Dispersal of disease agents by soil particles adhering to agricultural tools

Since agricultural tools are not usually washed or disinfected during the growing season, soil particles, especially mud, are very common on almost all tools. Analysis of the pathogenic populations showed that mud adhering to tools frequently employed in the field, e.g., tractor wheels, labor boots, and cultivators, contained more propagules or cells than infrequently used tools, such as plows or the wheels of our sampling car. However, the mud that adhered to every tool passing through the field had pathogenic populations of about the same level (Table 3).

Dispersal of disease agents by water

Several water sources were tested for plant pathogenic agents. All excess water from both sprinkler irrigation and rain contained high levels of the pathogens (Table 4). When other local water sources were tested for *A. macrospora*, it was observed that the fungus could be found in only 25 to 40% of the samples. Each of the water sources tested had infective propagules of this fungus. However, the *A. macrospora* population was relatively low in flowing water sources, such as channels, oxidization pools, river, and lake, and was massive in still swamp water.

Discussion

The field dispersal process of phytopathogenic agents is often complex. Disease agents can have a single or multiple modes of transmission and usually find their plant target by a random meeting or by the random action of specific and nonspecific vectors. The cultivation of one species of plant over a large area enables the pathogens to disperse in the fields via agricultural tools, insects, animals, or recycling water. The chemotactic motility of bacteria does not appear to be essential for successful dispersal since it is accepted that phytopathogenic bacteria do not move more than a few centimetres by their own motility (1,35). A very wide range of studies (19) elucidates the relationships between pathogens and their insect vectors. The insects help in bacterial survival, dissemination, and penetration into host tissue. Pathogen contamination on insects is probably common in nature. It seems that members of any insect group that commonly visits diseased and healthy plants can act as vectors of pathogens. Insects that are normally associated with specific crops are likely to be more important vectors than general insect visitors. However, the great abundance of the nonspecific insect visitors foraging for nectar or pollen makes them extremely important in the dispersal of phytopathogens. Any insect that does visit an inoculum source, such as diseased plant tissue, becomes contaminated and thus a potential vector (19). This study shows that almost every animal, insect, mite, tool, or person passing through an infested field can disseminate pathogenic agents. Vectors that are more prevalent in the fields, or crop-specific insect pests, are usually more contaminated with the respective pathogen. People working in the field or even light aircraft and birds

TABLE 4. Possible dispersal of disease agents by water

Water source	Disease agent*	Total no. of samples taken†	No. of contaminated samples	Mean no. of cells or propagules/positive sample
Excess irrigation water	AM	10	10	$5.47(\pm0.32)‡ \times 10^3$
	PST	10	10	$3.28(\pm0.46) \times 10^5$
	XCV	10	10	$4.76(\pm0.78) \times 10^4$
Excess rain drainage	PST	6	6	$7.63(\pm1.41) \times 10^5$
Flow water in an open channel in Bet She'an Valley	AM	5	2	$3.88(\pm0.48) \times 10^2$
Oxidization sewage water pools of Bet She'an town	AM	5	2	$8.8\ (\pm1.4\ ) \times 10^1$
Hadera natural swamp	AM	5	5	$2.64(\pm0.82) \times 10^4$
Jordan River	AM	4	1	1.4×10^1
Sea of Galilee	AM	4	1	2.6×10^1

*AM, *Alternaria macrospora;* PST, *Pseudomonas syringae* pv. *tomato;* XCV, *Xanthomonas campestris* pv. *vesicatoria.*
†10-day (±3) intervals.
‡Standard deviation given in parentheses.

flying low above the field can transfer pathogenic agents. These vectors are relatively more important, since they can carry the disease agents for long distances.

Soil, a common survival site of many disease agents (1,32), can act as a dispersal vector by adhering to everything which passes through it. Thus even random visitors, such as our laboratory car, can become pathogen vectors (Table 3).

Faulwetter (16) related rainfall and wind to the spread of *X. campestris* pv. *malvacearum.* Windblown rain was shown to be an effective vector of a number of bacterial diseases including XCV (38). Irrigation water provides not only the medium for bacterial transmission, but also the moisture essential for establishing infections (36). In some irrigation systems, runoff water is either passed through successive fields or collected in a pool and then reapplied to the cultivated field, thus enabling pathogens to spread easily from one field to another (9,21,22,35). In arid cultivation areas, such as Israel, irrigation water may be one of the most important disease-carrying agents. Though standing water contains more propagules, flowing water, i.e., river, lake, and oxidization pools, even far from the infested area, contain fungal propagules and may, when used for irrigation, act as a pathogen vector.

One main question remains unanswered in this dispersal study, and that is the ability of virulent propagules or cells to initiate the specific disease in the field that they have randomly reached. This depends on many environmental, biological, genetic, and agricultural factors. Therefore, studies such as this one can only reveal the possibility of dispersal of pathogenic cells, but not the actual danger resulting from such dispersal.

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