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Periodicity and gradients in dispersal of *Alternaria linicola* in linseed crops

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Abstract

Conidia of *Alternaria linicola* produced on infected linseed crops were mainly dispersed by wind. The numbers of conidia in the air above linseed crops collected by a Burkard spore sampler were greatest between 12:00 h and 13:00 h, when the relative humidity was lowest. Although numbers of conidia collected decreased with increasing height within and above the crop canopy, air-borne *A. linicola* conidia were present up to 80 cm above the crop canopy. Conidia of *A. linicola* were transported by wind up to at least 40 m downwind from an artificial line inoculum source, but their numbers decreased with increasing distance from the source. In 1991, 1992, and 1993, the dispersal of *A. linicola* conidia above linseed crops followed a seasonal periodicity which was influenced by weather conditions and cultural practices. The greatest numbers of conidia were collected during July, August and early September and coincided with periods favourable for sporulation and with an increase in the incidence of the disease in the senescent crop. Air-borne *A. linicola* conidia produced on point or line inoculum sources (naturally infected linseed stem debris) were responsible for the spread of the disease in linseed crops. In 1992 and 1993, the disease was first detected downwind from the sources, but by the end of the growing seasons, it had spread in all directions and up to 20 m and 60 m from the sources, respectively. Disease gradients were initially steep near the inoculum sources but they became flatter with time due to the secondary spread of the disease.

Introduction

Alternaria linicola Groves & Skolko, the most important seed-borne pathogen of linseed (*Linum usitatissimum* L.) in the UK, can decrease emergence by up to 50%, seed yield by up to 35%, and can also affect oil yield and quality [Mercer *et al.*, 1991]. *A. linicola* is also the main reason for the failure of the linseed seed to reach the UK certification standards, which require that less than 5% of the seed in total is infected. The severity of the disease caused by *A. linicola* in linseed crops during the growing season fluctuates from year to year, depending on the weather conditions [Fitt *et al.*, 1991a, b; Fitt and Vloutoglou, 1992, Mercer *et al.*, 1991]. However, infection of developing seeds is most frequent in areas with a wet period between flowering and harvest [Mercer *et al.*, 1991]. Conidia of *A. linicola*, like those of other *Alternaria* species, are mainly dispersed by wind [Fitt and Ferguson, 1993; Fitt and Vloutoglou, 1992]. The greatest concentrations in the air above linseed crops in 1990 were collected in July and August and coincided with an increase in the disease incidence in the senescent crops [Fitt and Ferguson, 1993]. The dispersal of conidia of many *Alternaria* species has been reported to follow seasonal and diurnal periodicities [Humpherson-Jones and Maude, 1982; Langenberg *et al.*, 1977; Meredith, 1966; Rotem, 1964, 1991]. The highest concentrations of air-borne *Alernaria* conidia are often observed late in the growing season, with the maximum numbers being dispersed at midday. However, most of these conidia are transported for only short distances

from the foci of their production and therefore can create only local epidemics [Bashan *et al.*, 1991; Humpherson-Jones and Maude, 1982].

Although air-borne *A. linicola* conidia are considered to be the principal method for the spread of the disease in linseed crops during the growing season, there is no information on the effects of environmental factors on the release and dispersal of *A. linicola* conidia or on the distances over which the conidia are transported by the wind. This paper describes experiments to investigate the seasonal and diurnal patterns of dispersal of *A. linicola* conidia in linseed crops and to study the *A. linicola* disease gradients and spore dispersal gradients from point or line inoculum sources.

Materials and methods

Seasonal and diurnal dispersal of A. linicola *conidia*

In 1991, 1992 and 1993 the seasonal and diurnal dispersal of *A. linicola* conidia were studied by using a 7-day recording volumetric spore sampler (Burkard Manufacturing Co. Ltd., Woodcock Hill, Industrial Estate, Rickmansworth, UK). The spore sampler was placed in the middle of the linseed crop (cv. Antares) in an area (diameter 2 m) free from plants, with the orifice 40 cm above ground level. In 1991, sampling began on 14 June, 65 days after the emergence of the crop, and finished on 16 October when the crop was harvested. In 1992 and 1993 the sampler was operated continuously; sampling started on 21 April 1992 when the first linseed crop was sown and finished on 10 October 1993, 23 days after the harvest of the second crop. The hourly changes in the concentration of *A. linicola* conidia in the air were estimated only in 1992 for the six selected days during which the greatest numbers of conidia were collected by the Burkard spore sampler.

In 1992 and 1993, to investigate if the Burkard spore sampler was efficient enough to detect air-borne *A. linicola* conidia above linseed crops early in the growing season (April–May) when their concentrations in the air were low, young linseed seedlings (bait plants) were exposed within the crop at weekly intervals. Six plastic trays (35×26×7 cm), containing a mixture of soil-less compost with a slow release fertilizer (Croxden compost produced by Nursery Trades (Lea Valley) Ltd, UK), were sown each time with linseed seed (cv. Antares, treated with prochloraz (4 g a.i. kg^{-1} seed, Prelude 20LF, Agrichem)) with no detectable *A. linicola* infection. The trays were placed in a glasshouse (temperature range 15–20 °C) with 7 h of additional light provided by two high pressure sodium plant irradiators with integral control (Thermoforce Ltd, Camplex Plantcare Division, Tetbury, UK). Ten days after sowing, when the seedlings had one pair of true leaves, four of the trays were transferred to the field. Two of the trays were placed at ground level and the other two at approximately 1 m above ground within the linseed crop. The remaining two trays (controls) were transferred to a glasshouse (temperature range 10–20 °C). After one week of exposure, all trays, including controls, were covered with polyethylene bags (100% r.h.) and left in the glasshouse for 5 days. 100 seedlings were then sampled at random from each tray and assessed for the presence of *A. linicola* conidia. The disease incidence (% plants infected) on the bait plants each week was compared with the number of air-borne *A. linicola* conidia collected by the Burkard spore sampler in the same week. Bait plants were exposed to the linseed crops continuously from April 1992 until November 1993.

Records of daily rainfall, mean temperature and hourly wind speed were obtained from a meteorological station situated 0.5–1 km from the experimental site. The wind speed was measured by a cup anemometer at a height of 1 m above ground and the relative humidity was measured by an aspirated psychrometer 30 cm above ground within the linseed crop. Both wind speed and relative humidity were recorded by a Campbell 21X data logger.

Disease gradients from a point inoculum source – 1992 field experiment

The experiment was sown on the Rothamsted farm, UK approximately 2 km south of the nearest linseed crop and after a crop of lupins. One plot (0.01 ha) was sown with untreated linseed seed (cv. Antares), with no detectable *A. linicola* infection on 14 April at a rate of 600 seeds m^{-2} (Fig. 1a). Nitram (34.5% N, ICI Agrochemicals Ltd) was applied on 14 April at 220 kg ha^{-1}. The herbicides bentazone (960 g a.i. ha^{-1}, Basagran, BASF) and bromoxynil + clopyralid (240:50 g a.i. ha^{-1}, Vindex, DowElanco) were applied on 2 June. The crop was irrigated by using an overhead oscillating system on 17, 18, 25 and 29 June, 9 and 28 July with 12 mm of water applied on each occasion.

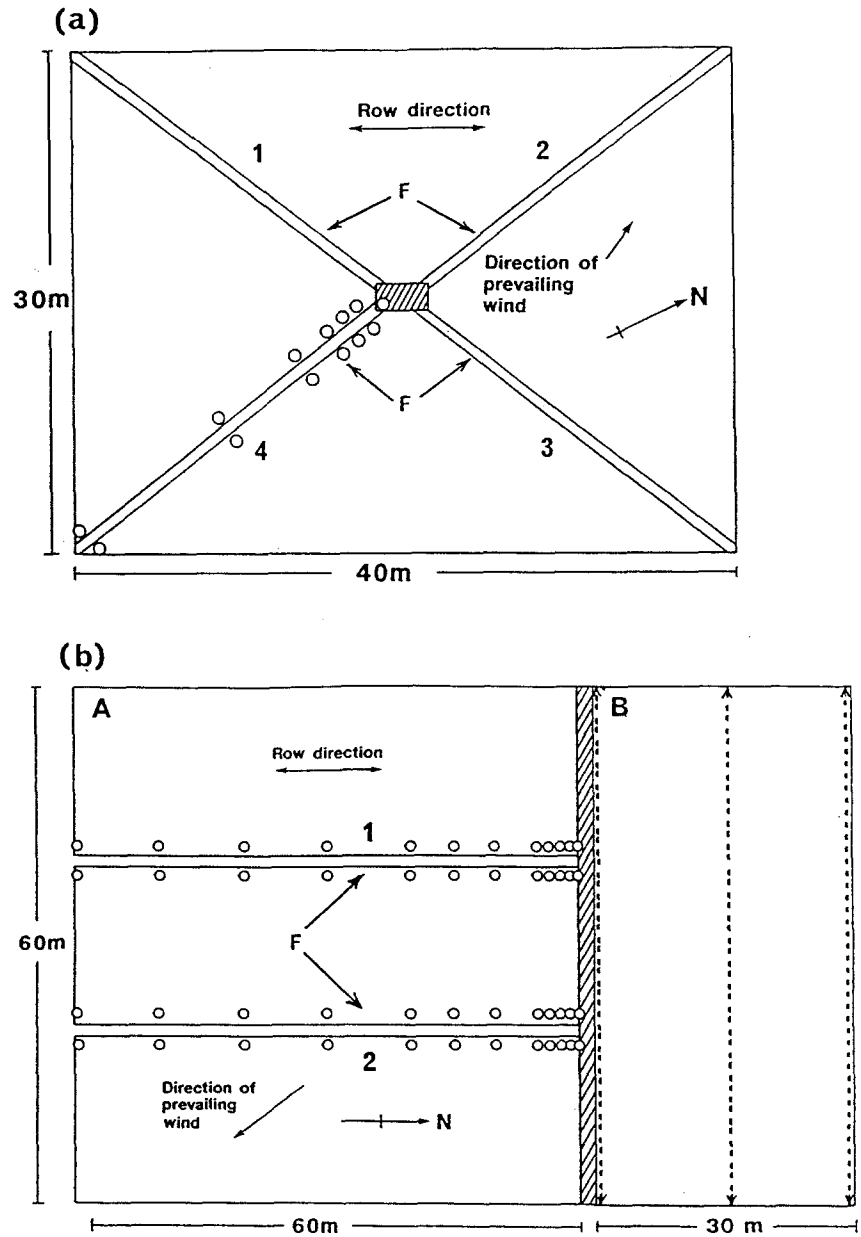

Fig. 1. Plans of the 1992 (a) and 1993 (b) field experiments for studying the *A. linicola* disease and spore dispersal gradients from a point (1992) or a line (1993) inoculum source. 1, 2, 3, 4: sampling directions; F: footpaths; ▨: inoculum source (1×2 m in 1992; 0.5×60 m in 1993); ○: sampling points in one direction; - - -: sampling directions in plot B.

On 8 July four diagonal paths (each 0.5×20 m) were cut to facilitate sampling (Fig. 1a).

The inoculum source consisted of linseed stem debris naturally infected by *A. linicola* and placed in 0.3×1 m nylon net bags. One day before the introduction of the inoculum into the crop, a sample of 100 plants was collected at random throughout the field in order to assess the incidence of *A. linicola* infection in the crop (background infection). On 9 July, approximately 14 days after full flowering, six bags with debris were placed at ground level in the central area (1×2 m) of the plot (Fig. 1a). To minimize the dispersal of *A. linicola* conidia from the infected debris during transport through the linseed crop, the net bags with the

debris were enclosed in polyethylene bags until they were placed at the central area of the field. After the introduction of the inoculum into the crop, no farm machinery entered the field.

Samples of plants were collected from all four directions along the paths at 0, 0.1, 0.3, 0.6, 1, 1.5, 2, 3, 5, 10 and 20 m distance from the inoculum source (central area) during the growing season. At each sampling point two plants were collected (one plant from each side of the path). Samples were taken by proceeding from the least (edge of the field) to the most severely infected area (central area) and care was taken to avoid brushing against the plants in order to minimize the spread of the inoculum by physical contact. A total of four samples were collected at approximately two-weekly intervals until harvest, starting one week after the introduction of the inoculum. The disease gradients were expressed as the percentage of plants infected at increasing distances from the inoculum source, calculated as averages over all four directions.

Disease gradients from a line inoculum source – 1993 field experiment

The field experiment was sown on the Rothamsted farm, UK in two plots (A: 0.32 ha and B: 0.16 ha) (Fig. 1b). The previous crops had been linseed for the last two years in plot B and oilseed rape in 1991 and potatoes in 1992 in plot A. Untreated linseed seed (cv. Antares), with no detectable *A. linicola* infection was sown on 21 April at a rate of 600 seeds m^{-2}. Nitram (34.5% N) was applied on 12 May at 217 kg ha^{-1}. The herbicide metsulfuron-methyl (6 g a.i. ha^{-1}, Ally, DuPont) was applied on 1 June. On 6 June two paths (0.5×60 m each) were cut along the plot A to facilitate sampling. The crop was irrigated by using an overhead oscillating system on 2 and 6 July with 12.5 mm water each time.

The inoculum source consisted of linseed stem debris naturally infected by *A. linicola* and placed in a nylon net bag (0.5×60 m). One day before the introduction of the inoculum into the crop, two samples of 100 plants each were collected at random throughout the two plots (one sample per plot) to assess the incidence of *A. linicola* in the crop (background infection). On 7 June, approximately two weeks before the start of flowering, the bag with the debris was placed at ground level between plot A and plot B (Fig. 1b) and held in place with wooden poles.

In plot A, samples of 10 plants each were collected from both sides of the paths (five plants from each side) at different distances (0, 1, 2, 3, 5, 10, 15, 20, 30, 40, 50 and 60 m) from the inoculum source. Samples were taken by proceeding from the least (60 m from the source) to the most severely infected area (next to the inoculum source) and care was taken to avoid brushing against the plants to minimize the spread of inoculum by physical contact. In plot B, samples of plants (20 plants per distance) were collected across the field at 0, 15 and 30 m from the inoculum source. A total of seven samples were collected from each plot during the growing season at approximately two-weekly intervals. The disease gradients in plot A (downwind from the inoculum source) were expressed as the average percentage of plants infected along the two paths at increasing distances from the inoculum source and in plot B (upwind from the inoculum source) as the percentage of plants infected at 0, 15 and 30 m from the source.

Spore dispersal gradients

The spore dispersal gradients were studied in plot A (Fig. 1b) by using five rotorod-type samplers [Perkins, 1957]. The samplers were operated from 10:00 h to 16:00 h on the first dry day after a period of rain. This period of the day was chosen because the greatest numbers of air-borne *A. linicola* conidia were collected by the Burkard spore sampler during this period. The horizontal spore dispersal gradients were studied by placing the samplers 30 cm above ground and at different distances from the inoculum source. For studying the vertical dispersal of *A. linicola* conidia, the samplers were placed in the middle of the field (approximately 30 m from the inoculum source); one of them was located at ground level (height 0 cm) and the others at 35, 70, 100 and 150 cm above ground level (mean height of the crop 70 cm). The samplings for studying the horizontal or vertical spore dispersal gradients began approximately 2 and 10 weeks, respectively, after the introduction of the inoculum into the crop. A total of six samplings were made before harvest.

Statistical analyses

Two empirical models [Fitt *et al.*, 1987] were used to describe the *A. linicola* disease or spore dispersal gradients with distance from the inoculum sources (point or line inoculum sources): the inverse power law model [Gregory, 1968] and the negative exponential model [Kiyosawa and Shiyomi, 1972]. For more pre-

cise comparison of the gradients the linearized forms of both models were used:

$$\ln (y) = \ln (a) - b \ln (x) \quad (1)$$
(inverse power law model)

and

$$\ln (y) = \ln (c) - d x \quad (2)$$
(negative exponential model)

in which y is the amount of disease or number of conidia, x is the disease from the inoculum source (m), a (Eq. 1) is a constant equal to the value of y at x = 1 m, c (Eq. 2) is equal to the value of y at x = 0 m and the exponents b and d are the slopes of the linear regressions describing the steepness of the gradients. The parameters a, b, c and d in Equations (1) and (2) can be estimated by plotting the linear regression of ln (y) on ln (x) and of ln (y) on x, respectively. For analyzing the data on the vertical dispersal of *A. linicola* conidia, the linear regression used was:

$$y = f - g z \quad (3)$$

in which y is the number of conidia collected at height z (cm) within or above the linseed crop, f is the intercept on the y-axis and g is the slope of the line. To test the goodness of fit of each model to data for the *A. linicola* disease or spore dispersal gradients, the percentage variance accounted for (r^2) was calculated for each linear regression.

Results

Seasonal and diurnal dispersal of A. linicola *conidia*

There was considerable variation in the numbers of *A. linicola* conidia collected above linseed crops in 1991, 1992 and 1993 (Fig. 2). Conidia of *A. linicola* were collected during the period July–September mainly on dry days following periods of rain, with the numbers gradually decreasing during extended dry periods. In 1991, the concentrations of air-borne *A. linicola* conidia above a linseed crop remained low throughout the collecting period (Fig. 2). There was a maximum concentration of 46 conidia m^{-3} on 14 July, which decreased rapidly over the next few days. Conidia of *A. linicola* were regularly collected during August with the highest concentration being observed on 25 August (40 conidia m^{-3}). July and August were generally hot (mean temperatures 16.9 °C and 17.4 °C, respectively) and dry (total rainfall 73.4 mm and 45.5 mm, respectively). No *A. linicola* conidia were collected during the first half of September, when the total rainfall was only 9.9 mm. However, a few conidia (mean daily concentration 1–5 conidia m^{-3}) were collected during the second half of September, when more rain fell (total rainfall 51.5 mm). Although the crop was not harvested until 10 October, no *A. linicola* conidia were collected by the Burkard spore sampler during the period between the end of September and 10 October. This period was generally dry and cold with a total rainfall of 3.3 mm and a mean temperature of 11.3 °C.

In 1992, the seasonal periodicity in concentrations of *A. linicola* conidia followed a pattern similar to that in 1991 (Fig. 2). However, the number of conidia collected during the growing season was greater than in 1991. Few *A. linicola* conidia were collected during May and June 1992 (mean daily concentration 1 conidium m^{-3}). Most days in May were dry and although a total rainfall of 103 mm was recorded during this month, most of the rain fell in the last three days. June was generally dry (total rainfall 37.5 mm) but the crop was irrigated three times during this period. Air-borne *A. linicola* conidia were consistently collected during July and August, with the highest concentrations being observed on 15 July, 14, 22 and 31 August (102, 113, 117 and 113 conidia m^{-3}, respectively). Both July and August were wet with a total rainfall of 62.2 mm and 114.2 mm, respectively. Although the crop was not harvested until 17 September, few *A. linicola* conidia were collected during this period (maximum daily concentration 36 conidia m^{-3}). No *A. linicola* conidia were collected between 22 September 1992 and 24 March 1993.

In 1993 the crop was sown on the same date as in 1992, but fewer conidia were collected by the Burkard spore sampler, because of differences in weather conditions between the two years (Fig. 2). Few conidia were collected during the period between the beginning of May and the end of July 1993. May was drier in 1993 than in 1992 (total rainfall 44.7 mm and 103 mm, respectively), but more rain fell during June 1993 than during June 1992 (total rainfall 131 mm and 35.7 mm, respectively). July was dry in both years (total rainfall 62.2 mm and 58.9 mm in 1992 and 1993, respectively). *A. linicola* conidia were consistently collected during August and September 1993, with the highest concentrations being observed on 14 and 19 August (84 and 74 conidia m^{-3}, respectively). August was drier in 1993 than in 1992 (total rainfall 39.3 mm and 114.2 mm,

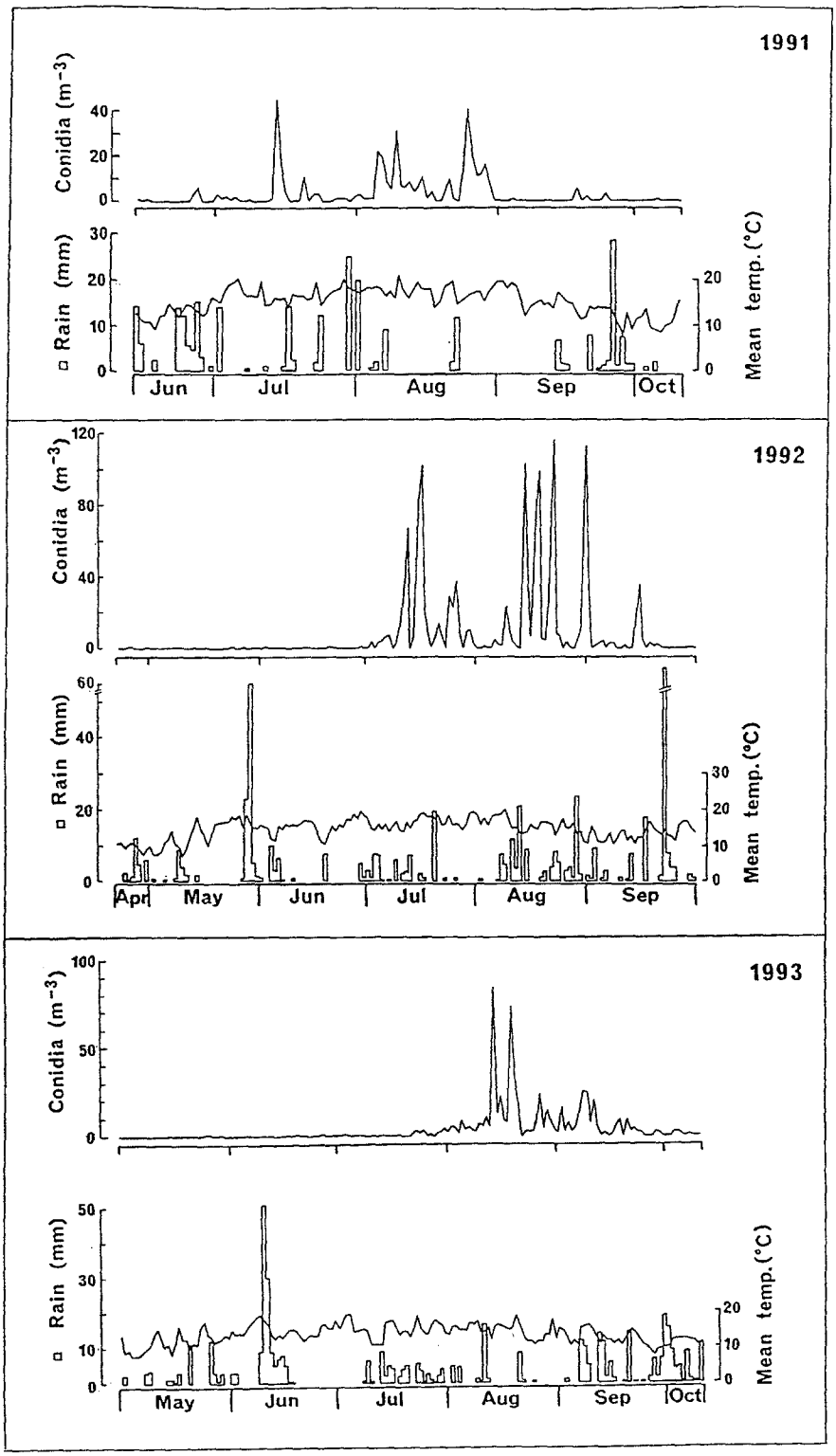

Fig. 2. Mean daily concentrations of air-borne *A. linicola* conidia above a linseed crop in relation to rainfall and temperature in 1991, 1992, and 1993.

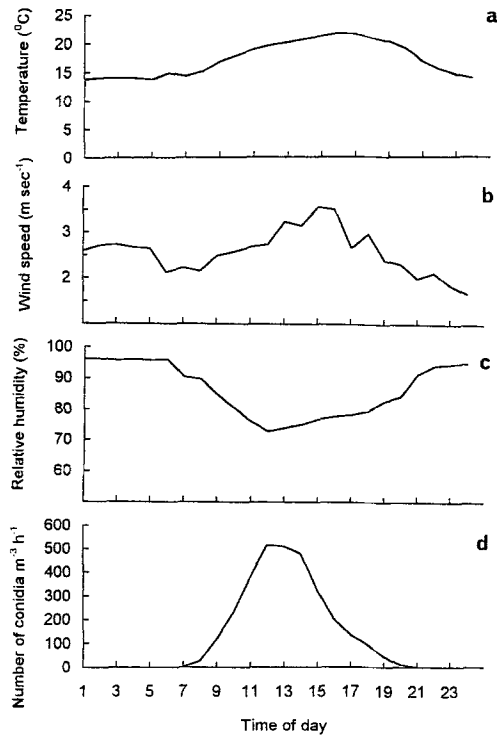

Fig. 3. Hourly concentrations of air-borne *A. linicola* conidia (d, average of 6 days) recorded by the Burkard spore sampler, temperature (a, average of 6 days), hourly wind speed (b, average of 6 days) and relative humidity (c, average of 6 days) above a linseed crop on 12 June, 15 June, 24 June, 14 August, 18 August and 22 August 1992.

respectively). No *A. linicola* conidia were collected after the crop was harvested (10 October).

The hourly concentrations of air-borne *A. linicola* conidia collected on 6 days in 1992 showed a well defined diurnal periodicity (Fig. 3). No *A. linicola* conidia were collected between 21:00 h and 07:00 h and few were collected between 07:00 h and 08:00 h (Fig. 3). The rapid increase in the number of air-borne conidia observed between 08:00 h and 12:00 h (from 120 to 514 conidia m^{-3} h^{-1}) occurred as temperature and wind speed increased and relative humidity decreased. The maximum concentration was observed between 12:00 h and 13:00 h, when relative humidity was lowest (73–74%). However, the highest concentration of *A. linicola* conidia dispersed above linseed crops preceeded the maximum wind speed (3.6 m sec^{-1}) and the maximum temperature (22 °C) by 3 and 5 h, respectively. As the number of air-borne conidia decreased after 13:00 h, the relative humidity increased.

In both 1992 and 1993, it was possible to detect air-borne *A. linicola* conidia above linseed crops much earlier in the growing season by using bait plants than by using the Burkard spore sampler (Fig. 4). Conidia of *A. linicola*, present in the field before the emergence of the crop (mid-April 1992 and early April 1993), infected bait plants exposed at ground level. In both years the incidence of *A. linicola* on the bait plants placed at ground level was slightly greater than on those placed 1 m above ground, especially early or late in the growing season. The highest incidences (100%) of *A. linicola* infection on the bait plants (either on those placed at ground level or on those placed 1 m above ground) were usually associated with periods when the greatest numbers of air-borne conidia were collected by the Burkard spore sampler (between July and early September in 1992 and between August and early October in 1993).

In both years, no *A. linicola* conidia were collected by the Burkard spore sampler after the harvest of the crop (harvest dates 17 September and 10 October in 1992 and 1993, respectively) (Fig. 4). However, the bait plants detected conidia produced on infected linseed stem debris left on the ground after harvest for two or three weeks after harvest in 1992 and 1993, respectively. No *A. linicola* conidia were either detected by the bait plants or collected by the Burkard spore sampler during the period between October 1992 and March 1993 and therefore data collected during this period have not been plotted. No *A. linicola* infection was detected on the bait plants not exposed in the linseed crops (controls).

Disease gradients from a point inoculum source – 1992 field experiment

In 1992, when the *A. linicola* disease gradients from a point inoculum source were studied, the percentage of plants infected decreased with increasing distance from the source. The inverse power law model fitted better than did the negative exponential model for all four sets of data. On average, the linear regressions of ln (y) on ln (x) (inverse power law model) accounted for 78% of the variance and the regressions of ln (y) on x (negative exponential model) accounted for 46% of the variance (Table 1). The disease was first detected downwind on 16 July, one week after the introduction of the inoculum into the crop (Fig. 5). Relatively steep disease gradients were observed on 16 July ($b = -0.29$) and on 13 August ($b = -0.26$) up to 1.5 m and 2 m from the inoculum source, respectively. Approximately one month after the introduction of the

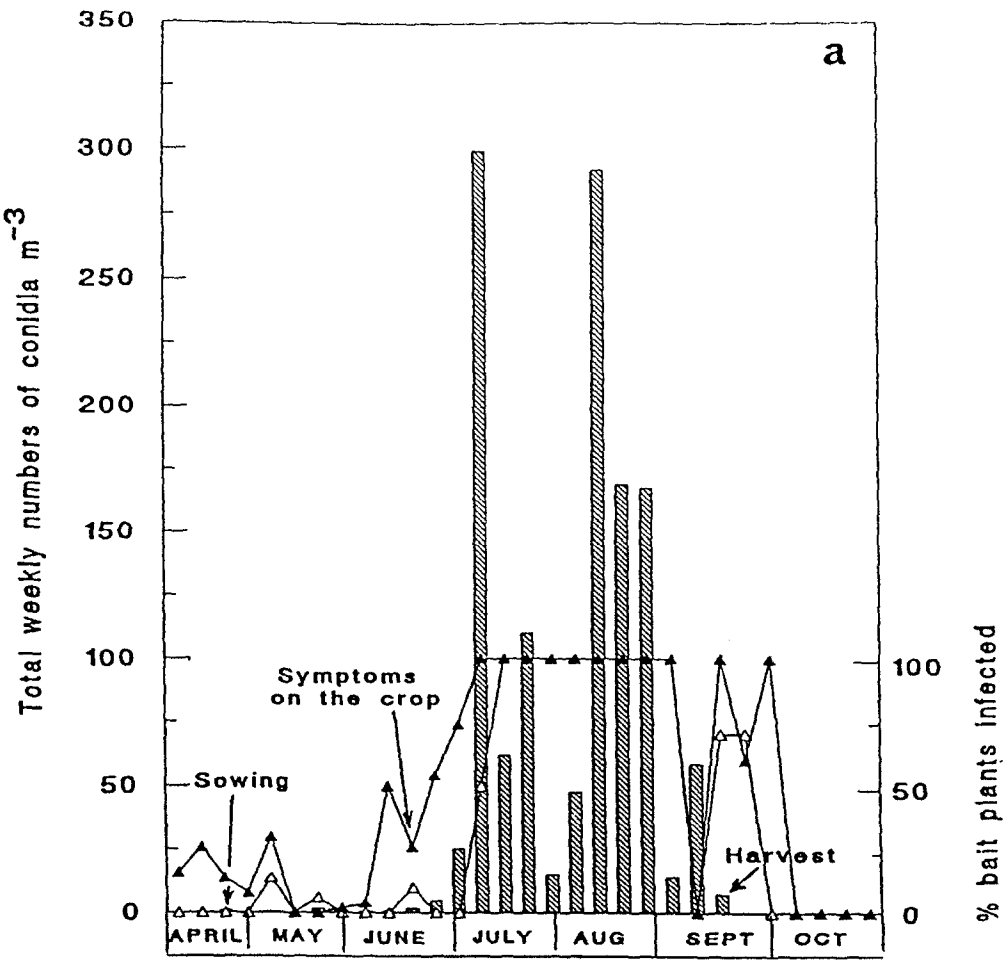

Fig. 4. Total weekly numbers of air-borne *A. linicola* conidia (▨) collected by the Burkard spore sampler above a linseed crop and disease incidence (%) on bait plants exposed in the same crop either at ground level (▲) or 1 m above ground (△) during the periods 1 April– 31 October 1992 (a) and 15 March–15 November 1993 (b).

inoculum, the disease was detected in all four directions. Gradients became flatter with time and values of the slopes increased (Table 1) due to the secondary spread of the disease. On 29 August and 12 September (45 and 65 days after the introduction of the inoculum into the crop, respectively) plants infected by *A. linicola* were detected up to 10 m and 20 m from the source, respectively. There was no background infection in the crop as no *A. linicola* infection was detected on the plants collected on the date when the inoculum source was introduced into the crop.

Disease gradients from a line inoculum source – 1993 field experiment

The negative exponential model gave a better fit than did the inverse power law model to the data for the *A. linicola* disease gradients downwind from the source. On average, the linear regressions of ln (y) on x (negative exponential model) and of ln (y) on ln (x) (inverse power law model) accounted for 92% and 49% of the variance (r^2), respectively (Table 1). The disease was first detected 2 weeks after the introduction of the inoculum into the crop and steep disease gradients were observed up to 3 m from the source (Fig. 6). Between 3 m and 30 m from the source the disease gradients appeared to be flatter. One month (8 July) after the introduction of the inoculum into the crop, the disease gradients were steep (b = −0.64) up to 3 m from the source, but they became flatter between 3 m and 15 m from the source. On 22 July disease gradients were relatively steep up to 5 m from the source (b = −0.20), but they became flatter beyond this distance up to 60

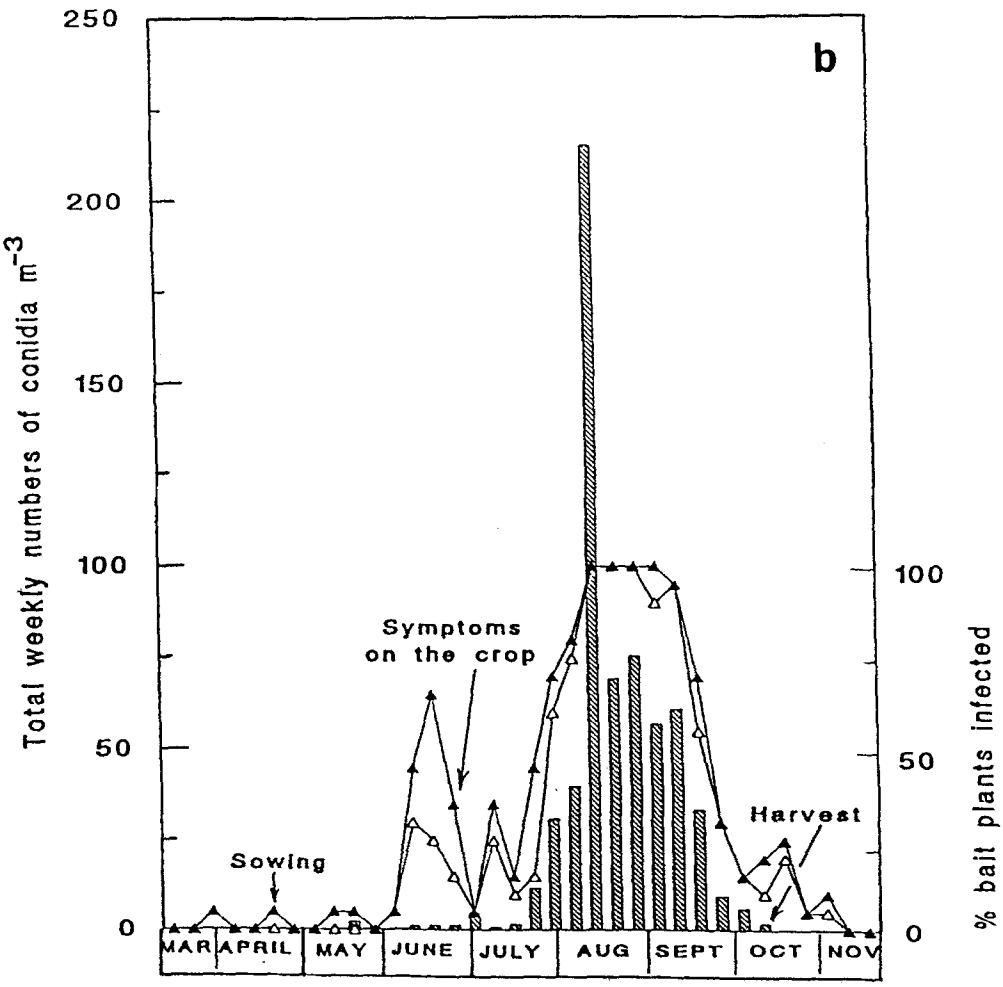

Fig. 4. Continued.

m. Gradients generally became flatter with time (Table 1) due to the secondary spread of the disease.

The *A. linicola* disease gradients upwind from the inoculum source (plot B) were fitted equally well by the inverse power law model and negative exponential model. The average percentage of the variance accounted for (r^2) by each model was 93% (Table 2). The disease was first detected up to 30 m from the inoculum source at a very low incidence (1%) on the same date (24 June) as in plot A, where the disease gradients downwind from the source were studied. The disease gradients were steep at the beginning of the growing season, but they became flatter with time due to the secondary spread of the disease (Table 2).

Spore dispersal gradients

Horizontal spore dispersal gradients. The negative exponential model gave a better fit to all sets of data than did the inverse power law model. On average, the linear regressions of ln (y) on x (negative exponential model) accounted for 73% of the variance (r^2), whereas the regressions of ln (y) on ln (x) (inverse power law model) accounted for 53% of the variance (Table 3). Steep dispersal gradients were observed on 24 June ($b = -0.44$) and on 22 July ($b = -0.30$) up to 2 m and 10 m from the source, respectively (Fig. 7). Spore dispersal gradients became flatter with time, due to the production and dispersal of secondary inoculum. On 14 August conidia of *A. linicola* were detected for the first time up to 40 m from the source.

Table 1. Parameters estimated from the regressions of disease incidence (%) (y) on distance from the inoculum source (m) (x) for the inverse power law model [ln (y) = ln (a) - b ln (x)] and the negative exponential model [ln (y) = ln (c) - dx] used to describe the *A. linicola* disease gradients downwind from a point or a line inoculum source in 1992 and 1993, respectively

Sampling date	Inverse power law model			Negative exponential model		
1992	ln (a)*	b**	r^2 ¶	ln (c)*	d**	r^2 ¶
16 July	2.13	−0.29	82.9	3.28	−1.11	57.4
13 August	2.86	−0.26	85.1	3.80	−0.74	55.3
27 August	4.08	−0.16	82.7	4.24	−0.06	61.4
12 September	4.20	−0.06	60.0	4.26	−0.01	10.1
1993						
24 June (1)***	2.58	−0.33	63.0	4.32	−0.95	95.0
24 June (4)***	1.61	0.00	100	1.61	0.00	100
8 July (2)***	3.34	−0.18	57.2	4.38	−0.64	94.3
8 July (5)***	2.30	0.00	100	2.30	0.00	100
22 July (3)***	3.97	−0.09	50.0	4.42	−0.20	95.6
22 July (6)***	2.47	−0.17	51.1	3.17	−0.19	79.6
5 August	3.89	−0.19	45.3	4.36	−0.04	96.6
19 August	4.15	−0.14	41.0	4.48	−0.03	91.7
2 September	4.32	−0.08	39.3	4.51	−0.02	86.6
17 September	4.37	−0.06	46.7	4.50	−0.01	96.0

* a and c: constants equal to the values of y at x = 1 and x = 0 m, respectively.
** b and d: slopes of the linear regressions.
¶ r^2: % variance accounted for.
*** disease gradients on 24 June, 8 July and 22 July each described by two regression lines (Fig. 6); (1), (2) & (3) show the primary disease gradients; (4) & (5) show the background infection and (6) shows the effect of the background infection (5%) on the disease gradients.

Table 2. Parameters estimated from the regression of disease incidence (%) (y) on distance upwind from the inoculum source (m) (x) for the negative exponential model [ln (y) = ln (c) - dx] and the inverse power law model [ln (y) = ln (a) - b ln (x)] used to describe the *A. linicola* disease gradients upwind from a line inoculum source in 1993

Sampling date	Negative exponential model			Inverse power law model		
	ln (c)*	d**	r^2 ¶	ln (a)*	b**	r^2 ¶
24 June	4.02	−0.14	98.2	1.84	−0.35	89.3
8 July	4.01	−0.11	89.4	2.21	−0.31	98.2
22 July	4.26	−0.08	86.7	3.01	−0.22	99.1
5 August	4.34	−0.06	95.0	3.33	−0.17	94.4
19 August	4.44	−0.04	84.5	3.87	−0.10	99.6
2 September	4.50	−0.03	95.6	4.05	−0.07	93.7
17 September	4.61	−0.02	99.8	4.25	−0.05	76.5

* a and c: constants equal to the values of y at x = 0 and x = 1 m, respectively.
** b and d: slopes of the linear regressions.
¶ r^2: % variance accounted for.

Vertical spore dispersal gradients. Linear regressions fitted all six sets of data quite well. On average, linear regressions of y (number of conidia m^{-3} h^{-1}) on x (height in cm) accounted for 82% of the variance (Table 3). The concentrations of *A. linicola* conidia decreased with increasing height within and above the

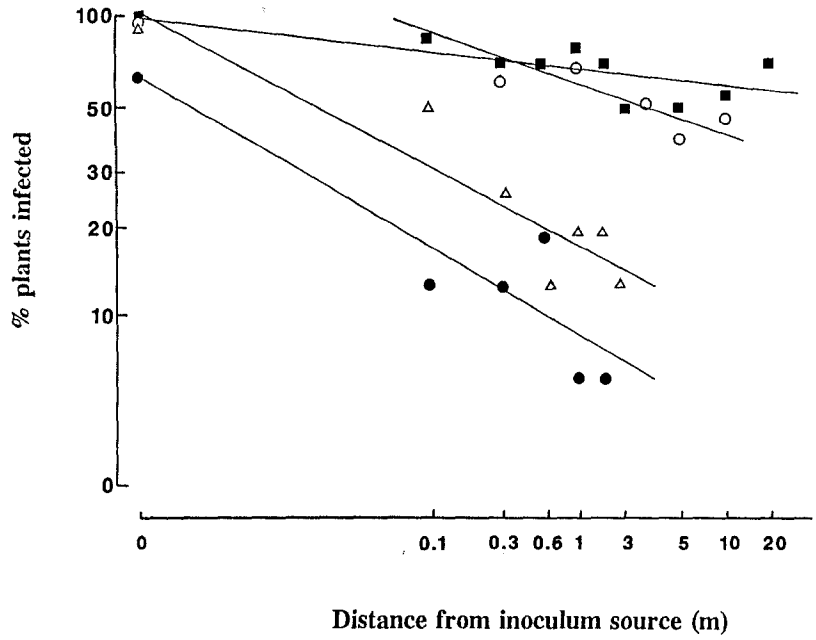

Fig. 5. A. linicola disease gradients from a point inoculum source (average of 4 directions around the source) on 16 July (●), 13 August (△), 27 August (○) and 12 September (■) 1992. The gradients were fitted by the inverse power law model [ln (y) = ln (a) − ln (x)]; the slopes of the regression lines (b) and the percentages of variance accounted for (r^2) are given in Table 1. Values on both axes are back-transformed.

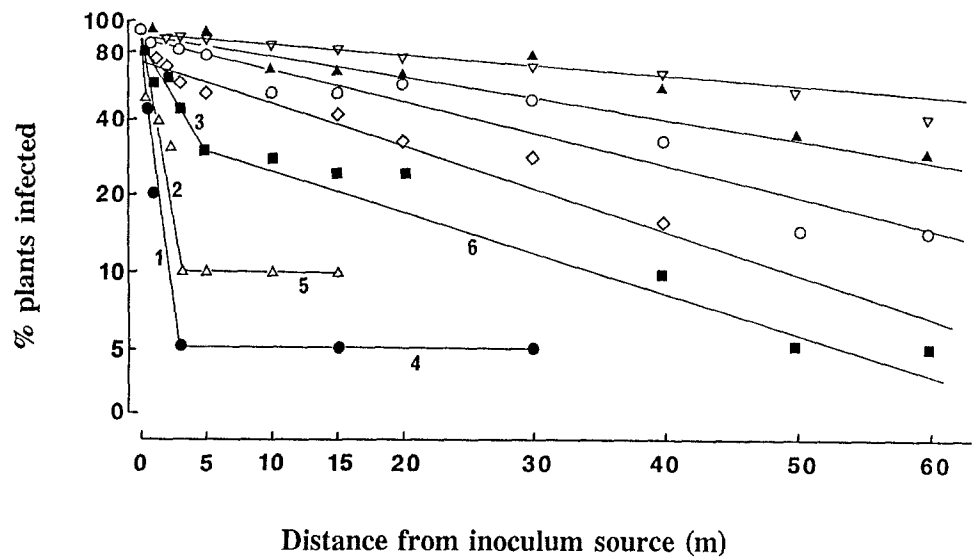

Fig. 6. A. linicola disease gradients downwind from a line inoculum source on 24 June (●), 8 July (△), 22 July (■), 5 August (◇), 19 August (○), 2 September (▲) and 17 September (▽) in 1993, fitted by the negative exponential model [ln (y) = ln (c) − dx]. The regression lines 1, 2, and 3 show the primary disease gradients, the lines 4 and 5 show the background infection, whereas the line 6 shows the effect of the background infection on the disease gradients. The slopes of the regression lines (d) and the percentages of variance accounted for are given in Table 1. Values on y-axis are back-transformed.

linseed crop (Fig. 8). Generally, the numbers of conidia collected during the sampling period were greater at ground level than at 150 cm above ground. There was also an increase in the number of conidia collected with time, with the greatest number being collected on 22 September, approximately 2 weeks before harvest.

Table 3. Parameters estimated from regressions of i) numbers of *A. linicola* conidia m^{-3} h^{-1} (y) collected by the rotorod spore samplers on distance from the inoculum source (m) (x) for the negative exponential model [ln (y) = ln (c) − dx], the inverse power law model [ln (y) = ln (a) − b ln (x)] and ii) numbers of conidia m^{-3} h^{-1} (z) collected by the rotorod spore samplers on height above ground (cm) (w) for the linear model (z = f − gw) used to describe the *A. linicola* horizontal and vertical spore dispersal gradients downwind from a line inoculum source in 1993, respectively

i)	Horizonal spore dispersal gradients					
Sampling date	Negative exponential model			Inverse power law model		
	ln (c)*	d***	r^2 ¶	ln (a)*	b***	r^2 ¶
24 June	4.86	−0.44	63.9	135.4	−45.15	63.9
22 July	5.83	−0.30	90.4	83.5	−6.41	23.3
2 August	5.72	−0.11	81.9	347.5	−40.12	67.8
7 August	5.07	−0.02	56.6	285.5	−13.64	72.3
14 August	3.67	−0.02	53.9	159.7	−2.25	53.9
18 August	5.83	−0.05	91.5	327.5	−7.84	83.2

ii)	Vertical spore dispersal gradients		
	Linear model		
	f**	g***	r^2 ¶
25 August	89.4	−0.55	76.9
31 August	249.8	−1.74	94.2
1 September	472.0	−2.47	90.8
2 September	771.9	−3.59	72.7
21 September	397.3	−2.08	90.4
22 September	1374.0	−6.42	66.9

* c and a: constants equal to the values of y at x = 0 and x = 1 m, respectively.
** f: constant equal to the value of z at w = 0 cm.
*** b, d and g: slopes of the linear regressions.
¶ r^2: % variance accounted for.

Discussion

The results of this study confirmed that conidia of *A. linicola*, like those of other *Alternaria* species, are mainly dispersed by wind. The dispersal of *A. linicola* conidia showed a diurnal periodicity which was influenced by the relative humidity and the wind speed. The numbers of conidia dispersed increased with decreasing relative humidity and increasing wind speed, reaching a maximum between 12:00 h and 13:00 h, when the relative humidity was lowest (73–74%) and the wind speed was 2–3 m sec^{-1}. The highest concentration of conidia in the air was observed 3 h before the highest wind speed, suggesting that although wind is required for the dispersal of *A. linicola* conidia, strong winds may remove a large proportion of the available reserves of conidia within a short time. The pattern of diurnal dispersal of *A. linicola* conidia is therefore similar to that of other *Alternaria* species, including *A. alternata* [Pearson and Hall, 1975], *A. brassicicola* [Humpherson-Jones and Maude, 1982], *A. dauci* [Langenberg *et al.*, 1977] and *A. porri* f. sp. *solani* [Rotem, 1964]. However, no *A. linicola* conidia were dispersed between 21:00 h and 07:00 h, although there was an increase in the wind speed between 24:00 h and 05:00 h. Rain, dew or high relative humidity have been reported to inhibit the release and subsequent dispersal of conidia of *A. dauci* [Langenberg *et al.*, 1977] and *A. porri* f. sp. *solani* [Meredith, 1966; Rotem, 1964].

As the results of this study showed, the Burkard spore sampler was less efficient than the bait plants in detecting *A. linicola* conidia early or late in the growing season, when their concentrations in the air were very low. In both years the Burkard spore sampler detected air-borne *A. linicola* conidia at least one month before the appearance of symptoms on the linseed crop. However, by exposing bait plants, air-borne *A. linicola* conidia could be detected up to three months before the symptoms were observed on the linseed crop. Furthermore, in both years, air-borne *A. linicola*

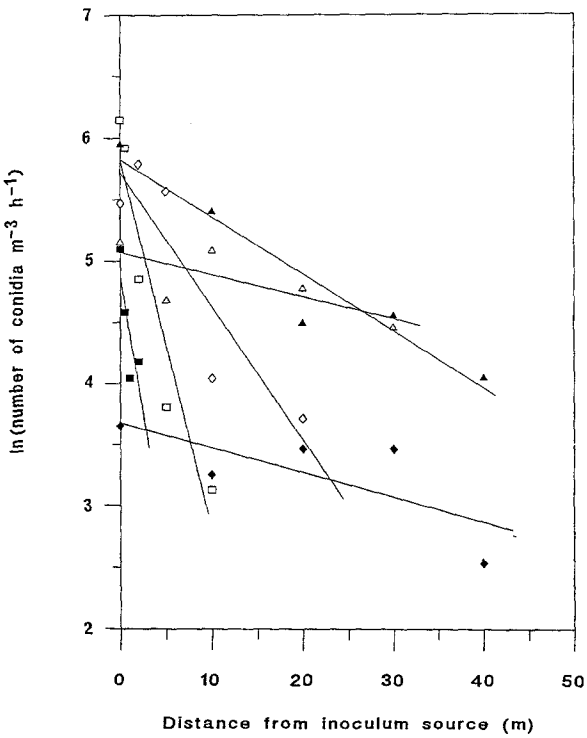

Fig. 7. *A. linicola* horizontal spore dispersal gradients downwind from a line inoculum source as measured by the rotorod samplers at 30 cm above ground level on 24 June (■), 22 July (□), 2 August (◇), 7 August (△), 14 August (♦) and 18 August (▲) 1993. The gradients were fitted by the negative exponential model [ln (y) = ln (c) − dx]; the slopes of the regression lines (d) and the percentages of variance accounted for (r^2) are given in Table 3.

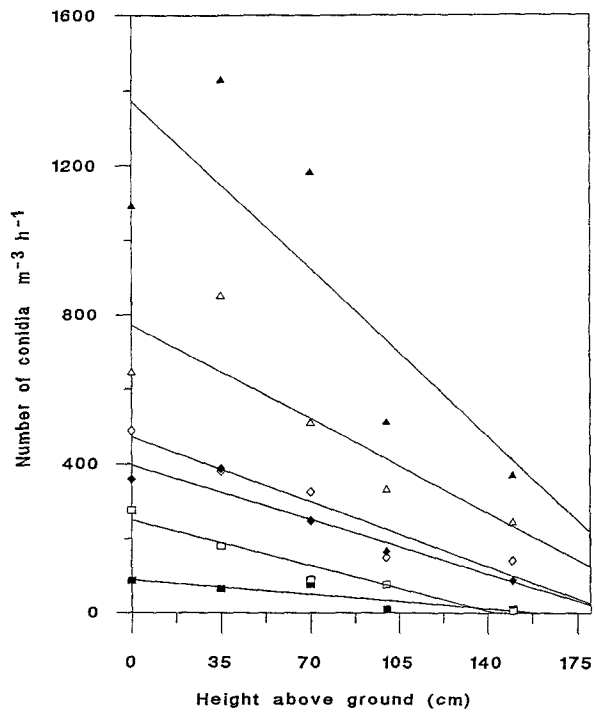

Fig. 8. Vertical dispersal of *A. linicola* conidia as measured by the rotorod samplers on 25 August (■), 31 August (□), 1 September (♦), 2 September (◇), 21 September (△) and 22 September (▲) 1993. The samplers were operated within the linseed crop from 10:00 h until 16:00 h at 0, 35, 70, 100 and 150 cm above the ground level. The slopes of the regression lines (b) and the percentages of variance accounted for (r^2) are given in Table 3.

conidia present above linseed crops were deposited on the bait plants for 2 or 3 weeks after harvest, although they were not then detected by the Burkard spore sampler. The incidence of *A. linicola* infection may have been greater on the bait plants at ground level than on those 1 m above ground early in the growing season because conidia produced on the infected linseed stem debris may have been deposited by splash dispersal on the bait plants at ground level but not at those at a height of 1 m.

Further evidence for the dispersal of *A. linicola* conidia by wind was provided by the rotorod spore samplers which collected air-borne conidia up to 80 cm above the canopy, above the height to which spores were dispersed by splash [Fitt and Bainbridge, 1983]. However, numbers collected decreased with increasing height both within and above the crop canopy, like those of air-borne *A. brassicae* and *A. brassicicola* conidia [Humpherson-Jones, 1992]. The numbers of *A. linicola* conidia collected by sticky-slide spore samplers 20 cm above ground were also greater than those collected above the linseed crop by Mercer *et al.* [1992]. These results suggest that more conidia were produced on the old, senescent leaves at the base of the plants than on the younger leaves at the top of the plants. Moreover, as the wind speed is greater above than within the canopy, it is possible that the concentration of *A. linicola* conidia above the canopy was diluted. This small number of conidia which escape the crop canopy may be involved in a long-distance dispersal of the pathogen. Evidence for wind dispersal of *A. linicola* conidia was also provided by the horizontal spore dispersal gradients in 1993, when the numbers of conidia collected decreased with increasing distance up to 40 m downwind from the inoculum source.

The seasonal periodicity in numbers of air-borne *A. linicola* conidia above linseed crops was influenced by the prevailing weather conditions, although conidia were collected during the entire growing season (April–September) in 1991, 1992 and 1993. The greatest numbers of *A. linicola* conidia in the air above

linseed crops were collected in July and August when average temperatures were high. Large numbers of conidia were collected by the Burkard spore sampler on the first dry day following a period of rain, whereas few or no conidia were collected during rainy days or extended dry periods. Similar seasonal periodicities in the concentrations of air-borne conidia associated with periods of rain or prolonged leaf wetness have been reported for *A. brassicicola* [Humpherson-Jones and Maude, 1982], *A. helianthi* [Allen *et al.*, 1983], *A. porri* [Meredith, 1966], *A. carthami* and *A. alternata* [Mortensen *et al.*, 1983]. Generally, dispersal of large numbers of *A. linicola* conidia on a particular day was associated with the occurrence during the pervious day or night of conditions that favoured sporulation (leaf wetness, 100% relative humidity, temperature $\geq 15\,^{\circ}C$ [Vloutoglou, 1994].

The numbers of air-borne *A. linicola* conidia dispersed above linseed crops also differed between years, presumably due to differences in climatic conditions. Greatest numbers of *A. linicola* conidia were recorded in 1992 when June was drier and hotter than in 1991 and August was wetter. The low mean temperature in June 1991 compared with that in June 1993 might have decreased the sporulation of the pathogen on the plant tissues during that period. Differences in the numbers of conidia between different years might have also been due to differences in the amounts of primary inoculum or in cultural practices. The amounts of primary inoculum present in the field at the beginning of the growing season were probably greater in 1992 and 1993 than in 1991 due to the presence of infected debris. In both years linseed stem debris, naturally infected by *A. linicola* the previous year, was left on the ground after harvest and the field was cultivated just before the sowing of the subsequent linseed crop. Moreover, the irrigation applied to the crop in 1992 and 1993 during the dry periods in June and July might have favoured the production of greater numbers of *A. linicola* conidia on the infected plant tissues.

The results of this study suggest that the disease caused by *A. linicola* on leaves and capsules of linseed crops is mainly spread by air-borne conidia. In 1991, 1992 and 1993 the seasonal increase in the disease incidence on the linseed crops coincided with the greatest concentrations of air-borne *A. linicola* conidia (July, August and early September) [Vloutoglou, 1994]. In 1991, when few *A. linicola* conidia were collected by the Burkard spore sampler above the linseed crop, the disease incidence on the plants was very low (4% by mid-August). In 1992, when greater numbers of conidia were dispersed above the linseed crop than in 1991, the disease incidence was also greater (60–80% by mid-August). Correlation between conidial dispersal and disease incidence has been reported not only for *A. linicola* [Fitt and Ferguson, 1993], but also for *A. dauci* on onions [Langenberg *et al.*, 1977], *A. alternata* and *A. solani* on tomatoes [Pearson and Hall, 1975; Rotem, 1964], *A. brassicicola* on oilseed rape [Humpherson-Jones and Maude, 1982] and *A. macrospora* on cotton [Rotem, 1991]. In 1993, however, disease incidence on the plants was high despite the small numbers of conidia collected. In all years there was an increase in the incidence of the disease on the senescent crop at the end of the growing season just before harvest, despite an unexpected decrease in the numbers of air-borne *A. linicola* conidia. It appears that low temperatures during that period suppressed sporulation of the pathogen on the infected plant tissues.

Furthermore, the *A. linicola* disease gradients in 1992 and 1993 followed patterns similar to those of the spore dispersal gradients; disease incidence decreased with increasing distance from the inoculum source. However, in 1993, two sources of inoculum could be distinguished: a major source (artificial line inoculum source), which gave very steep primary gradients up to 3 or 5 m from the source and a minor source, uniformly distributed in the field (infected stem debris left on the ground after harvest of the previous linseed crop or a small undetected infected proportion of the seed used for sowing), which flattened the gradients. In both years, the disease was first detected downwind from the inoculum source, suggesting that wind was the main agent for the dispersal of the inoculum. However, as the direction of the local wind varied constantly not only between days, but also within the day, the disease spread in all directions later in the season. These results suggest that, although wind is required for the dispersal of *A. linicola* conidia and subsequently for the spread of the disease in a linseed crop, the direction of the prevailing wind is not an overriding factor.

The empirical models which fitted the *A. linicola* disease gradient data best were different in 1992 and 1993. Several factors (geometry of the source, distance over which the gradients are studied, weather conditions, background infection, etc.) may affect the values of b and d [Gregory, 1968] and therefore disease gradients may be described best by different models on different occasions. Such factors were possibly responsible for the differences in the best models between 1992 and 1993. In 1992, the disease gradients were

studied from a point inoculum source, whereas in 1993, they were studied from a line inoculum source. The distance over which the gradients were measured from the source was shorter in 1992 (20 m) than in 1993 (60 m). Moreover, in 1992, the inoculum source was introduced into the crop late in the growing season (24 days after full flowering), whereas in 1993, the inoculum source was introduced very early (14 days before the start of flowering).

The results of this study suggest that conidia of *A. linicola* produced on inoculum sources early in the growing season can be transported by wind and subsequently create a disease epidemic near the foci of their production. However, even under environmental conditions favourable for the spread of the disease, factors such as the size of the inoculum source, the number of conidia available for dispersal, the crop density, the direction of the rows of the plants, the amount of the background inoculum and the wind speed may influence the development of an epidemic in linseed crops.

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