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A model of the escape of *Sclerotinia sclerotiorum* ascospores from pasture

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Abstract

A multi-layer physical model, SPORESIM-1D, based on the gradient transfer theory (K-theory) of turbulent dispersal (analogous with the molecular diffusion of gasses) is described for the transport of *Sclerotinia sclerotiorum* ascospores within and above a grass canopy following their release from apothecia at ground level. The 'steady-state' diffusion equation is solved numerically and the spore escape fraction is estimated. SPORESIM-1D's context is the risk analysis of *S. sclerotiorum* used as a mycoherbicide to control *Cirsium arvense* in pasture. In validation tests SPORESIM-1D was internally consistent and produced a vertical wind speed profile similar to that measured in a grassland. In further validation tests, measured vertical profiles of atmospheric concentrations of *Lycopodium clavatum* spores in a wheat crop, and *Venturia inaequalis* spores in an apple orchard and in a grassland, were closely approximated by the model, as was measured data on the concentration of *S. sclerotiorum* ascospores deposited downwind of a small area source in a grassland. Escape fractions for grassland predicted by SPORESIM-1D, were 50% lower than predicted by both a Lagrangian model (Plant Disease 82 (1998) 838) and a one-layer version of SPORESIM-1D, SPORESIM-1L, indicating that the vertical compartmentalisation in SPORESIM-1D, allowing wind speed and pasture leaf area index (LAI) to vary with height, results in a more realistic estimate of the escape fraction. Simulations using SPORESIM-1D revealed an increase in the escape fraction with increasing wind speed, and an order-of-magnitude fall with increases in LAI from values typical of a closely grazed sheep pasture (ca. 2) to those of more laxly grazed cattle pastures and intact grassland (ca. 7). This result implies that any additional risk of disease in a susceptible crop growing downwind of a pasture treated with a *S. sclerotiorum* mycoherbicide may be reduced by grazing management. Reduction in the risk of sclerotinia rot in kiwifruit (*Actinidia deliciosa*) vines, and in apple scab disease in apple trees, caused by *V. inaequalis*, appears possible by maintaining a dense grass under-storey. A simple empirical model for spore escape with one parameter and two variables (LAI and wind speed) derived from the mechanistic model provided a good description ($r^2 = 0.998$) of simulated escape fraction. Combined with information on release rates of *S. sclerotiorum* spores at a biocontrol site, this model will enable a times-series analysis of spore emission, and coupled with a

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Gaussian plume model, prediction of minimum isolation distances between a biocontrol site and a susceptible crop.
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1. Introduction

The Ascomycete, *Sclerotinia sclerotiorum*, has potential as a mycoherbicide for the control of *Cirsium arvense* (L.) Scop., and other weeds in pastures in New Zealand (Bourdôt et al., 1995; Bourdôt and Harvey, 1996). However, this fungal pathogen has a very wide host range including many economically important crops (Pennycook, 1989) and the artificially increased inoculum in treated pastures may increase the disease risk in susceptible crops downwind of the biocontrol site (Bourdôt et al., 2000). Quantification of this risk is necessary for an informed judgement about the safety and management of this form of weed control.

Sclerotia deposited in the pasture at a biocontrol site over-winter in the soil (Bourdôt et al., 2000) and form apothecia in the spring releasing ascospores into the air at the base of the pasture (Bourdôt et al., 2001). A fraction of these spores may escape the pasture and be dispersed beyond the biocontrol site on air currents, thereby adding to the natural background levels of *S. sclerotiorum* spores in the neighbourhood of susceptible crops. Using exponential decay models describing the gradient in the measured density of ascospores deposited downwind of pastures treated with *S. sclerotiorum*, Bourdôt et al. (2001) derived a safety zone of 8 m. The general applicability of this safety zone is, however, questionable because these empirical models provide no information about how spore liberation, transport and deposition is influenced by environmental conditions. In general these processes are influenced particularly by wind and air turbulence (McCartney and Fitt, 1985) as well as density of the vegetation. de Jong et al. (1999) have outlined an alternative, mechanistic approach employing a Gaussian plume model for dispersal that uses as input the emission rate of spores from a pasture (or 'source strength'), the product of the release rate of spores from the apothecia, a process quantified empirically by Bourdôt et al. (2001) and the 'escape fraction'.

The escape fraction (Gregory, 1961) cannot be measured directly (Aylor and Taylor, 1983; Aylor and Ferrandino, 1985) but may be evaluated given a mechanistic understanding of the interacting processes that control the movement of spores within a vegetation canopy. An existing statistical model of spore release from apothecia, the 'volcano-model' (Kohli et al., 1995), is not appropriate for this purpose. A physical mathematical model of spore dispersal in and above a vegetation canopy based on the physics of air movement is required. To this end we have adapted an existing model of the transport of *Chondrostereum purpureum* basidiospores in a forest (de Jong et al., 1991) to simulate the transport of the ascospores of *S. sclerotiorum* within a grass canopy. The principles of this model have been widely accepted by the scientific community (de Jong, 1992; Teng and Yang, 1993; Sawyer et al., 1994; Shaw, 1994; Barlow, 1999; Evans, 2000). Our simulation model (SPORESIM-1D) uses concepts from models of spore transport in a wheat crop (Rijsdijk and Rappoldt, 1979) and in plant canopies in general (Legg, 1983; Legg and Bainbridge, 1978; Raupach, 1989; Davis and Monahan, 1991; Flesch and Wilson, 1992; Yao et al., 1997; Aylor, 1999). It also includes ideas from models for barley (Legg and Powell, 1979; Aylor, 1982) and rice (Park and Kim, 1995), and elements from models of pollen transport in the air inside a forest (Di-Giovanni et al., 1989) and of spore dispersal via rain-splash (Pielaat et al., 1998). It uses numerical methods for the simulation of spore dispersal (Yang et al., 1998).

SPORESIM-1D may be considered as a second-generation model after Legg and Powell (1979) for three reasons. Firstly, it uses the micro-

weather formula of Goudriaan (1977) in order to calculate the wind and turbulence profile in a grass sward from a known wind speed at a reference height above the pasture. Secondly, an elegant and quick numerical method is used for solving the finite difference equations (de Jong et al., 1991). Thirdly, the vegetation canopy (pasture containing grasses and clovers) is divided vertically into many horizontal layers. This modification of the 'one-layer' model SPORESIM-1L, used in de Jong et al. (1999), allows the vertical profile of pasture leaf area density to be taken into account when calculating the deposition of spores onto foliage due to turbulent impaction. In SPORESIM-1D, impaction is adequately treated and the spore source can be vertically shifted, making it a very flexible tool that has relevance for a wide range of dispersal phenonema in addition to the escape of *S. sclerotiorum* spores from a pasture.

In this paper, we describe three versions of SPORESIM-1D that we validate according to defined performance criteria, comparing simulated and measured data on the dispersal of the ascospores of *Venturia inaequalis* and *S. sclerotiorum*, and the spores of *Lycopodium clavatum*. We also compare SPORESIM-1D with another spore transport model and derive a mechanistically based expression that gives the escape fraction as a simple function of wind speed and pasture leaf area per unit ground surface area (leaf area index (LAI)), providing a simple basis for calculating the emission rate of ascospores from a model pasture.

SPORESIM-1D is written in Visual FORTRAN (Version 6), and is operational and available on request from the senior author. The source listings are in de Jong et al. (2002).

2. Methods

2.1. Notation and model versions

Three versions of the model SPORESIM-1D varying in dimensionality (vertical and downwind directions) and discretisation (horizontal layers) are considered in this paper. The simplest version of the model is SPORESIM-1L. It is a one-dimensional one-layer model that describes the vertical flux of spores within and outside an area source of spores. The second version is SPORESIM-1D, also a one-dimensional model for an area source of spores, but partitioned vertically (with height, z) into many horizontal layers. Both versions are suitable for numerical evaluation and estimate the fraction of spores escaping vertically from a grassland canopy (the escape fraction, E_v). The third version of the model, SPORESIM-2D, evaluates spore concentration in two dimensions, height above ground (z) and distance downwind of the source (x), and is used for simulation of a line source of spores.

The descriptions and units for the parameters and the variables used in SPORESIM-1L, SPORESIM-1D and SPORESIM-2D are in Table 1. Parameter values are shown in Table 2. Other details of the models are introduced as they are discussed in the succeeding sections.

2.2. The partial differential equation for spore dispersal

Within a pasture undergoing biological control of thistles, the concentration of airborne *S. sclerotiorum* ascospores, C, depends on air currents (wind speed), deposition (onto plant and soil surfaces), and sedimentation (falling by gravity in still air). McCartney and Fitt (1985) extensively describe the diffusion equation for these processes, in which the turbulent dispersal of airborne particles is based on an analogy with the molecular diffusion of gasses (gradient transfer or K-theory). Assuming that release of ascospores from apothecia occurs continuously at a constant rate, C reaches a steady-state in seconds or less. Ascospore concentration, C, is then in equilibrium with input of ascospores from apothecia on one hand, and losses by vertical transport, by sedimentation, and by deposition on the other. The steady-state diffusion equation for a pasture considered as a single layer and assuming zero concentration of spores in the external air, is:

$$u\frac{\partial C}{\partial x} = R_{spor}\delta(z - z_r) + \frac{\partial}{\partial z}\left[K(z)\frac{\partial C}{\partial z}\right] + v_s\frac{\partial C}{\partial z} - v_d A_d C \quad (1)$$

with boundary conditions

$$C(x=0,z)=0 \text{ and } \frac{\partial C}{\partial z}(x,z=0)=0.$$

Here, u is the wind speed within the layer (m s^{-1}), C is the spore concentration (spores m^{-3}), x_l is the downwind length of the pasture (m), R_{spor} is the release rate of ascospores per unit ground area (ascospores m^{-2} s^{-1}) at a reference height (z_r) above ground level, K is the turbulent diffusion coefficient (m^2 s^{-1}), z is the height (vertical dimension within layer (m)), v_s is the sedimentation velocity (m s^{-1}), v_d is the deposition velocity (m s^{-1}), and A_d is the deposition-area density (m^2 m^{-3}). The value of parameter A_d was approximated using the LAI (leaf area per unit ground area) of the pasture as discussed in Section 3.5.

2.3. Derivation of a discrete model

To define a discretised version of Eq. (1) suitable for numerical evaluation, consider a spatial discretisation with constant spacing:

$$x_n = n\Delta x, \quad x_o = 0, \quad x_N = x_l$$

$$z_i = i\Delta z, \quad z_o = 0, \quad z_I = h,$$

and define

$$C_{i,n} = C\left(z_i + \frac{\Delta z}{2}, x_n + \frac{\Delta x}{2}\right).$$

Table 1
Notation list for parameters and variables used in SPORESIM-1L, SPORESIM-1D, and SPORESIM-2D

Symbol	Units	Description
Δx	m	downwind length of a layer in the model
Δy	m	cross-wind length of a layer in the model
Δz	m	height of a layer in the model
A_d	m^2 m^{-3}	deposition-area density
C	spores m^{-3}	spore concentration
C_n	spores m^{-3}	spore concentration in nth layer in model
D_{leaf}	–	fraction of spores deposited on leaves
D_{soil}	–	fraction of spores deposited on soil
E_h	–	fraction of spores escaping horizontally
E_i	–	efficiency of impaction on leaf surfaces
E_v	–	fraction of spores escaping vertically
g	m s^{-2}	acceleration due to gravity
h	m	pasture height (above which spores are released)
i_w	–	turbulence intensity
K	m^2 s^{-1}	Eddy diffusivity of spores in the pasture
k	–	Karman constant
LAI	m^2 m^{-2}	Pasture leaf area index
Q	spores s^{-1}	emission rate of spores from pasture canopy
r	s m^{-1}	exchange resistance
R_{spor}	spores m^{-3} s^{-1}	sporulation rate
Stk	–	Stokes' number
u	m s^{-1}	wind speed in and above the pasture
$u*$	m s^{-1}	friction velocity
u_n	m s^{-1}	wind speed in the nth layer in the model
u_r	m s^{-1}	wind speed at reference height above the pasture
u_z	m s^{-1}	wind speed at height z in the pasture
v_d	m s^{-1}	deposition velocity of spores
v_s	m s^{-1}	sedimentation velocity of spores
w	m	leaf width
x	m	horizontal downwind distance within pasture
x_l	m	length of pasture
z	m	vertical distance within pasture

Table 2
Parameter values and constants used in SPORESIM-1L, SPORESIM-1D, and SPORESIM-2D

Symbol	Description	Value
k	Von Karman constant	0.35 [−]
w	leaf width	0.01 m
i_w	turbulence intensity	0.6 [−]
v_s	sedimentation velocity	0.002 m s^{-1}
LAI	leaf area index	2–7 [−]
v_d	deposition velocity	0.01 m s^{-1}
h	pasture height	0.25 m
R_{spor}	ascospore release rate of source	10^2 m^{-2} s^{-1}
x_l	downwind length of biocontrol site	100 m
g	acceleration due to gravity	9.8 m s^{-2}
L	numerical stability	~1.0 [−]

Integrating Eq. (1) in the box defined by $[x_n,x_{n+1}] \times [z_i,z_{i+1}]$ and taking $C_{i,n}$ to be the spatial average of the concentration over the box gives

$$u\frac{\Delta z}{\Delta x}(C_{i,n}-C_{i,n-1}) \cong R_{spor,i}-\Delta z v_d A_d C_{i,n}+v_s(C_{i+1,n}-C_{i,n}) + K(z_{i+1/2})\frac{\partial C}{\partial z}(z_{i+1/2})-K(z_{i-1/2})\frac{\partial C}{\partial z}(z_{i-1/2}).$$

The approximation is correct to error terms of order Δx and Δz^2 assuming that the terms corresponding to vertical diffusive flux (the last two terms on the right hand side) are evaluated with comparable accuracy. The discrete terms $R_{spor,i}$ are either R_{spor} (for the first grid box, corresponding to the spore source), or zero (for all layers above). Applying a centred discrete approximation for the vertical flux terms and taking $K(z_{i+1/2})$ to be evaluated at the boundary between cells gives a discrete equation

$$u\frac{\Delta z}{\Delta x}(C_{i,n}-C_{i,n-1}) \cong R_{spor,i}-\Delta z v_d A_d C_{i,n}+v_s(C_{i+1,n}-C_{i,n}) + K(z_{i+1/2})\frac{C_{i+1,n}-C_{i,n}}{\Delta z} - K(z_{i-1/2})\frac{C_{i,n}-C_{i-1,n}}{\Delta z}.$$

This amounts to a second order (in z) implicit discretisation of Eq. (1). The first two terms on the left hand side describe the horizontal loss from the cell and flux into the cell, respectively. Values of $C_{i,n}$ are determined from upwind spore inputs by inverting a tri-diagonal matrix using the Gauss–Jordan elimination procedure (Waggoner et al., 1969; Ward et al., 1989). With this method, the steady-state concentrations for each layer can be found very rapidly. Let K_{max} denote the maximum eddy diffusivity. Provided

$$\frac{K_{max}\Delta x}{u\Delta z^2}\leq\frac{1}{2}$$

this approach is stable (DuChateau and Zachmann, 1986). Since the crop is much smaller in the vertical direction than the horizontal, the vertical discretisation is correspondingly small, allowing a relatively coarse discretisation in the downwind direction.

In fact, it is often useful to use only a single column of vertical layers (that is, $\Delta x = x_1$), corresponding to horizontal integration across the entire crop. In this case, since we assume no horizontal flux of spore into the crop from the left, the discrete model becomes

$$u\frac{\Delta z}{x_1}\ C_i \cong R_{spor,i}-\Delta z v_d A_d C_i+v_s(C_{i+1}-C_i) + K(z_{i+1/2})\frac{\partial C}{\partial z}(z_{i+1/2}) - K(z_{i-1/2})\frac{\partial C}{\partial z}(z_{i-1/2}), \quad (2)$$

with

$$\frac{\partial C}{\partial z}(z_{i+1/2})=\frac{C_{i+1}-C_i}{\Delta z}.$$

2.4. Implementation of the discrete model

To allow for the considerable vertical gradient in spore concentration that may exist, the single layer model, SPORESIM-1L, was extended to many thin layers in SPORESIM-1D (Fig. 1). The bottom layer only contained spore-releasing apothecia, and so the term $R_{spor,i}$ was set to zero for all other layers. Wind speed and the turbulent diffusion

coefficient for each layer were calculated from the wind speed u_r at a reference height above the crop (Goudriaan, 1977). The velocities of deposition and sedimentation were based on theoretical considerations and existing data. The elliptical ascospores of *S. sclerotiorum* measure 9–13 by 4–6.5 μm (Dennis, 1968). They have a theoretical sedimentation velocity (i.e. their rate of fall in still air due to gravity according to Stokes' Law, cf. Gregory (1961)), v_s of 0.002 m s^{-1} based on McCartney and Fitt (1985). Deposition on surfaces such as leaves and stems is defined here as turbulent impaction and occurs at a theoretical velocity, v_d of 0.01 m s^{-1} based on Fig. 9 in Chamberlain (1975), Fig. 1 in Bache (1981) and Fig. 7 in Slinn (1982). In testing the model we used data on the dispersion of *V. inaequalis* and *L. clavatum* spores in addition to data from *S. sclerotiorum*. Ascospores of *V. inaequalis* have about the same dimensions as *S. sclerotiorum* ascospores, and hence the same v_s and v_d. The theoretical sedimentation velocity, v_s, of *L. clavatum* spores is 0.0197 m s^{-1}.

The assumption of a continuous release of *S. sclerotiorum* ascospores, explosively ejected from the apothecia to a height of several centimetres and often in clumps of two or four (Ingold, 1971), seems reasonable. While on occasions of still-air

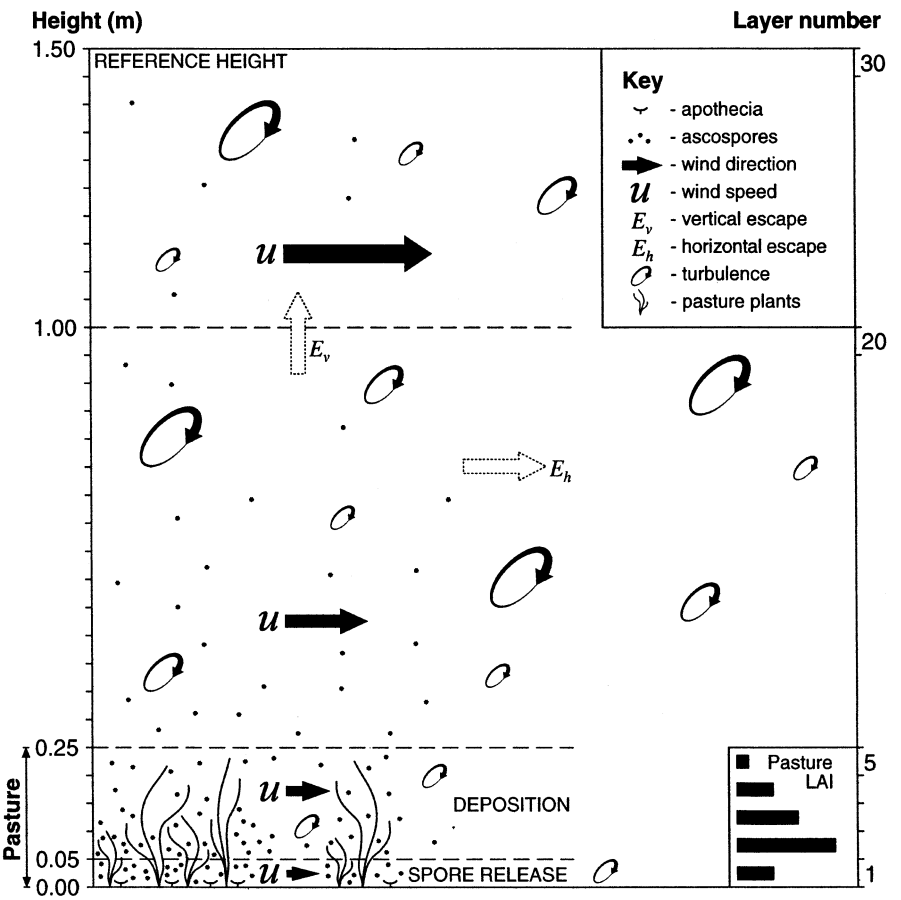

Fig. 1. SPORESIM-1D, a multi-layer model for the transport of *Sclerotinia sclerotiorum* ascospores within, and escape from, a pasture sward. The air within and above the pasture, to a reference height of 1.5 m for wind speed, is divided into many layers. Ascospores are released by apothecia in the bottom layer. The fraction escaping (above layer 20) is a function of turbulence, wind-speed (u), and the rate of deposition onto soil and plant surfaces (v_d); the latter a function of pasture leaf area index (LAI) that varies vertically within the pasture.

conditions large numbers of spores may be released simultaneously by 'puffing' (Hartill and Underhill, 1976), release occurs continuously under the windy spring-time conditions prevailing in pastures in Canterbury, New Zealand (Bourdôt et al., 2001).

Wind, u, and turbulence, K, are calculated from one wind speed at a reference height above the crop using a micro-weather simulator (Goudriaan, 1977; Stigter et al., 1977). The vertical distribution of LAI in the pasture was taken from Fig. 1 in Nassiri et al. (1996). The bottom-line predictions from the model are phrased in terms of the fraction of spores, released at the reference height, z_r, which escape from the crop. The vertical escape fraction, E_v, is defined by the vertical flux of spores through a surface at the top of the crop at $z = h$, divided by the total spore production. Thus

$$E_v = \frac{\int_0^{x_l} \left(-K \frac{\partial C}{\partial z} - v_s C \right) \Big|^{z=h} \mathrm{d}x}{(x_l R_{spor})}.$$

The horizontal escape fraction, E_h, relates to the number of spores being conducted downwind and escaping through a surface located at the downwind edge of the crop at $x = x_l$. This gives

$$E_h = \frac{\int_0^{h} \left(u \frac{\partial C}{\partial x} \right) \Big|^{x=x_l} \mathrm{d}z}{(x_l R_{spor})}.$$

The total escape fraction is then defined as $E = E_v + E_h$.

In SPORESIM-1D the per-cell vertical escape fraction, E_v, from layer n into layer $n+1$ at a particular height, z, is defined as

$$E_v = \left[\frac{C_n}{r_{n+1}} - \frac{C_{n+1}}{r_n} \right] \times \Delta z$$

where Δz is the difference in height between two layers ($z_{n+1} - z_n$), i.e. the thickness of a layer. C_n is the concentration of spores in the nth layer in the model and r is the resistance to exchange of spores between layers (s m^{-1}). E_v may be used to estimate the rate of emission of spores from a biocontrol site, thus providing the input term Q, for a long-distance dispersal model such as the Gaussian Plume model (Erbrink, 1995).

The per-cell horizontal escape fraction, E_h, is defined as

$$E_h = \left[\frac{C_n \times u_n}{x_l} \right]$$

where u_n is the wind speed in layer n. E_h is used in transforming the one-dimensional (area source) model SPORESIM-1D into a two-dimensional (line source) model, SPORESIM-2D, to describe the downwind dispersal of spores (Section 3.4.1).

2.5. Verification and validation procedures

The purpose of SPORESIM-1D is to provide a good description of spore dispersal phenomena in a pasture, so that an accurate estimate of the fraction of spores escaping above the pasture canopy can be obtained. Our basic assumption is that if the model gives a good prediction of spore concentrations in the air above and downwind of spore sources, then we suppose that it also gives a reliable estimate of the escape fraction.

The context in which SPORESIM-1D is to be used is a risk analysis of the biocontrol of the pasture weed, *C. arvense*, using the fungus *S. sclerotiorum* as a mycoherbicide. For this reason validation was considered an essential requirement (Rykiel, 1996), and the key performance criteria SPORESIM-1D must meet to be acceptable for use are:

1. The model is verifiably correct mechanically and logically.
2. The model correctly simulates wind speed in a pasture; wind is the driving force in the model.
3. Model estimates of escape fraction are not unduly affected by wind gustiness.
4. Modelled spore concentrations are in close agreement with measured spore concentrations in field experiments and the general behaviour of the escape fraction is similar to that in an existing model.

3. Verification and validation results

3.1. Verification

The internal validity of SPORESIM-1D was tested using the guidelines in Wagenmakers (1984), setting v_s and v_d to zero, r to100 and x_l to 10^6. This resulted in a linear profile of spore concentration versus height (Fig. 2). Beginning at the top layer (layer 20), above which 'escape' occurs in SPORESIM-1D, spore concentration (spores m^{-3}) declined linearly (by 10 spores m^{-3} per layer) as is to be expected from theoretical considerations when the pasture area has an almost infinite length and there is neither deposition nor sedimentation. The consistent occurrence during all simulations of the condition,

$$E_h + E_v + D_{leaf} + D_{soil} = 1.0$$

where E_h and E_v are as defined above and D_{leaf} and D_{soil} are the proportions of spores deposited on foliage and soil, verifies that the computer programme is internally valid and accounts for all spores generated under all test conditions (See Fig. 9 for an example).

A sensitivity analysis of SPORESIM-1D was conducted as outlined by Wagenmakers (1984) and de Jong (1988) with respect to model structure (model reaction to different equations for the same physical processes) and model parameters (model reaction to changes in parameter values).

3.2. Wind speed profile in pasture-comparison of model output with field data

The movement of air within a canopy plays an important role in the dispersal of spores (Legg and Bainbridge, 1978; McCartney, 1994), and wind speed is particularly important (Leffelaar, 1993). Consequently, our escape model must simulate wind speed adequately. The vertical profile of wind speed in SPORESIM-1D (and in SPORESIM-2D) is calculated from measured wind speed at a reference height, $h = 1.0$ m according to the equations in Goudriaan's micro-weather simulator (Goudriaan, 1977). Aylor et al. (1993) measured wind speed at several heights in and above a grass canopy of *Festuca arundinacea* using sensitive cup

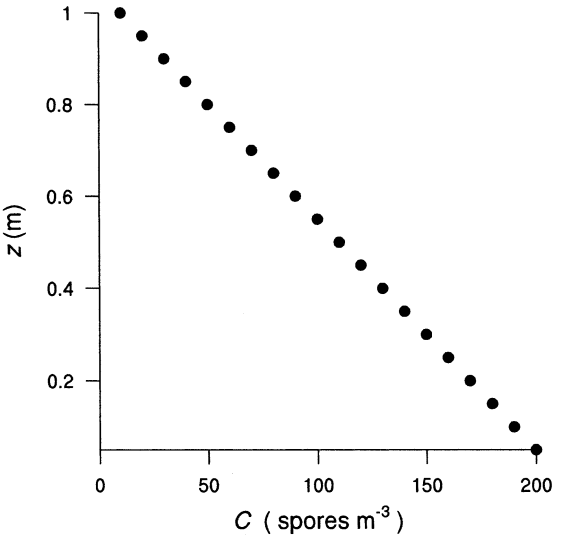

Fig. 2. Internal validity of the one-dimensional model SPORESIM-1D is demonstrated by the expected linear relationship between the simulated density of spores and height above ground, z. Points on the graph are layers in the model. Exchange resistance in all layers was set at $r = 100$ s m^{-1}, with $v_s = 0$ and $v_d = 0$.

anemometers above the canopy and vertically deployed hot wire anemometers below the canopy. The measured wind speeds from Fig. 4 in Aylor et al. (1993), averaged for each of nine sets of measurements, were compared with wind speeds simulated by SPORESIM-1D. Canopy parameters (LAI = 4.7 and $h = 0.28$m) in Aylor et al. (1993) were incorporated in the simulation model and the parameter for turbulence intensity ($i_w = 0.6$), was selected by calibration whereby its value was adjusted to maximise the agreement between the windspeeds from the model and the mean data values in Aylor et al. (1993).

Field data and model data match reasonably well (Fig. 3). Both modelled and measured vertical profiles of mean horizontal 'cup' wind speed, u, expressed as a ratio with friction velocity, (u/u^*) increased exponentially with relative height (z/h) within the canopy ($z/h < 1.0$) and logarithmically with height above the canopy.

3.3. Wind gustiness and spore escape

Wind speed u, is a constant in SPORESIM-1D (and in the other versions of the model), but in

reality is highly variable in time. The distribution of hourly mean and gust wind speeds from the Broadfields weather station in Canterbury, New Zealand, measured in spring 1996 illustrate this time-dependence of u. Hourly mean wind speeds varied from 0 to 17.3 m s^{-1} over 2184 h of measurement with a mean of 4.2 m s^{-1} while maximum hourly gusts varied in speed from 4 to 24.7 m s^{-1} over 2117 h of measurement (Table 3).

To investigate the consequences for the escape fraction of ignoring wind gusts, a sensitivity analysis was conducted using SPORESIM-1D in which the escape fraction, E_v, for a time period during which gusty conditions persisted, was compared with escape when the wind speed was steady and equal to the mean wind speed for the time interval. To simulate escape during a period of gusty conditions, the time period was arbitrarily divided into three fractions of different duration (0.89, 0.10 and 0.01). These time fractions were periods of 'steady wind', moderate gusts' and 'heavy gusts', respectively. The periods of moderate and heavy gusts were assigned wind speeds of 7 and 24.7 m s^{-1} (mean and maximum gust speeds in spring 1996 in Canterbury (Table 3)). The 'mean' wind speed for the time period was set equal to 4.2 m s^{-1} (the mean hourly wind speed for the spring of 1996 (Table 3)) and, as a consequence of this, the wind speed for the 0.89 'steady' fraction of the time period was required to be 3.7 m s^{-1}. SPORESIM-1D, with LAI = 0 to 10, was used to simulate escape for each of the three wind speeds representing the steady, moderate gust and heavy gust fractions of the time period, and for the mean wind speed. The escape fraction for the gusty period was estimated as the sum of the escape fractions for each of the three time fractions after scaling them by their respective fractions of time.

The results for the sensitivity analysis using an LAI of 5 are in Table 4. They suggest that during

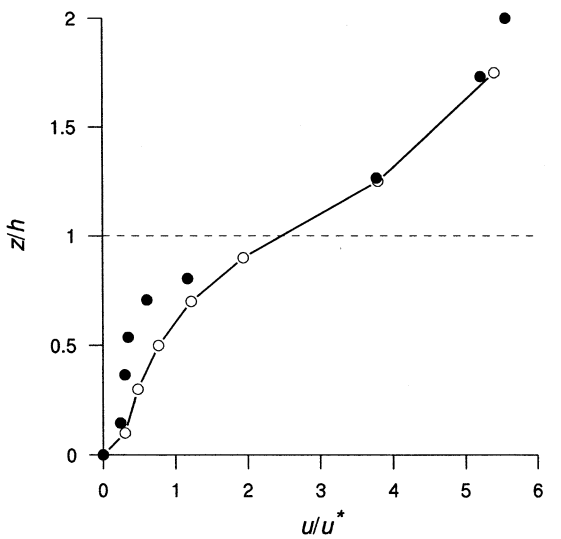

Fig. 3. Comparison of the vertical profile of wind speed:friction velocity ratio, u/u^*, as measured in a *Festuca arundinacea* grassland Connecticut, USA (means for each of nine sets of data from Fig. 4 in Aylor et al., 1993) (●), with simulated data using the one-dimensional model SPORESIM-1D (○—○). The vertical axis gives height on a relative scale as distance above ground, z, divided by the height, h, of the grassland canopy.

Table 3
Wind speed statistics for Canterbury, New Zealand for the period 1 September–30 November (spring) for 1996

Wind speed class interval (m s^{-1})	Frequency (h)	
	Hourly mean	Maximum gust
0	19	4
2	544	123
4	595	441
6	518	392
8	289	404
10	185	292
12	24	208
14	8	152
16	1	67
18	1	24
20	0	4
22	0	4
24	0	1
26	0	1
Total hours	2184	2117[a]

Maximum hourly mean wind speed (17.3 m s^{-1})
Mean wind speed (4.2 m s^{-1})
Maximum gust speed (24.7 m s^{-1})
Mean gust speed (7.0 m s^{-1})

Data are from Broadfields weather station H32642 in Canterbury and were recorded on an hourly basis.
[a] Gusts not recorded for 67 consecutive hours (2200 hours 21 Sept.–1600 hours 24 Sept.).

a period of intermittent gusty wind conditions, the escape fraction may be the same as that during a period when the wind speed is steady at the mean wind speed for the gusty period. The same result was obtained for LAI values up to eight, while at LAI values of 9 and 10 escape was 2 and 6% greater under the gusty conditions (data not given). These results imply that the higher the wind speed, the less rapidly escape increases with increasing wind speed, and that overall, gusty wind conditions have little influence on the escape fraction. However, gusty winds could cause differential spore release (from apothecia) and deposition rates and result in entrainment of spores in large eddies. This could alter the escape fraction and is not accounted for in the above sensitivity analysis using a steady-state model. Thus it is with some degree of uncertainty that we conclude that SPORESIM-1D gives realistic estimates of the escape fraction during gusty wind conditions.

3.4. Comparison of simulated data from SPORESIM-1D and SPORESIM-2D with measured data

Three independent sets of spore data measured under field conditions were compared with data produced by simulations using SPORESIM-1D and SPORESIM-2D. The procedures used and the results of the comparisons are discussed in the next three sections. The value of the parameter, R_{spor}, the driving force in SPORESIM-1D (and SPORESIM-2D), was not available in two of the field data sets. In these cases the value of R_{spor} was estimated by adjusting it to maximise agreement, judged visually, between the model output and the data set; a 'calibration' procedure often used to estimate otherwise unknown parameter values in ecological models (Rykiel, 1996).

Table 4
Analysis of the effect of wind gusts on the proportion of spores escaping vertically from a grass canopy using SPORESIM-1D

Wind gust specification	u (m s^{-1})	Proportion of time	E_v[a]
Steady	3.7	0.89	0.088
Moderate gusts	7.0[b]	0.10	0.171
Heavy gusts	24.7[b]	0.01	0.391
Combined conditions			0.100[c]
Mean	4.2[b]	1.0	0.104

[a] The values of E_v for 'steady', 'moderate', 'heavy' and 'mean' values of u were calculated by SPORESIM-1D with LAI = 5.

[b] Wind speeds for 'moderate' and 'heavy' gusts were set equal to the mean and maximum wind gust speeds for Canterbury in spring 1996 (Table 3) and the speed of the 'steady' wind was a consequence of setting the 'mean' wind speed to 4.2 (from Table 3) [$4.2 = (0.89 \times 3.7) + (0.1 \times 7) + (0.01 \times 24.7)$].

[c] The overall escape fraction was calculated as $E_v = (0.89 \times 0.088) + (0.1 \times 0.171) + (0.01 \times 0.391)$.

3.4.1. Artificial line source of Lycopodium clavatum spores with known release rate

The measured data used in this comparison with model-generated data consisted of aerial concentrations of *L. clavatum* spores at seven heights and at distances of 2 and 4 m downwind of an artificial line source (with a release height of 0.4 m) within a 0.8 m tall wheat crop in Connecticut, USA, in 1986 (Table IV, Aylor and Ferrandino, 1989). The spores were released at a constant rate from artificial sources. The concentration of the spores was measured with rotorods (Rotorod Sampler, Sampling Technologies Inc., Minnetonka, MN, USA) placed at four heights above the canopy (0.85, 1.10, 1.35 and 1.60 m above the ground) and with small suction traps at two heights inside the canopy (0.26 and 0.58 m); concentrations near the ground (0.03 m) were measured from deposits on glass microscope slides placed on the ground.

In order to compare the performance of SPORESIM-1D against these data, it was converted from its one-dimensional form (in which x and y are considered to be infinitely large and $0 < z <$ infinity), to the two-dimensional form, SPORESIM-2D, (where only y is considered to be infinitely large and $0 < z <$ infinity and $0 < x <$ infinity) capable of simulating spore dispersal (to a height, z, of 2.0 m) for a distance, x, of 5 m downwind of a line source. This version of the model consisted of 20 horizontal layers each of 10 adjacent square cells that were 0.5 m wide (Δy) $\times$ 0.5 m long (Δx) $\times$ 0.1 m thick (Δz); a cell size resulting in an

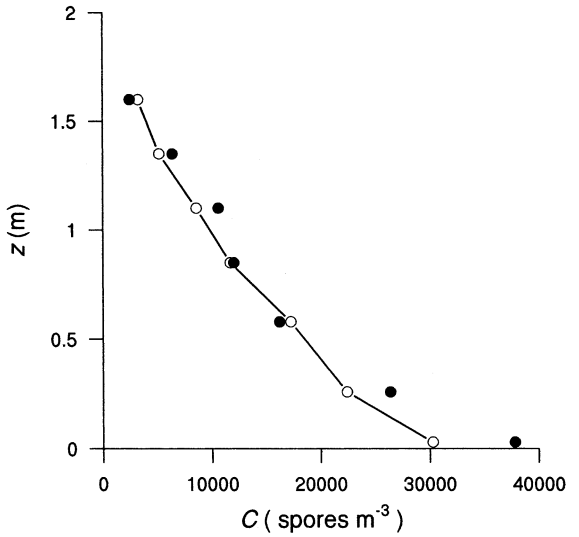

Fig. 4. Comparison of the aerial concentration, C, of artificially released spores of *Lycopodium clavatum* measured in a wheat crop in Connecticut, USA, in 1986 (from Table IV, Aylor and Ferrandino, 1989) (●) with simulated data using the two-dimensional line source version of the model, SPORESIM-2D (○—○).

acceptable numerical stability value of $L \sim 12$ (DuChateau and Zachmann, 1986). The first column of 20 cells represented the source in which the release of spores occurred at a height, z, of 0.4–0.5 m (i.e. in the fifth layer of the model) and the release rate, R_{spor}, was taken from Aylor and Ferrandino (1989). In the other 49 cells (those downwind of the source) R_{spor} was set to zero. The horizontal escape of spores from each column of 20 cells, E_h, provided the spore input to successive cells downwind. For this simulation, LAI, u and v_s were also taken from Aylor and Ferrandino (1989).

The simulated data for spore concentration at each of the seven heights above ground at 3 m downwind of the source were in very good agreement with the mean of the measured concentrations at 2 and 4 m (Fig. 4). Since SPORESIM-2D modelled the measured spore concentrations in the wheat crop with a high degree of precision, we can assume that it, and its one-dimensional form, SPORESIM-1D, adequately model both the horizontal and vertical escape fractions, E_h and E_v.

3.4.2. Natural area sources of Venturia inaequalis spores

The ascospores of *V. inaequalis*, the fungus that causes apple scab disease in apple trees (Aylor, 1998), are similar in density and size (6×13 μm) to those of *S. sclerotiorum*, 9–13 by 4–6.5 μm (Dennis, 1968), and may be considered analogues of the latter with respect to dispersal. Their aerial concentration at different heights above sources has been measured in a variety of dispersal experiments. During the course of our model validation study, we compared simulated data from SPORESIM-1D with various sets of measured data published by Aylor (1995) and by Aylor and Qiu (1996). SPORESIM-1D, calibrated for the particular data sets by adjusting the value of R_{spor}, provided reasonably good predictions of the vertical variation in the measured spore concentrations. Here, we have selected two particular data sets as examples to illustrate the level of agreement between simulated and measured data.

3.4.2.1. Apple orchard. Our first example uses the spore concentration data, C (ascospores m^{-3}), for *V. inaequalis* presented in Fig. 3 in Aylor (1995) measured at six heights above the ground (0.15, 0.30, 0.50, 0.80, 1.50, 3.0 m) on the 101st day of 1993 in an orchard of dwarf apple trees in Mt. Carmel, Connecticut, USA. The ascospore source was the grassed areas of land (grass height, $h =$ 0.1–0.25 m) between the trees that had been 'seeded' uniformly with apple leaves containing scab lesions: ascospores were released into the air from asci on the pseudothecia contained in the lesions. The concentration of the ascospores in the air above the source was measured with rotorod samplers for 2 h starting after rain began. The one-dimensional area source version of the model, SPORESIM-1D, was used with parameter values (grass LAI, u) taken from measurements made in the orchard by Aylor (1995). The release rate of the ascospores in the orchard was not known and the value of this parameter, R_{spor}, was estimated by calibration using the six spore concentration data values from Aylor (1995).

The spore concentration, C, simulated by SPORESIM-1D, behaved in a similar manner to the observed C, declining rapidly with increasing

height above the ground (Fig. 5a). While the model simulated the data from the experiment well below a height of 0.5 m and at heights above 2 m, it over-estimated the observed values of C at intermediate heights. It seems probable that this was a consequence of SPORESIM-1D not accounting for the presence of the trees. The 'absence' of trees in the model could have resulted in incorrectly modelled vertical wind speed profile and a lower than expected rate of spore deposition, thus a higher than expected concentration of spores in the air.

3.4.2.2. Grass field. Our second example uses the spore concentration data, C (ascospores m^{-3}), for *V. inaequalis* presented in Fig. 6 A in Aylor and Qiu (1996) measured on the 119th day of 1993 in a 0.5 ha field of 'mixed fescue and orchard grasses' in Mt. Carmel, Connecticut, USA. The height, h, of the top of the grass ranged from 0.06 m at the beginning of the season to about 0.25 m at the end of the season. The ascospore source comprised of scabbed apple leaves spread over a 30 m × 30 m area in the middle of the field. The concentration of the ascospores in the air above the source was measured with a vertical array of rotorod samplers (at heights, z, above ground of 0.15, 0.30, 0.50, 0.80, 1.50, 3.0 m) placed near the centre of the field and operated for 2 h following the start of rain. The one-dimensional area source version of the model, SPORESIM-1D was used with parameter values (grass LAI, u) taken from measurements made in the grass field by Aylor and Qiu (1996). The spore release rate, R_{spor}, was not measured in the grassland and this parameter was estimated in a model calibration procedure in which the vertical profile of C produced by SPORESIM-1D was scaled until the modelled values of C were in good agreement, as judged by visual comparison, with the six measured values of C in Aylor and Qiu (1996). This resulted in an R_{spor} value of 0.44×10^5 ascospores $m^{-2}\,s^{-1}$; a rate of spore release of the same order-of-magnitude as that estimated by Aylor and Qiu (1996) using the 'integrated horizontal flux' and the 'laboratory spore tower' methods.

The modelled vertical concentration profile in the grass field was very similar to the measured concentration profile from near ground level to a height, z, of 1.5 m (Fig. 5b). The generally lower values of the simulated data probably reflect under-estimation of the spore release rate, R_{spor}, during model calibration. Nevertheless, the result indicates that SPORESIM-1D is a valid model for estimating the vertical concentration of spores within and above a grass community, and hence

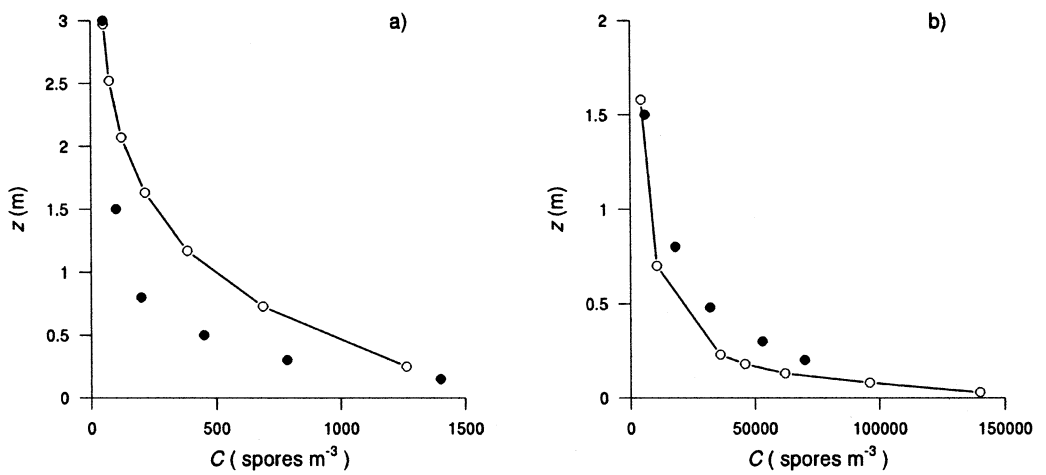

Fig. 5. Comparison of simulated aerial concentrations of the ascospores of *Venturia inaequalis* using the one-dimensional, ground-level area-source version of the model SPORESIM-1D (○—○), with concentrations measured (●) in (a) an apple orchard in Connecticut, USA (data from Aylor, 1995) and in (b) a fescue grassland (data from Aylor and Qiu, 1996).

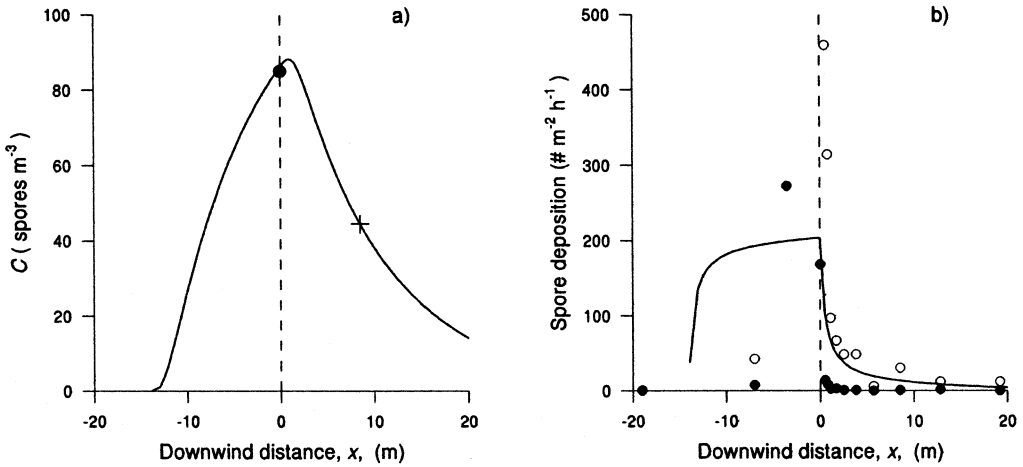

Fig. 6. Measured and modelled dispersal of *S. sclerotiorum* ascospores within and downwind of a 14 m diameter patch of *C. arvense* (-14 to 0 m on bottom axis) treated previously with a *S. sclerotiorum* mycoherbicide in Canterbury. In (a): (—) steady-state atmospheric concentration, C, of spores at height, z, of 0.6 m predicted by the two-dimensional version of the model, SPORESIM-2D; (●) measured concentration, C, of 85 spores m^{-3} (from Table 2, Bourdôt et al., 2001) used to calibrate the model; (+) half distance, $d_{1/2}$. In (b): (●) measured spore deposition (weighted mean over 9 days) during the interval 1000–1400 h, back-transformed from Fig. 3, Bourdôt et al. (2001); (○) measured deposition for the day when C of 85 was determined (two extreme values of C (6531 at x of -3.5 m and 6216 at x of 0.0 m) are not shown); (—) deposition predicted by SPORESIM-2D.

also for estimating the fraction of spores that escape from the pasture.

3.4.3. Biocontrol source of Sclerotinia sclerotiorum spores in a pasture

Spore deposition data from Experiment 3 in Bourdôt et al. (2001) was utilised as an independent test of SPORESIM-1D. The data from this experiment consisted of the average density of *S. sclerotiorum* ascospores deposited on a selective agar in Petri dishes placed in lines radiating 19.2 m downwind of a circular 14 m diameter patch of *C. arvense* in the centre of an irrigated sheep-grazed pasture. The spores were collected between 1000 and 1400 h on nine days in the spring/early summer (Sept., Oct., Nov., Dec.) of 1997 and the *C. arvense* patch had been treated in the spring of 1994 and 1995 with high doses of a mycoherbicide preparation based on *S. sclerotiorum*. A substantial soil-borne sclerotium population, and hence also, a large apothecium population, were assumed to exist within the *C. arvense* patch. The deposition data are given as ascospores deposited per m^2 per hour in Bourdôt et al. (2001) Fig. 3. Additionally, the average density of the ascospores in the air at a height 600 mm at the downwind edge of the ascospore source on one of the nine days, 27 Nov. 1997, was found to be 85 m^{-3} using a Burkard High Throughput 'Jet' Spore Sampler and the selective agar (Table 2 of Bourdôt et al., 2001).

In order to compare the performance of the model against these deposition data, it was converted to its two-dimensional form, SPORESIM-2D, capable of simulating dispersal, within (to a height of 1.6 m), and downwind (for 19.2 m) of a 14 m diameter spore source. This version of the model consisted of 32 horizontal layers each of 340 adjacent square cells each 0.1 m wide (Δy) $\times$ 0.1 m long (Δx) $\times$ 0.05 thick (Δz); this cell size gave an acceptable numerical stability value of $L < 1$ (DuChateau and Zachmann, 1986). The first 140 of the cells represented the 14 m diameter spore source in which the release rate of spores, R_{spor}, (in the bottom layer) was greater than zero; in the other 200 cells (those downwind of the source) $R_{spor} = 0$. The horizontal escape of spores from each column of 32 cells, E_h, provided the spore input to successive cells downwind. For this simulation pasture height, h, was 0.25 m, wind

speed, u, was 3.9 m s^{-1} (mean wind speed measured for 27 Nov. 1997; Table 2, Bourdôt et al. (2001)) and pasture LAI, was 2.0, a value typical for sheep pasture in Canterbury (Fig. 8). Other parameter values were set as in Table 2.

The model was calibrated by varying the value of R_{spor} until a value of C of 85 spores m^{-3} was obtained at a height, z, of 0.6 m in cell 140 representing the downwind edge of the 14 m spore source being simulated where the single data value of 85 spores m^{-3} had been measured.

The value of R_{spor} estimated by this calibration procedure was 255 spores m^{-2} ground surface s^{-1}; a value that is biologically reasonable in a pasture treated twice with high doses of *S. sclerotiorum* as we now illustrate. R_{spor} (spores m^{-2} soil surface), may be given by

$$R_{spor} = S \times A \times f$$

where S is the density of sclerotia ($\#$ m^{-2}) in the soil in the autumn preceding the spring-summer season when they will produce apothecia in the base of the pasture (Bourdôt et al., 2001), A is the size of the sporulating apothecial disc surface (mm^2 sclerotium^{-1}) and f is the rate of discharge of ascospores from the apothecia (spores mm^{-2} disc surface s^{-1}). Taking the measured daily mean value of f of 0.08242 for a frost-free day and the November value for A of 2 from Figs. 9 and 5, respectively, in Bourdôt et al. (2001), an R_{spor} of 255 in November requires an autumnal sclerotium density, S, of 1547 sclerotia m^{-2}. While 1547 sclerotia m^{-2} is above the upper limit of 360 sclerotia m^{-2} estimated for a single application of *S. sclerotiorum* to *C. arvense*-infested pasture (Bourdôt et al., 2000), such a high density might be expected from the multiple high dose applications made to the *C. arvense* patch modelled here.

The spore concentrations, C, at steady-state calculated for each of the 340 cells at height, z, of 0.6 m, is shown in Fig. 6a. The spore concentration, C, which is 85 spores m^{-3} at the downwind edge of the source, increases to a maximum of 88.2 spores m^{-3} at 0.8 m downwind. The 'half distance' for *S. sclerotiorum* of 8.6 m is in good agreement with the d_{half} of 9 m measured for the ascospores of *Pyrenopeziza brassicae* (McCartney, 1994). This similarity is explained by *P. brassicae* spores being of similar size and thus similar settling velocity (v_s 0.1 cm s^{-1}, Lacey et al. (1987)), to those of *S. sclerotiorum*.

Using the simulated values of C, the deposition of spores onto Petri dishes on the ground (spores m^{-2} h^{-1}) was calculated for the 340 bottom cells in the model as

$$\text{Deposition} = C_1 \times T \times \frac{v_s}{\Delta z}$$

where C_1 is the spore concentration in the bottom cells, T is the deposition interval (60^2 s), v_s is 0.002 m s^{-1}, and the thickness of the cells, Δz, in the bottom layer is 0.05 m. The model was in generally good agreement with the field deposition data for 27 Nov. 1997, the day for which the model was calibrated with a measured value of C and u. Although, under-estimating four very high deposition data values near the source's downwind edge, it did mimic the relatively high measured deposition within the spore source and the steep gradient in deposition downwind of the edge of the source (Fig. 6b). By contrast, the model generally over-estimated the deposition data averaged over nine days of measurement. This suggests that the value of $C = 85$ for the downwind edge of the spore source used to calibrate the model was unrepresentatively high; this is supported by the lower values for C measured on other days in the experiment conducted by Bourdôt et al. (2001).

Overall, it appears that SPORESIM-1D, modified to allow downwind dispersal, adequately predicts spore deposition gradients and atmospheric concentrations over short distances downwind of a ground-level source. We may assume then, that it also provides realistic estimates of the spore escape fraction, E_v.

3.5. Comparison of SPORESIM-1D with alternative models

The purpose of SPORESIM-1D is to predict the fraction of spores that will escape a pasture canopy under varying environmental conditions. The escape fraction, E, cannot be easily measured and there is therefore no data with which the escape fractions predicted by SPORESIM-1D can be

tested against. Under these conditions, it is appropriate to use the predictions of other models as validation criteria (Rykiel, 1996). According to a Lagrangian simulation model of spore deposition and escape that uses a wind speed average within the grass canopy (Aylor, 1998), the fraction of ascospores escaping the canopy is very sensitive to the friction velocity (u^*), a measure of the retardation of the wind by the ground (Goudriaan, 1977). The Lagrangian model showed that for a canopy 0.5 m high, simulated escape fraction increased from 0.3 to 0.75 as friction velocity increased from 0.1 and 0.5 m s^{-1} (Fig. 7). Spore escape also increased with u^* in SPORESIM-1D (u was varied to obtain a range in u^* (McIntosh and Thom, 1978); other parameter values as in Table 1), but by contrast with Aylor's Langrangian model, the escape fraction was consistently much lower in SPORESIM-1D (Fig. 7).

To test the hypothesis that the lower escape fraction is a result of the vertical compartmentalisation in SPORESIM-1D that allows wind speed and pasture LAI to vary with sward height (as occurs in pastures), its results were compared those of

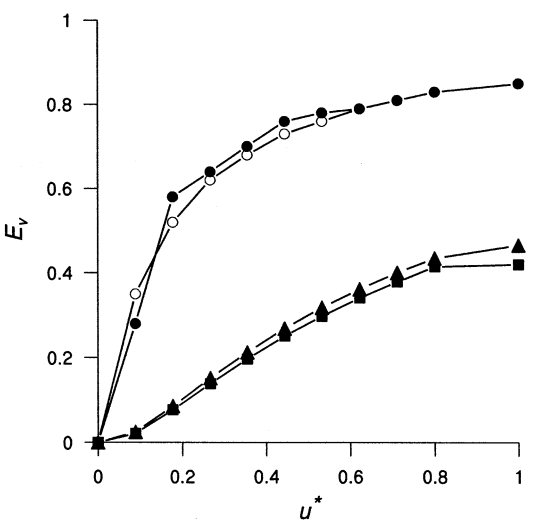

Fig. 7. Comparison of four models for the fraction, E_v, of *Venturia inaequalis* ascospores escaping a grass canopy with increasing friction velocity, u^*: (●—●) Lagrangian simulation model (Aylor 1998); (○—○) the one-layer model, SPORESIM-1L; (▲—▲) the multi-layer model, SPORESIM-1D using A_d and E_i to estimate spore deposition; (■—■) SPORESIM-1D using LAI to estimate deposition.

the one-layer version of the model, SPORESIM-1L. The one-layer model assumes a homogenous spore concentration throughout the pasture. This is not justified since there are indeed vertical gradients in both LAI and u that can be expected to result in higher spore concentrations near the ground when the source is at ground level. SPORESIM-1L resulted in escape fractions that were higher than those predicted by the multi-layer SPORESIM-1D, but very similar to those predicted by Aylor's model (Fig. 7). This result provides support for our hypothesis that a lower and more realistic estimate of escape is obtained by allowing LAI and u to vary with height in the pasture as is achieved with SPORESIM-1D.

In a further test of SPORESIM-1D, the method by which it calculates spore deposition was examined. SPORESIM-1D calculates deposition on the ground and on leaves in a rather simple way. It approximates deposition-area density, A_d, a difficult-to-measure parameter, using the more readily measured parameter, LAI, and the constants v_d and v_s. This simple method was compared with a mechanistically more correct method that used measurements of the vertical profile of A_d in a grassland (Aylor personnel communication) (A_d of 20, 11, 5, 2.5 and 1 for the five, 50 mm deep layers from a height, z, of zero up to 250 mm), and a measure of the efficiency with which spores are impacted (captured) on leaves, E_i, calculated when friction velocity, u^*, is 0.5 m s^{-1} as

$$E_i = \frac{0.86}{\left[1 + \frac{0.66}{\mathrm{Stk}}\right]^{1.967}},$$

Stk is Stokes' number, calculated as

$$\mathrm{Stk} = \frac{v_s u_z}{wg},$$

w is the leaf width (m) and g is the acceleration due to gravity (m s^{-2}) with a friction velocity, u^*, of 0.5 m s^{-1}. Deposition onto the soil surface was calculated by the 'deposition velocity method' with the help of v_d calculated as $v_d = 3 \times v_s =$ 0.006 m s^{-1} (Aylor, personnel communication). The escape fraction given by SPORESIM-1D using the simple method of calculating deposition was

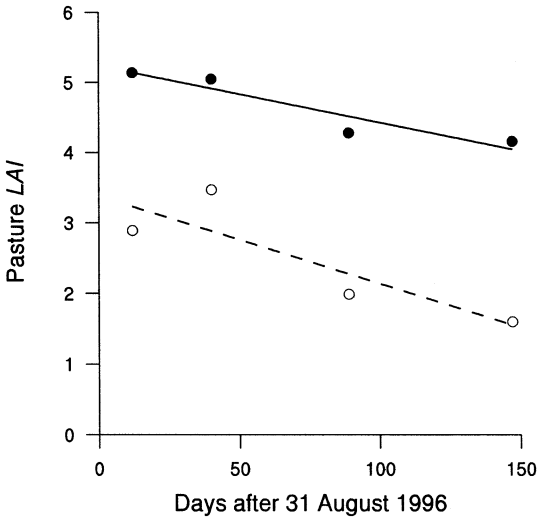

Fig. 8. The progression of LAI of pastures rotationally grazed by either sheep (○----○) or dairy cattle (●—●) in Canterbury, New Zealand from 11 September 1996 until 16 January 1997. For sheep pasture, the fitted linear regression is LAI = 3.38–0.0124t ($R^2 = 0.747$) and for dairy pasture LAI = 5.24–0.0081t ($R^2 = 0.885$) where t is days after 31 August 1996.

equal to the escape fraction given by SPORESIM-1D using the more complex method of calculating deposition (Fig. 7). Thus, we conclude that the simple method for deposition using the readily measured parameter, LAI, in conjunction with and v_d, is satisfactory.

4. Simulating escape of *Sclerotinia sclerotiorum* ascospores from pasture under different grazing management regimes

The validation tests in Sections 3.1 and 3.5 indicate that SPORESIM-1D is an acceptable model for estimating the fraction of spores escaping a grass canopy. Thus, we can use it with some confidence to investigate how pasture management may influence the escape of ascospores produced at the base of a pasture following the application of *S. sclerotiorum* as a weed biocontrol agent. Since spores are removed from the air inside a pasture by impaction onto plant surfaces and the size of this surface will vary greatly between types of grazing systems and their management, we can expect that there will also be differences in the escape fraction between these systems.

Before using SPORESIM-1D to determine the extent to which pasture grazing management will influence the escape of *S. sclerotiorum* ascospores following an earlier weed biocontrol application, knowledge of the LAI of such pastures is necessary. To this end the seasonal patterns in the LAI of pastures on dairy and sheep farms in Canterbury, New Zealand, were measured during the spring and summer of 1996–1997; the period when sporulation of *S. sclerotiorum* occurs in pasture (Bourdôt et al., 2001). Ten fields under grazing on each of ten dairy and ten sheep farms were selected at random from the area of the Canterbury Plains delineated by the topographical map (NZMS 1 S83 (BURNHAM) scale 1:63 360). On each of four occasions (11–13/9/96, 9–11/10/96, 28–29/11/96 and 15–16/1/97) in each of the twenty fields, six quadrat areas, 150 mm × 150 mm, were positioned ca. 10 m apart along a diagonally positioned transect line. The pasture plants in each quadrat were removed by cutting at the soil surface and the sample was weighed. The surface area of the plants in a sub-sample from each sample was measured with a planimeter, scaled up by weight to the area sampled, and divided by the quadrat area to calculate the pasture LAI.

Linear regressions of LAI against time showed a tendency for LAI to decline during the season in both the sheep and dairy pastures (Fig. 8). The overall mean for the LAI of sheep-grazed pasture was 2.8, but individual fields varied from 0.2 to 6.3. By contrast the overall mean for the LAI of cattle-grazed pasture was 4.9 with individual fields varying from 1.7 to 9.4.

To model the effect of variation in pasture LAI on the escape of ascospores from pasture, SPORESIM-1D was parameterised using values of LAI of 2–7, encompassing the range of the means of the measured LAI values (Fig. 8). Other parameter values used were windspeed, u_r, of 3 m s^{-1} and pasture height, h, of 0.25 m. With these parameter settings wind speed near the ground (layer 1 of the model) declined from 0.38 m s^{-1} at an LAI value of 2 to a very low speed of

0.05 m s^{-1} when LAI was 7. Exchange resistance, r, increased from 5.5 to 77.6 s m^{-1} and the concentration of ascospores, C, in the bottom layer increased 1.61 fold, from 1952 to 3144 spores m^{-3}, as LAI increased from 2 to 7. The fraction of ascospores escaping vertically from the model pasture declined by an order-of-magnitude as LAI increased from 2 to 7 as a result of increasing deposition of spores on the pasture plant surfaces and on the ground (Fig. 9). These results imply that under the wind speed conditions typical of Canterbury, the fraction of ascospores escaping a pasture where the biocontrol agent has been used will be substantially lower when cattle rather than sheep are being grazed. Additionally the results reveal a potential for limiting spore escape by reducing the frequency and/or intensity of grazing to maintain a high pasture LAI from late September until mid November in the year after *S. sclerotiorum* has been applied; the period within which sporulation occurs in Canterbury pastures (Bourdôt et al., 2001).

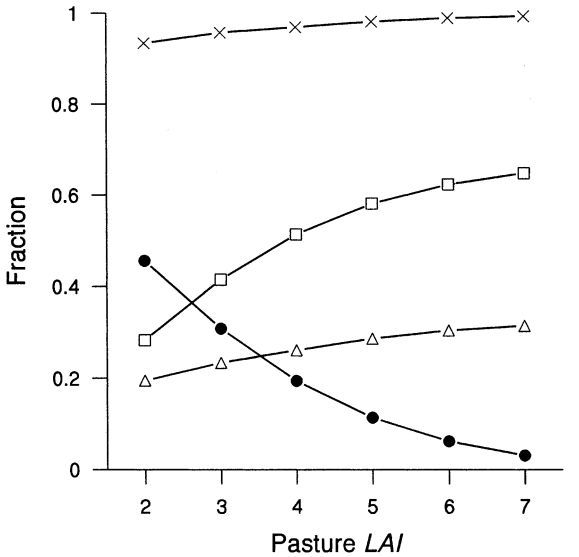

Fig. 9. The effect of pasture LAI on the fraction of spores escaping vertically above the pasture (E_v) (●—●), depositing on pasture plant surfaces (D_{leaf}) (□—□), and depositing on the soil (D_{soil}) (△—△) as determined using SPORESIM-1D. The sum of all fractions (excluding E_h) given as × — × .

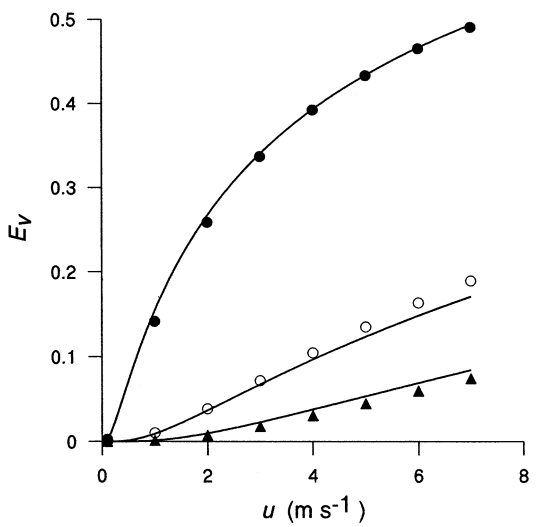

Fig. 10. The effect of wind speed, u, on the fraction of spores, E_v, escaping vertically from a pasture for LAI values of 2 (●), 5 (○) and 7 (▲) representing sheep-grazed, cattle-grazed and un-grazed pastures, respectively, as simulated by the one-dimensional area-source version of the model, SPORESIM-1D. Curves are fitted values using Eq. (8).

In a further simulation using SPORESIM-1D we investigated the interacting effects of wind speed and pasture density management on the escape fraction, E_v, by varying wind speed, u, (from 0.1 to 7 m s^{-1}; representative of commonly occurring hourly mean values in Canterbury; Table 3), and LAI (2, 5 and 7; representing sheep-grazed, cattle-grazed and non-grazed pasture, respectively). In this simulation an escape height, h, of 1.5 m was chosen, resulting in slightly reduced escape fractions compared to the previous analysis where the escape height was 0.25 m. Escape heights greater than 1 m are required for generating valid point-source spore emission rates as input for a Gaussian model (Erbrink, 1995) an intended elaboration of the current study to evaluate long-distance dispersal and minimum isolation distances (de Jong et al., 1999). The simulated data (symbols in Fig. 10) reveal that spore escape increases with wind speed and that escape is reduced by increasing pasture LAI over the range of wind speeds tested. It is also evident that the proportional reduction in escape with increasing pasture LAI is greater the lower the wind speed (i.e. the spore trapping effect of pasture vegetation appears to be greatest at low wind speeds). For example, at a wind speed, u, of 2 m s^{-1}, the

escape fraction when LAI is 5 is only 7% of that when LAI is 2, but when u is 7 m s^{-1} the escape fraction when LAI is 5 is 39% of that when LAI is 2.

5. A simple model for escape fraction as a function of wind speed and pasture LAI

The escape fraction data generated by SPORESIM-1D (symbols in Fig. 10) indicate that there is a relationship between E_v and u and LAI. A simple description of this relationship would be a useful tool for calculating the escape fraction and hence the emission rate, Q, of a biocontrol site for input into the Gaussian Plume model. We derive an expression for this relationship below.

5.1. Steady-state spore dispersal and the vertical eigenfunction

To derive a simple formula relating escape fraction, in-crop deposition, wind speed and diffusivity we return to Eq. (1) and make the further assumption that all parameters are spatially invariant. If the downwind length of the crop, x_l, is large, then it is reasonable to assume that the majority of the spore concentration downwind is at a 'steady-state;' that is

$$\frac{\partial C}{\partial x} = 0 \text{ for large } x.$$

Let $C = F(z/h)$ denote this steady vertical eigenfunction. Written in terms of F, Eq. (1) becomes

$$\frac{1}{h^2}F'' - \frac{v_s}{hK}F' - \frac{v_d A_d}{K}F = -\frac{R_{spor}}{K}\delta(z), \tag{3}$$

where h is the height of the pasture canopy. Consider the time scale of spore deposition within the crop as compared with the time scale of settling. On the one hand, the time scale for settling within the crop can be estimated by

$$t_{settling} \sim \frac{h}{v_s}.$$

The time scale of deposition, by contrast, scales as

$$t_{deposition} \sim \frac{1}{v_d A_d}.$$

If we assume that $t_{deposition} \ll t_{settling}$ then we can deduce that

$$\frac{v_s}{h} \ll v_d A_d.$$

Consequently the second term on the left hand side of Eq. (3) can be neglected, giving a reduced equation for the vertical eigenfunction:

$$F'' - \frac{v_d A_d}{K}h^2 F = F'' - \lambda^2 h^2 F = -\frac{R_{spor}}{K}h^2\delta(z/h). \tag{4}$$

Eq. (4) can be solved directly

$$F\left(\frac{z}{h}\right) = \frac{R_{spor}}{K\lambda}\,e^{-\lambda h(z/h)} = \frac{R_{spor}}{\sqrt{K v_d A_d}}\exp\left[-h\sqrt{\frac{v_d A_d}{K}}\frac{z}{h}\right]$$

Using $C(z) = F(z/h)$ gives

$$C_{steady} = \frac{R_{spor}}{\sqrt{K v_d A_d}}\exp\left[-\sqrt{\frac{v_d A_d}{K}}z\right] \tag{5}$$

which is an approximation for the vertical eigenfunction.

5.2. Escape fraction for the steady-state

The escape fraction, E_v, can be defined as the ratio of spores outside the crop and the total number of spores. On a per-time basis this is the ratio of the rate of spore escape and the rate of spore release, and since the rate of spore escape is the rate of release ($x_l R_{spor}$) less the rate of deposition within the crop, we may write

$$E_v = \frac{x_l R_{spor} - \text{Rate of deposition}}{x_l R_{spor}}.$$

The rate of spore deposition within the crop can be written

$$\text{Rate of deposition} = v_d A_d \int_0^h \int_0^L C\,dx\,dz.$$

Using Eq. (5) to approximate the integral on the right hand side, we get

$$\text{Rate of deposition} = v_d A_d L \int_0^h \frac{R_{spor}}{K\lambda} e^{-\lambda z} dz$$

$$= x_l R_{spor}\left(1 - \exp\left[-h\sqrt{\frac{v_d A_d}{K}}\right]\right).$$

Substituting this into the expression for E_v gives

$$E_v = \frac{x_l R_{spor} - x_l R_{spor}\left(1 - \exp\left[-h\sqrt{\frac{v_d A_d}{K}}\right]\right)}{x_l R_{spor}}$$

$$= \exp\left[-h\sqrt{\frac{v_d A_d}{K}}\right]. \quad (6)$$

5.3. Escape fraction, leaf area and wind speed

It remains to determine how the escape fraction depends on crop LAI and wind speed. If the eddy diffusivity varies directly with wind speed and inversely with the average vertical density of leaves, the diffusivity becomes

$$K = \kappa \frac{u}{A_d} = \kappa \frac{uh}{\text{LAI}}.$$

We have assumed that the average vertical leaf density can be written $A_d = \text{LAI}/h$. Using these assumptions the escape fraction (6) becomes

$$E_v = \exp\left[-h\sqrt{\frac{v_d \text{LAI}}{\frac{h}{\frac{\kappa u h}{\text{LAI}}}}}\right] = \exp\left[-\text{LAI}\sqrt{\frac{v_d}{\kappa u}}\right]. \quad (7)$$

This provides a relatively simple, mechanistically derived model for escape fraction in terms of LAI, crop height and wind speed.

5.4. Fitting the model to data

To test the goodness-of-fit of Eq. (7), a version,

$$E_v = \exp\left[-b\frac{\text{LAI}}{\sqrt{u}}\right], \quad (8)$$

was fitted to the escape fraction data generated by the simulation model SPORESIM-1D in Section 4 (Fig. 10). A nonlinear least-squares procedure gave a 'best' value of $b = 0.934 \pm 0.013$ for a 95% confidence interval. Letting $b = 0.934$ gave a correlation coefficient $r^2 = 0.998$, meaning that at least 99% of the variance was described by the model. The goodness-of-fit of the simple model Eq. (8), is illustrated in Fig. 10 where the model is plotted along with the simulated escape fraction data.

6. General discussion and conclusions

In this paper, we have described SPORESIM-1D, a simulation model for the dispersal of the ascospores of *S. sclerotiorum* within and above (escaping) a grass canopy based on the gradient transfer theory (K-theory) of turbulent dispersal (McCartney and Fitt, 1985). This mechanistic model includes the effects of wind, turbulence and deposition and is intended as a tool to assist our understanding and management of the non-target crop disease risk that may be associated with the use of *S. sclerotiorum* as a mycoherbicide for the control of *C. arvense* in pastures in New Zealand (de Jong et al., 1999). It also provides general insights into the mechanisms of spread in this pathogen, and thus satisfies some of the deficiency in our knowledge of *S. sclerotiorum* outlined by Wegulo et al. (1999). The model's context or domain (Rykiel, 1996) is therefore the risk analysis of weed biocontrol. Its specific purpose is to determine the fraction of *S. sclerotiorum* ascospores released into the air at the base of a pasture that escape from the canopy under a range of wind speeds and pasture cover densities typical of grazing lands. Given the biological risk analysis and management context of this model, its validation (acceptability for its intended purpose) was considered essential. To this end we have conducted various comparisons of data simulated by SPORESIM-1D (and two other versions of the model) with field data (Figs. 3–6) and with other models (Fig. 7), and these have provided convincing evidence that SPORESIM-1D is indeed a valid model for calculating the fraction *S. sclerotiorum* spores that escape a pasture canopy.

Understanding the behaviour of the 'escape fraction' enables us to conduct two key components of a thorough risk analysis. One of these is to determine the extent that grazing management, by controlling the leaf area density of the pasture

in which the *S. sclerotiorum* ascospores are being released, may influence the deposition of ascospores on the leaves of pasture plants and hence also the escape fraction. We have used SPORESIM-1D for this purpose and have found that the escape fraction is reduced an order-of-magnitude as the pasture LAI is increased from a value of 2, typical of rotationally grazed sheep pastures in Canterbury, New Zealand, to 7, a value typical of non-grazed pasture (Fig. 9). This result leads to two conclusions. Firstly, the escape of *S. sclerotiorum* ascospores, and hence the risk of additional disease in susceptible non-target crops planted beyond a mycoherbicide-treated pasture, will be substantially lower if the pasture is either not grazed or grazed by dairy cattle rather than by sheep during the spring period when ascospores are being formed. Secondly, the intensity and timing of grazing in the year following the use of *S. sclerotiorum* in a pasture will have a pronounced influence on the numbers of ascospores escaping, and hence also on the risk of additional disease in non-target crops beyond the biocontrol site. Since sporulation in *S. sclerotiorum* in non-irrigated pasture in Canterbury is confined almost entirely to the three-month period from mid September to mid November (Bourdôt et al., 2001), stopping grazing during that period, or grazing moderately, will significantly reduce the numbers of ascospores available for dispersal from the biocontrol site.

The other essential component of a risk analysis is the definition of a 'minimum isolation distance' (safety zone) for growing susceptible crops (de Jong et al., 1999). The product of the escape fraction and the rate of release of the *S. sclerotiorum* ascospores from apothecia at the base of a pasture is the emission rate of the ascospore source at the biocontrol site. This emission rate may be used as the source term, Q, in a Gaussian plume model (McCartney and Fitt, 1985) to determine the concentration of these 'additional' ascospores at distances beyond the source. Using a time series approach in which Q is calculated on a small time step (hourly) for the period of the year when ascospores are formed (1 September until 30 November in pasture in Canterbury, New Zealand (Bourdôt et al., 2001)), the average concentration of ascospores dispersed beyond the biocontrol site may be obtained for a particular set of time-varying environmental conditions (including pasture LAI as affected by phenological and managerial processes). By comparison with measured or modelled concentrations of 'naturally occurring' *S. sclerotiorum* ascospores, a safety zone may be determined (de Jong et al., 1999). To facilitate such an analysis, it is desirable to have a simple yet adequate model for the escape fraction rather than a complex simulation model; a point of view expressed also by McCartney and Fitt (1985) in respect to developing general models of disease development for disease forecasting. To this end we have derived from K-theory a simple one-parameter model that gives the escape fraction as a function of pasture LAI and wind speed (Eq. (8)). This model provided a good-fit to escape data simulated by SPORESIM-1D for a wide range of wind speed and pasture LAI (Fig. 10), indicating that it would provide acceptable estimates of the escape fraction for a time series analysis leading to the definition of a safety zone. Such an analysis will be the subject of a further contribution on the risk analysis of *S. sclerotiorum* as a mycoherbicide for pasture weed control.

While the primary context of SPORESIM-1D is the risk analysis of *S. sclerotiorum* used as a mycoherbicide for controlling a *C. arvense* in pastures, the model's context may also be considered to include the management of sclerotinia blossom and fruit rot caused by *S. sclerotiorum* in kiwifruit vines (*Actinidia deliciosa* (A. Chev.) Liang et A.R. Ferg. [Syn. *A. chinensis* Planchon]). The incidence of this disease in kiwifruit vines in New Zealand has been observed to be lower in orchards under 'organic' management than under conventional 'Kiwigreen' management. It has been suggested that this may, in part, be a consequence of the tall (up to 1.0 m) within row herb lay composed of a wide variety of plant species that is usually present in organic orchards. By contrast, in conventional kiwifruit orchards, either a bare strip is maintained by herbicide under T-bar vine support systems, or a very low (ca. 10 cm) grass sward is maintained under a pergola system. The tall under-storey vegetation in organic kiwifruit orchards

is adopted primarily to promote high populations of insect predator species and plant beneficial organisms. However, it has been speculated it may also be preventing the escape of *S. sclerotiorum* ascospores from near ground level to the kiwifruit flowers in the canopy in the spring, thereby reducing disease incidence (Elmer personnel communication). The results of our simulations with SPORESIM-1D where LAI has been varied support this hypothesis (Fig. 9). SPORESIM-1D thus provides an explanation for the observed reductions in disease in organic kiwifruit. Experimental manipulation of under-storey vegetation in kiwifruit orchards could be conducted to provide empirical data to test this hypothesis.

The context of SPORESIM-1D also includes management of apple scab disease in apple trees caused by the ascomycete, *V. inaequalis*. Like *S. sclerotiorum*, this fungus also releases ascospores (of similar density to those of *S. sclerotiorum*) into the air at ground level and they must escape the vegetation layer beneath the apple trees to infect the apple fruit (Aylor, 1998). SPORESIM-1D suggests that the incidence of apple scab disease will be reduced by the maintenance of a dense vegetation canopy beneath the trees in an apple orchard. This hypothesis is being tested in field research programmes conducted by the Department of Biological Farming Systems of Wageningen University in collaboration with the Dutch Fruit Growing Experiment Station in Randwijk, and in an organic apple orchard at the Lincoln University Biological Husbandry Unit, Canterbury, New Zealand.

The maintenance of a dense vegetation cover to minimise the escape of the ascospores of both *S. sclerotiorum* and *V. inaequalis* may have additional effects. For example, in the case of the use of *S. sclerotiorum* in pastures to control *C. arvense*, the reduction in ascospore escape in SPORESIM-1D coincides with a higher deposition of ascospores near the base of the pasture. This may potentially promote new infections in the year after application of the mycoherbicide (when sporulation occurs), enhancing the level of biological control. Another possible effect of high pasture cover densities could be a reduction in the numbers of ascospores released by apothecium populations as a result of low-light levels at ground level. Low-light levels inhibit apothecial initial development in the sclerotia of *S. sclerotiorum* (Letham, 1975; Thaning and Nilsson, 2000) and ascospore liberation is also inhibited under dark conditions (Hartill, 1980). While these low-light-induced effects of high pasture cover may cancel out any enhancement of weed biocontrol resulting from a greater fraction of spores being deposited in the pasture, they would reduce the rate of release of ascospores per unit pasture surface, thereby lowering the emission rate of the biocontrol site; an effect additional to that resulting from the reduction in the escape fraction. Similarly, in *V. inaequalis* ascospores are released in fewer numbers under dark conditions (Brook, 1969), again implying reductions in the emission rate from a vegetation canopy in addition to reductions mediated by the lowered escape fraction.

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