A theory on the vertical dispersal of splash-borne pathogen units influenced by arable crop characteristics

Chapter 6

A theory on the vertical dispersal of splash-borne pathogen units influenced by arable crop characteristics

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Abstract

An analytical mechanistic model was proposed to study the vertical spread of splash-borne spores in arable crop canopies. Three crop types were considered, with different LAI distributions. The influences of crop characteristics and rain properties on vertical spread were investigated. The LAI affected the amount of rain being intercepted by the canopy and the vertical displacement of splashed spores. Splash dispersal was concentrated in the upper canopy layers in a crop having LAI constant or increasing with height. Splash probabilities were greatest and most spores were intercepted in the layers just beneath the upper layers in a crop having LAI decreasing with height.

6.1 Introduction

Spores of many plant pathogens are dispersed in the splash droplets which are formed when raindrops hit the water film formed on the surface of arable crop canopies during rain events. Important fungal plant pathogens for which the main dispersal mechanism is by rain-splash are *Phytophtora* spp. on citrus, rhododendron, apples, black pepper and strawberry, *Colletotrichum* spp. on citrus, onion, rice and strawberry, *Fusarium* spp. on cereals, *Pseudocercosporella* spp. on wheat and oilseed rape, *Septoria* spp. on wheat and tomatoes and *Diaporthe* spp. on soybean. However, the spatial spread of spores in a canopy by rain-splash is affected not only by fungus-specific mechanisms for spore release and the properties of the rain. Different plants each have characteristic morphologies, which play an important role in spore dispersal, because of the different wetting of surface areas in the canopy. Potential splash events depend on the PAI (Plant Area Index, total surface area of plant tissue per surface area of ground; Pielaat, van den Bosch, Fitt and Jeger, chapter 5).

In crops, infected plant debris on the soil surface often forms the primary source of inoculum for these pathogens and gradual upward and lateral spread of disease in the canopy is by rain-splash (Ramachandran *et al.*, 1990 and Linders *et al.*, 1996). The influence of soil types on disease spread has formerly been investigated for a variety of soils and crops (Berrie and Luton, 1996; Madden and Ellis, 1990; Yang and TeBeest, 1992). Further spread in the canopy has also been studied for different crops and different results have been reported (Okayama, 1994; Ferrandino and Elmer, 1996; Fitt *et al.*, 1992 and Freitas *et al.*, 1998).

The objective of those experiments has been to understand the spatial spread of disease in different plant-pathogen systems, so as to improve disease control procedures. For example both chemical and biological treatments have been introduced to control diseases spread by rain-splash (Stobart *et al.*, 1999; Chauhan and Singh, 1991; Soleimani *et al.*, 1996). Another option has been the introduction of physical barriers, which was tested by Okayama (1994) in strawberry crops. Nevertheless, optimal disease management strategies can be developed only when mechanisms of disease spread in all of these crops during the growing season have been quantified. Disease spread in the different crops, with a wide range of specific morphological characteristics which change during the growing season, cannot be quantified adequately by experimental research alone. The development of physical models helps to improve understanding of the general mechanisms of splash dispersal of pathogens in a range of crops. A simulation model has been developed to study the vertical spread of light leaf spot on winter oilseed rape, where both plant growth and rain-splash influenced disease dispersal (Pielaat, van den Bosch, Fitt and Jeger, chapter 5). It was shown that spores were splashed to the plant apex and directed upwards by stem extension.

In this paper an analytical model is proposed and the influence of crop canopy structure on the vertical dispersal of splash-borne pathogens is investigated, for crops with Leaf Area Index (LAI, cm^2 leaf per cm^2 ground per cm plant height) constant, increasing or decreasing with height above the ground. For this purpose the influence of rain properties on the separate terms in this model describing the physical splash process are investigated qualitatively for the three crops.

6.2 The model

Consider a crop in which spores are dispersed vertically in the canopy by rain-splash. Spores are splashed to sites on the upper and lower leaves or to the ground, and re-splashed on the plants during rain events. This process was modeled by subdividing the splash dispersal process into its component mechanisms, 1. A raindrop hits the water film formed on a leaf or the ground and spores are dispersed in the splashing rain droplets. 2. Splashed spores are redistributed in the crop and on the soil surface by secondary splash. These two mechanisms were translated into probabilities and formed the basis of the model. A distinction was made between the probabilities that a rain droplet was splashed from the ground and splashed from the plant leaves in the crop because the physical surface structure of plants differed from that of the ground. In addition, spores splashing from the ground can only be dispersed upwards into the canopy or horizontally to stay on the ground, whereas spores splashing from plants can be dispersed both upwards and downwards in the canopy. Two separate equations were therefore formulated for redistribution of spores splashing from the ground and spores splashing from the plants.

First let us consider the redistribution of spores present at a certain height h (for h>0) in the canopy during a rain event. The spore density at height h and time t during a rain event was denoted by $H_{h,t}$ (i.e. number of spores per LAI per cm plant height at height h). By multiplying $H_{h,t}$, with the probability per unit time of a spore being hit (γ t^{-1}) and a splash probability (λ_h), the density of spores that splash away from height h per unit time (first term on the right in eq. 6.1) was described.

In addition, a fraction of the spores splashed from other heights in the crop during this time are deposited at height h. The water surface surrounding the ground is hit and subsequently spores are splashed from the ground with a probability $\gamma\lambda_g$ t^{-1} and from any other height in the crop with a probability $\gamma\lambda_n$ t^{-1}. A probability density function (p.d.f.) $D_{n,h}$ described the likelihood that a spore was deposited at height h when splashed from any height n. Multiplying $\gamma\lambda_g$ t^{-1} by $D_{0,h}$ gave the fraction of spores being deposited at height h when splashed from the ground per unit time during the rain event. The integral of $D_{n,h}$ $\gamma\lambda_n$ t^{-1}, with respect to n, gave the fraction of spores deposited at height h when splashed from any other site n in the crop (where n > 0). The actual number of spores deposited at height h in the splash process was obtained by multiplying the appropriate dispersal function by the spore density on the ground (i.e. number of spores per cm^2 soil at time t) denoted by G_t (last term on the right in eq. 6.1), and by spore density at any other height in the crop ($H_{n,t}$) respectively (second term on the right in eq. 6.1). The vertical redistribution of spores on the plants per unit time during a rain event was therefore formulated as

$$\frac{\partial H_{h,t}}{\partial t} = -\gamma_t\,\lambda_h\,H_{h,t} + \int_0^{max} \gamma_t\,\lambda_n\,H_{n,t}\,D_{n,h}\,dn + \gamma_t\,\lambda_g\,G_t\,D_{0,h}\,, \tag{6.1}$$

where max represents the maximum height of the crop (in cm).

By analogy with spore redistribution on the plants, a mathematical expression was derived for the change in the number of spores on the soil surface. This redistribution was defined by the number of spores that splashed away from the ground and the number of spores that splashed from the plants or the ground to the ground per unit time ($\mathcal{X}$). Thus

$$\frac{dG_t}{dt} = -\gamma_t \lambda_g G_t + \mathcal{X} . \tag{6.2}$$

An expression for $\mathcal{X}$ was found when the total number of spores during a rain event was considered. If no spores are lost from the system, the total number of spores in the crop and on the ground is constant in time, so

$$\frac{dG_t}{dt} + \int_0^{max} \frac{\partial H_{h,t}}{\partial t} dh = 0 . \tag{6.3}$$

Substituting equations 6.1 and 6.2 in equation 6.3 gave

$$\begin{aligned} -\gamma_t \lambda_g G_t + \mathcal{X} - \int_0^{max} \gamma_t \lambda_h H_{h,t} dh \quad + \quad & \int_0^{max} \gamma_t \lambda_n H_{n,t} \int_0^{max} D_{n,h} dh\, dn \\ + \quad & \gamma_t \lambda_g G_t \int_0^{max} D_{0,h} dh = 0 . \end{aligned} \tag{6.4}$$

As $\int_0^{max} D_{0,h} dh = 1 - \mathrm{D}_{0,0}$,

$$X = \int_0^{max} \gamma_t \lambda_h H_{h,t} dh - \int_0^{max} \gamma_t \lambda_n H_{n,t} \int_0^{max} D_{n,h} dh\, dn + \gamma_t \lambda_g G_t D_{0,0} . \tag{6.5}$$

This indicates that the number of spores reaching the ground per unit time consists of the spores that are not intercepted by the crop when splashing from the plants, and spores that are redeposited on the ground when splashing from the ground.

With this model (6.1) and (6.2), the influence of crop characteristics on the vertical dispersal of pathogen spores during rain events was studied. Crop types differed in leaf structure and leaf surface area distribution and this affected the splash process. Therefore, both the probabilities that a spore was splashed and that a spore was deposited differed between crops. Crop characteristics were expressed by the parameters λ_h, λ_g and the p.d.f. $D_{n,h}$ for spore deposition. In this research three crop types, which differ in leaf area distribution, were considered. The three crops had a Leaf Area Index (LAI, cm^2 leaf per cm^2 ground per cm crop height) constant, decreasing or increasing with height. Expressions for λ_h, λ_g and $D_{n,h}$ were derived from a simple stochastic model for the different crop types in order to study the splash process.

6.3 Results and Discussion

6.3.1 The probability that a spore was splashed in different crops.

Before a spore can be splash dispersed from a particular layer with thickness ξ in the crop, a raindrop has to penetrate the canopy down to this layer. It was assumed that the likelihood that a raindrop penetrated the crop down to the base of the canopy was proportional to the LAI the raindrop encounters from the point where it entered the crop. Thus,

$$\frac{dP_h}{dh} = LAI_h\, P_h, \quad P_{max} = 1$$

The probability that a raindrop penetrated the crop to below height h was therefore

$$e^{-\int_h^{max} LAI_\sigma\, d\sigma}.$$

A raindrop will be intercepted in the crop canopy layer between h and h-ξ according to P_h - $P_{h-\xi}$ and so the probability that a raindrop was intercepted in this layer became

$$e^{-\int_h^{max} LAI_\sigma\, d\sigma}\,(1 - e^{-\int_{h-\xi}^{h} LAI_\sigma\, d\sigma}).$$

With the Taylor approximation for $1 - e^{-\int_{h-\xi}^{h} LAI_\sigma\, d\sigma}$, it followed that

$$e^{-\int_h^{max} LAI_\sigma\, d\sigma}\, LAI_h\, \xi\,.$$

The probability that a raindrop was intercepted in the layer between h and h-ξ was multiplied by the probability that a spore was incorporated into the splash droplets (l_h)

to give the probability ($\lambda_h \xi$) that a spore was splashed from this layer with thickness ξ in the canopy, and therefore

$$\lambda_h = l_h \, LAI_h \, e^{-\int_h^{max} LAI_\sigma \, d\sigma} . \tag{6.6}$$

In equation (6.6) the term $e^{-\int_h^{max} LAI_\sigma \, d\sigma}$ can be interpreted as the probability that a raindrop was not intercepted between the point where it entered the canopy (max) and height h. $\xi \, LAI_h$ indicates interception between h and h-ξ. The parameter l_h was replaced by l_g when spores were splashed from the ground (where h=0).

Crop characteristics, expressed in terms of LAI and the leaf structure, influence the value of λ_h. Different equations for λ_h were therefore derived from the different LAI distributions of the three crops in Appendix A. The equations (6.8), (6.9) and (6.10) of Appendix A were used for the analysis.

Figure 6.1 shows the distributions for probabilities that a spore was splashed from different heights in the canopy (where h > 0) when different values of c (the total LAI of a plant) and different values for l_h (the rebound probability) were applied. Raindrops can penetrate the canopy less easily when relatively more surface area is present in the upper layers. Many raindrops were already intercepted in the upper layers of a crop having a constant LAI. The probability that a spore was splashed from a height layer therefore decreased rapidly with decreasing height in this crop (Figure 6.1 a,b), particularly when the total LAI, c, was large (Figure 6.1b). The effect of having more surface area in the upper layers was even stronger in a canopy having an increasing LAI. Therefore, splash probabilities decreased rapidly towards the ground in this canopy (Figure 6.1 e,f). When the crop had a decreasing LAI the probability that a spore was splashed first increased down to some layer and then decreased below this layer (Figure 6.1 c,d). The LAI was large and it was less likely for a drop to penetrate to the lower layers of this crop. A large value of c increased the probability that a spore was splashed from the upper leaves (Figure 6.1 b,d,f) relative to the crops with a low value of c (Figure 6.1 a,c,e). The total probability distribution increased when the probability of a spore being rebounded (l_h) increased.

6.3.2 Vertical spread of splashed spores in different crops.

By analogy with the procedure for obtaining expressions for λ_h in the three crops, equations for the p.d.f. $D_{n,h}$, describing the likelihood that a spore was deposited between height h and h-ξ when splashing from height n with thickness ξ, were formulated.

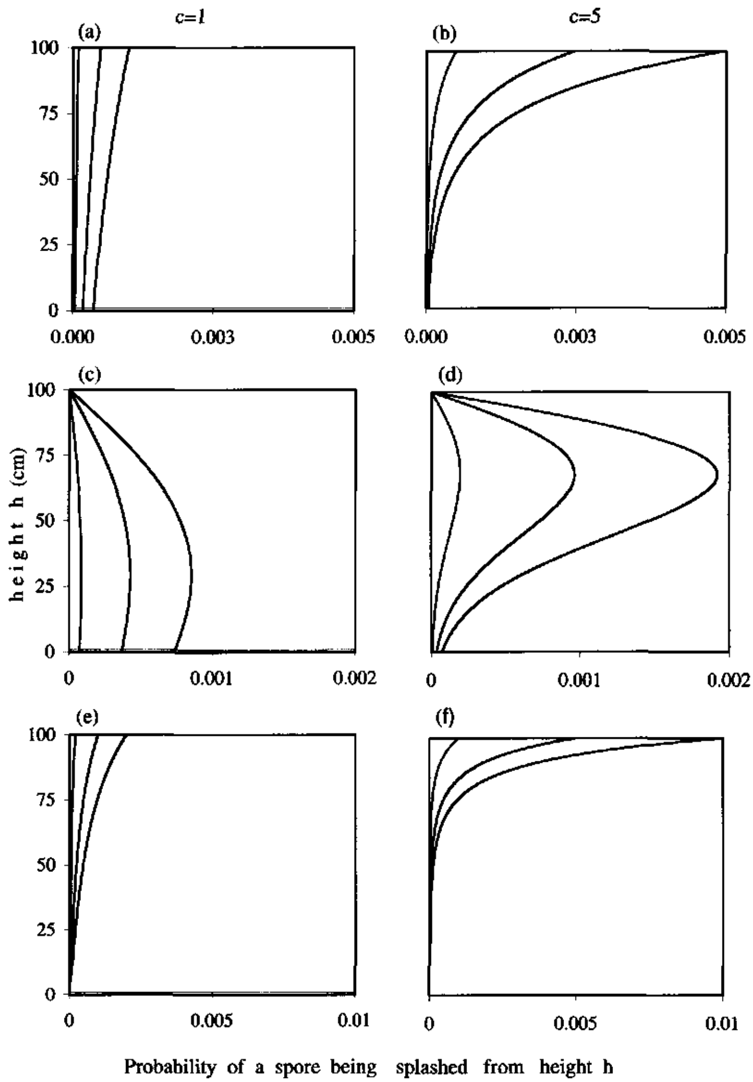

Figure 6.1: The probability of a spore being splashed from height h with thickness ξ in a crop having LAI constant (a,b),decreasing (c,d), or increasing (e,f) with height, and a total LAI, c=1 (a, c, e) or 5 (b, d, f) and a rebound probability, l_h=0.1 (left line), 0.5 (middle line) or 1.0 (right line). Crop height was 100 cm.

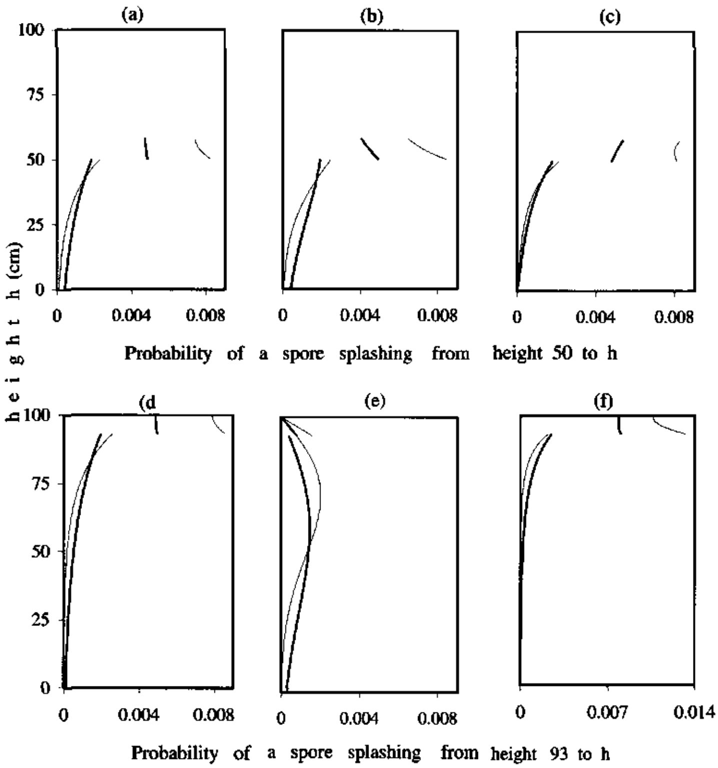

Figure 6.2: P.d.f. for the probability that a spore is deposited at height h with thickness ξ when splashed from height category n=50 cm (a,b,c) or n= 93 cm (d,e,f) in a crop having LAI constant (a,d), decreasing (b,e) or increasing (c,f) with height, and a total LAI, c=3 (solid line) or 6 (dotted line). Crop height was 100 cm and splash height was 8 cm.

The term

$$e^{-\int_{n}^{n+a} LAI_\sigma \, d\sigma}$$

was used to describe the likelihood that a spore was not intercepted between height n and its maximum splash height n+a. The mean maximum height (a) of spore splashes was calculated from experimental results in which ballistic trajectories of spores splashing from different plant parts were estimated (Pielaat, Marshall, McCartney, van den Bosch and Fitt, chapter 4). The p.d.f. $D_{n,h}$ for spore deposition was composed of three parts; a spore can be deposited at a vertical distance which is higher than, lower than or equal to the original point of drop impaction. Therefore

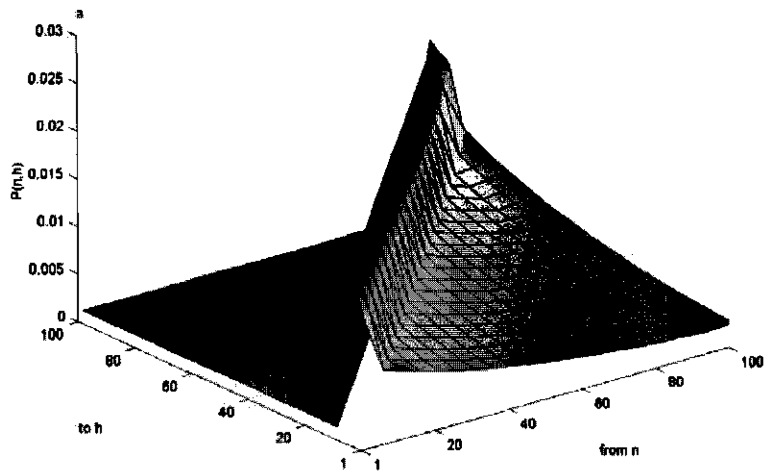

Figure 6.3: Probability density function for a spore being deposited at height h with thickness ξ when splashed from height n with thickness ξ in a crop having a with height constant LAI and a total LAI, c=2. Crop height was 100 cm and splash height was 8 cm.

$$D_{n,h} = \begin{cases} \xi LAI_h\left(e^{-\int_n^h LAI_\sigma \, d\sigma} + e^{-\int_n^{n+a} LAI_\sigma \, d\sigma} e^{-\int_h^{n+a} LAI_\sigma \, d\sigma}\right) & \text{if } h > n \\ \xi LAI_h \, e^{-\int_n^{n+a} LAI_\sigma \, d\sigma} e^{-\int_h^{n+a} LAI_\sigma \, d\sigma} & \text{if } h < n \\ \xi LAI_h\left(1 + e^{-2\int_n^{n+a} LAI_\sigma \, d\sigma}\right) & \text{if } h = n \end{cases} \tag{6.7}$$

The term n+a was replaced by max when spores splashed from a height where max < n+a . A more detailed explanation of the p.d.f. $D_{n,h}$ can be found in Pielaat, van den Bosch, Fitt and Jeger, chapter 5. When the corresponding LAI distributions for the three crops were substituted in these equations, different p.d.f.s for spatial spread were obtained as described in Appendix B. The equations of Appendix B were used for the analysis.

Figure 6.2 shows examples of the p.d.f.s for the vertical spread of a spore splashing either from a layer at height 50 cm in the canopy, where max > n+a, or from a layer at height 93 cm in the canopy, where max < n+a. Transition probabilities were plotted for

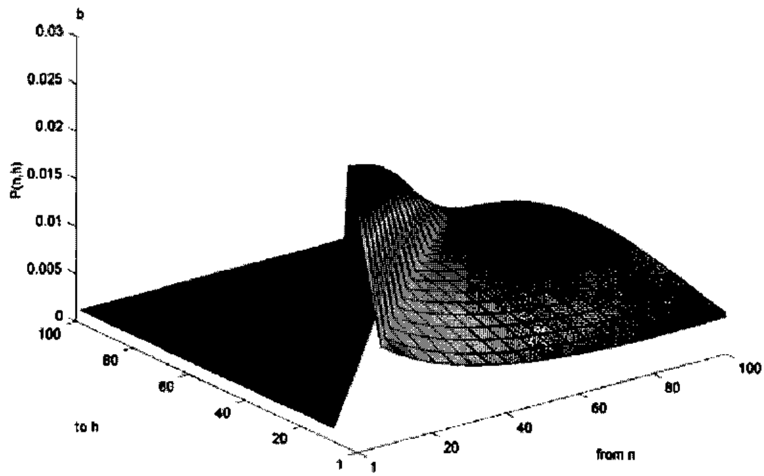

Figure 6.4: Probability density function for a spore being deposited at height h with thickness ξ when splashed from height n with thickness ξ in a crop having a with height decreasing LAI and a total LAI, c=2. Crop height was 100 cm and splash height was 8 cm.

the three different crops (where $h > 0$) and two values of c (the total LAI of a plant). A maximum mean splash height of 8 cm was used. The largest deposition probabilities were in the height layers above or level with the original drop impact point, with more spores being deposited when the LAI in the layers above the impact point increased and when the total LAI, c, of a crop increased. Apparently the LAI above each impact point was large enough to incorporate many of the splashed spores. The greater the surface area above the impact point the greater the deposition probabilities. As a consequence the probability of a spore being deposited increased towards the maximum splash height when a spore was splashed from 50 cm in a crop having an increasing LAI (Figure 6.2c). This trend was not observed when spores were released from a layer at height 93 cm in this crop. The LAI was already so large at height 93 cm that transition probabilities had a maximum value just above the impact point when splashed from this layer.

Although individual transition probabilities were smaller, most of the spores released were splashed to a layer beneath the impact point. The LAI below each impact point was large enough to prevent many splash droplets from penetrating down to the ground. Splash to the lower layers decreased gradually with decreasing deposition probabilities towards the ground when the LAI, c, was large (Figure 6.2 a,b,c,d,f). The more surface area just beneath the impact point the faster the deposition probabilities decreased.

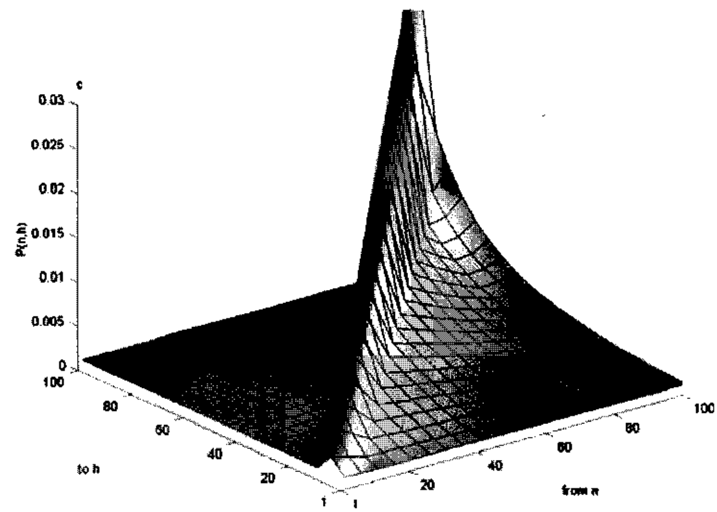

Figure 6.5: Probability density function for a spore being deposited at height h with thickness ξ when splashed from height n with thickness ξ in a crop having a with height increasing LAI and a total LAI, c=2. Crop height was 100 cm and splash height was 8 cm.

An exception to this result was observed in a crop having LAI decreasing with height, where splash to the lower layers first increased and then decreased. The surface area was too low in the upper layers for spore deposition in a crop having a decreasing LAI, therefore more spores were deposited in the lower canopy with relatively slow decreasing probabilities when the total LAI was low. This trend was more apparent when the total LAI, c, was larger.

The p.d.f.s for deposition in height layer h (for $h > 0$) when splashing from an arbitrary layer n (for $n > 0$) are shown in Figures 6.3, 6.4 and 6.5 for the three different crop types. Transition probabilities are largest in those layers having the largest LAI.

In this paper we have shown how leaf area index distribution (constant, decreasing, or increasing with height) affect key parameters involved in the splashing of spores within and beneath a crop canopy. This should form a basis for evaluating the consequences of breeding programmes leading to different plant architecture or new cropping practices where splash-dispersed pathogens are constraints to production.

Acknowledgements

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Appendix A

The LAI distribution was specified for three crop types to study the influence of crop morphology on the probability that a spore was splashed from height h with thickness ξ per time unit during a rain event.

Crop 1
The first crop had LAI constant with height, defined by

$$LAI_h = \begin{cases} c & \text{for } h \leq max \\ 0 & \text{for } h \geq max \end{cases}$$

So, $\int_0^{max} LAI_\sigma \, d\sigma = c\,max$ and

$$\lambda_h \;=\; l_h \, \xi \, c \, e^{-c(max-h)}. \tag{6.8}$$

Crop 2
The second crop had a LAI decreasing with height, defined by

$$LAI_h = \begin{cases} \alpha(max - h) & \text{for } h \leq max \\ 0 & \text{for } h \geq max \end{cases}$$

So, $\int_0^{max} LAI_\sigma \, d\sigma = \int_0^{max} \alpha(max - \sigma) d\sigma$. Since the three crops did not differ in total LAI, $\alpha = \frac{2c}{max}$ and

$$\lambda_h \;=\; l_h \, \xi \, 2c \, (1 - \frac{h}{max}) \, e^{-c\,max(1-\frac{h}{max})^2}\,. \tag{6.9}$$

Crop 3
The third crop had a LAI increasing with height, defined by

$$LAI_h = \begin{cases} \alpha \, h & \text{for } h \leq max \\ 0 & \text{for } h \geq max \end{cases}$$

So, $\int_0^{max} LAI_\sigma \, d\sigma = \int_0^{max} \alpha\sigma \, d\sigma$ and

$$\lambda_h = l_h \, \xi \, 2c \, \frac{h}{max} \, e^{-c\,(1-\frac{h}{max})(max+h)} \, . \tag{6.10}$$

Appendix B

Specified p.d.f.s $D_{n,h}$ for the vertical deposition of spores splashing between two layers n and h both with thickness ξ for the three crop types with LAI distributions as presented in Appendix A.

Crop 1

$$D_{n,h} = \begin{cases} \xi \, c\,(1 + e^{-2c(n+a-h)})\, e^{-c(h-n)} & \text{if } h > n \\ \xi \, c \, e^{-c(2a+n-h)} & \text{if } h < n \\ \xi \, c\,(1 + e^{-2ca}) & \text{if } h = n \end{cases}$$

If a spore splashed from a height where max < n+a, then n+a was replaced by max in the equation where h > n; the term 2a+n was replaced by 2max-n in the equation where h < n and the term -2ca was replaced by -2c(max-h) where h=n.

Crop 2

$$D_{n,h} = \begin{cases} \xi\,(1 + e^{-4c(n+a-h-\frac{(n+a)^2-h^2}{2max})})\, e^{-2c(h-n-\frac{h^2-n^2}{2max})}\, 2c(1-\frac{h}{max}) & \text{if } h > n \\ \xi\, e^{-ca(2-\frac{a+2n}{max})}\, e^{-2c(n+a-h-\frac{(n+a)^2-h^2}{2max})}\, 2c(1-\frac{h}{max}) & \text{if } h < n \\ \xi\,(1 + e^{-2ca(2-\frac{a+2n}{max})})\, 2c(1-\frac{h}{max}) & \text{if } h = n \end{cases}$$

If a spore splashed from a height where max < n+a, the equations became

$$D_{n,h} = \begin{cases} \xi\,(1 + e^{-2c(max-2h+\frac{h^2}{max})})\, e^{-2c(h-n-\frac{h^2-n^2}{2max})}\, 2c(1-\frac{h}{max}) & \text{if } h > n \\ \xi\, e^{-c(max-2n+\frac{n^2}{max})}\, e^{-c(max-2h+\frac{h^2}{max})}\, 2c(1-\frac{h}{max}) & \text{if } h < n \\ \xi\,(1 + e^{-2c(max-2h+\frac{h^2}{max})})\, 2c(1-\frac{h}{max}) & \text{if } h = n \end{cases}$$

Crop 3

$$D_{n,h} = \begin{cases} \xi\,(1 + e^{-\frac{2c}{max}((n+a)^2-h^2)})\,e^{-\frac{c}{max}(h^2-n^2)}\,2ch/max & \text{if } h > n \\ \xi\,e^{-\frac{c}{max}((n+2a)^2-h^2)}\,2ch/max & \text{if } h < n \\ \xi\,(1 + e^{\frac{-2c}{max}((n+a)^2-h^2)})\,2ch/max & \text{if } h = n \end{cases}$$

If a spore splashed from a height where max $<$ n+a, then n+a was replaced by max in the equation where h $>$ n; the term $(n+2a)^2$ was replaced by $2max^2$-n^2 in the equation where h $<$ n and the term $(n+a)^2$ was replaced by max^2 where h = n.

Chapter 7

General conclusions

This work shows that mechanistic models allow detailed examination of the biological and physical factors influencing the spatial spread of splash dispersed fungal plant pathogens. The main mechanisms underlying splash dispersal are: 1. A raindrop hits the water film formed on a leaf or the ground and spores are dispersed in the splashing rain droplets, and 2. Splashed spores are redistributed in the crop and on the soil surface by secondary splash. These two mechanisms were translated into probabilities and formed the basis in modelling horizontal and vertical spread of splash dispersed pathogens.

Horizontal disease spread

Analysis of a mechanistic random 'jump' model showed that the effects of rain properties and ground cover on the splash process could be seen in their effects on the model parameters. For high rain intensities the probability that a spore was splashed increased and simultaneously more spores were removed from the system. The mean dispersal distance varied according to the size of the splash droplets.

The diffusion approximation for the mechanistic model showed that for splash dispersal a diffusion model is in most situations not a useful approximation. The main problem in using a diffusion model for splash dispersal is that the initial inoculum source is depleted instantaneously at $t=0$. Only in the limit for $t \to \infty$ does the diffusion model describe the process as well as the mechanistic model. Still we would like to emphasize that during an average rain event spores are dispersed over relatively short distances; this process is best described by the mechanistic approach.

The model was compared to experimental data on spore dispersal from a point source. For this purpose composite variables were derived from the model that are of direct biological relevance. For instance, equations were derived for the total number of spores surrounding the source and distances spores travel during rain events. A description