Managing for Fine-Scale Differences in Inoculum Load: Seeding Patterns to Minimize Wheat Yield Loss to Take-all

K. A. GARRETT, M. KABBAGE AND W. W. BOCKUS   kgarrett@ksu.edu
Department of Plant Pathology, 4024 Throckmorton Plant Sciences Center, Kansas State University, Manhattan, KS 66506-5502

Abstract. For pathogens with highly localized inoculum, controlled positioning of susceptible plants can be used to delay exposure to the pathogen. For example, when wheat is direct-drilled in fields where wheat was infected by *Gaeumannomyces graminis* var. *tritici* (*Ggt*) in the previous season, the remaining rows of wheat crowns serve as an inoculum source for the new wheat planting. In order to determine how different seeding patterns of wheat might affect yield loss to *Ggt*, we constructed a mathematical model in three stages. First, we calculated the probability density function for the distance between a new seed and the nearest old row of crowns for two main planting scenarios: parallel to the previous year's rows or at an angle to them. Second, we used estimates from Kabbage and Bockus [Kabbage, M. and Bockus, W. W. 2002. Plant Disease **86**, 298–303] of the yield loss to *Ggt* as a function of the distance between wheat seed and inoculum source. Third, we combined these two models to estimate the average yield loss for different planting patterns. We estimated that planting parallel to and between the previous year's rows would cut yield loss almost in half for a typical row spacing compared to angled planting, provided there was not an important offset, or bias, in the position of the parallel planting. Planter wobble was relatively unimportant if there was no systematic bias in position.

Keywords: reduced tillage, spatial variability, plant disease, phytopathology

Introduction

Precision agriculture approaches offer benefits when separate units of a field are best managed in different ways. Whelan and McBratney (2000) proposed as a null hypothesis for precision agriculture that "Given the large temporal variation evident in crop yield relative to the scale of a single field, then the optimal risk aversion strategy is uniform management." In this work, we propose consideration of the environment that crop plants experience at a small spatial scale. The null hypothesis for our scenario might be stated as: "Given that disease inoculum is associated with the rows from the previous year in a no-till system, the optimal strategy is seeding without regard to position of the old rows." In this paper, we use a mathematical modeling approach to predict under what circumstances different seeding patterns might be useful for reducing loss to such localized inoculum, using take-all of wheat as an example.

Time of infection has been used successfully to predict yield loss to systemic disease (Madden *et al.*, 2000). For crown-borne inoculum, the distance between a newly planted seed and an infected crown functions similarly as a predictor since this

distance will determine how quickly growing plant tissues encounter the inoculum. For example, for wheat take-all epidemics, caused by *Gaeumannomyces graminis* var. *tritici* (*Ggt*), infection takes place when growing wheat roots and the pathogen come into contact, and the time it takes for this to occur will be closely tied to the distance between seed and pathogen. The age of a plant when it encounters *Ggt* can be an important factor in determining the yield loss it will experience (Garrett, 1948). In direct-drill (no-till) conditions, the distance between seed and inoculum source can be managed by controling planting patterns when wheat is sown into a field previously planted to wheat infected with take-all. This is because the most significant inoculum source for *Ggt* is infected, intact crowns from the previous crop; roots and root fragments are unimportant sources of inoculum (Cotterill and Sivasithampa-ram, 1988; Moore and Cook, 1984; Wilkinson *et al.*, 1985). Therefore, under direct-drilled conditions, *Ggt* inoculum occurs as rows of undisturbed crowns of the previous crop.

Take-all offers incentives to the development of new cultural techniques such as this, since there are limited management alternatives. Management is currently based primarily on cultural practices because of the lack of effective host resistance or chemical controls (Colbach *et al.*, 1997). Inoculum in crop residue typically initiates epidemics; primary infection occurs when susceptible roots encounter *Ggt* in the infected crowns (Bailey and Gilligan, 1999). Crop rotation has an important effect on *Ggt* because, while *Ggt* can survive to a limited extent as a saprophyte (Hornby, 1975), it does not compete well with other soil microflora (Butler, 1953; Cook, 1981; Garrett, 1940; Hornby, 1975) and populations of *Ggt* decline to levels insufficient to initiate epidemics during periods without a susceptible host (Cotterill and Sivasi-thamparam, 1988). However, growers do not necessarily use rotation; for example, repeated wheat monoculture is popular in many areas of Kansas due to the current lack of alternative winter crops (Bockus, 1983).

Additionally, rotation from winter wheat to a summer crop such as corn, sorghum, or soybean usually results in the loss of one cropping season in three. Another cultural practice, delayed planting in fall, can provide escape from the pathogen because its survival in the absence of wheat is so tenuous (Bailey and Gilligan, 1999). Extending the length of the saprophytic period by delayed planting results in a greater reduction in the *Ggt* population. However, delayed planting is not popular because it increases the likelihood of soil erosion and can also lead to reduced yields (Bockus, 1983). A third cultural practice, tillage, has the potential to control take-all. Tillage breaks up the residue with *Ggt* into smaller pieces that are more quickly degraded by other soil microorganisms (Wilkinson *et al.*, 1985) and eliminates the shading of inoculum that can help it avoid thermal inactivation and so survive through the summer (Bockus *et al.*, 1994). But because of concerns about soil erosion, growers are increasingly adopting reduced tillage practices. Due to these constraints, problems with take-all are likely to increase (Moore and Cook, 1984; Scott, 1969) and other possibilities for cultural control of take-all are needed.

We propose the manipulation of planting patterns as a prospective management tool for pathogens such as *Ggt*. Current precision planting technology makes this a more feasible approach than it might have been in the past. It is clear that planting exactly between the previous year's rows would maximize the distance between seed

and infected crowns from the previous year. But we also wished to consider the following questions:

(1) If planting cannot be done perfectly (without any bias, or offset, and without any variance in position, or planter wobble), then what planting pattern, relative to the previous year's rows, would be expected to minimize yield loss?
(2) How would the optimal planting pattern be expected to change as a function of the bias and precision in planting and as a function of the row spacing?
(3) How much difference in yield loss can be expected depending on planting pattern? (Is the difference large enough to motivate more attention to seeding pattern?)

To address these questions, we have used mathematical modeling to develop predictions based on our current understanding of the system. We constructed probability density functions for the distance between seed and old crowns corresponding to different planting arrangements. We considered the main planting patterns possible for this system: planting parallel to the previous year's rows compared to planting perpendicular to the previous year's rows or at another nonzero angle. By combining these probability density functions with estimates of yield loss as a function of distance between seed and inoculum (Kabbage and Bockus, 2002), we predicted the average yield loss for direct-drill areas with take-all inoculum for the different planting patterns.

Model

Position of seed relative to crowns from previous year

The probability density function (Ross, 1997) for the shortest distance between a newly planted seed and the nearest row of crowns from a previous wheat planting ($f(x)$) was constructed for different planting patterns. This distance (x) was modeled as a continuous random variable and expressed as a function of the row spacing of the wheat (s) and the planting pattern. The greatest possible distance a seed can be from the previous year's row is $\frac{1}{2} s$, when it is positioned exactly at the midpoint between the previous year's rows. We assumed that the row spacing was the same in both years and modeled $f(x)$ for both planting at an angle ($0° < \theta \le 90°$) to the old rows and planting parallel to the old rows with attention to planting as close to equidistant from the two old rows as possible (Figure 1). We treated the width of the
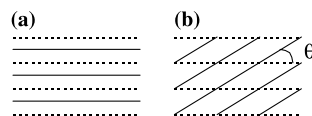

Figure 1. Illustration of (a) new parallel planting (solid lines) relative to previous season's rows (dotted lines) and (b) new planting at an angle θ relative to previous season's rows, where one common form of planting would be with $\theta = 90°$, or perpendicular to the previous year's crop.

crown as negligible; incorporating a nonzero crown width (typically around 2 cm) would simply reduce the functional row spacing by the width of the crown in our model. Crowns from the previous year may occasionally be moved in the process of planting the current year's crop; the effect of this on the distance between new seed and old crown would be similar to including a greater planter wobble in the model, as described below.

If the new planting is at an angle $\theta > 0$ to the old rows, the shortest distance between a new seed and the old row is equally likely to be any distance between 0 and $\frac{1}{2} s$ (Figure 2). This will be the case if the angle is 90°, or perpendicular, or if $0° < \theta \leq 90°$. The main difference between these two scenarios, $\theta = 90°$ and $0° < \theta < 90°$, is that for perpendicular planting ($\theta = 90°$) there will be only short intervals of plants close to the old rows and of plants farther from the old rows while for a small angle there will be longer intervals of plants close to the old row and of plants farther from the old row. Though the spatial clumping of plants near versus far from the old row will be different, the distribution of distances between seed and old row for any angle $0° < \theta \leq 90°$ can be expressed using a uniform distribution (Ross, 1997) as

$$f(x) = 2/s\, I_{[0,1/2\,s]}(x), \tag{1}$$

where I is an indicator function such that $I_{[0,\ \frac{1}{2}\,s]}(x) = 1$ when x falls within the interval $[0,\ \frac{1}{2}\,s]$ and $I_{[0,\ \frac{1}{2}\,s]}(x) = 0$ when x falls outside the interval. (We assume that the field is large enough that, even for values of θ near zero, new rows will cross from one old row to another old row.) The same distribution will also be produced by planting parallel to the old rows but with no other attention to placement relative to the old rows.
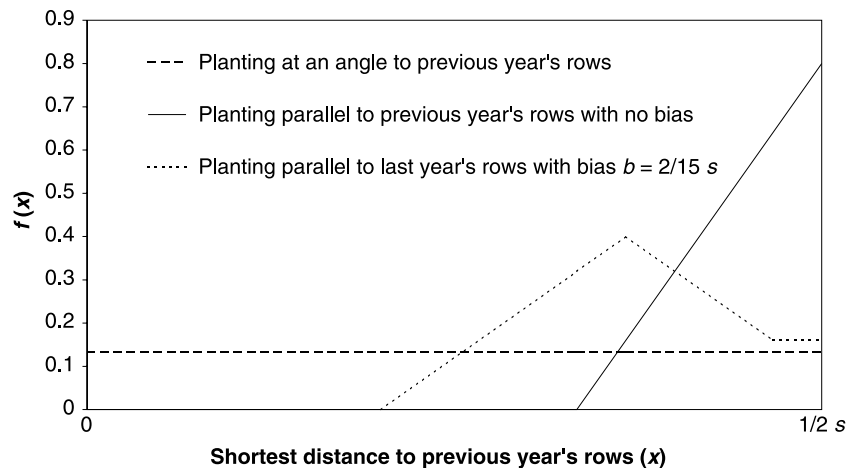

Figure 2. Probability density function for the distance between a new seed and the nearest point in one of the previous year's rows ($f(x)$) for angled planting ($0° < \theta \leq 90°$), parallel planting ($\theta = 0°$) with no bias, and parallel planting with bias $b = 2/15\ s$, where s denotes the row spacing. The bias is the distance between the actual center of planting and the intended center of planting at the point equidistant between the old rows. For this example, the range of planting wobble is $r = 1/3\ s$.

If the new planting is parallel to the old rows with attention to planting as close to equidistant from the two old rows as possible, there are several other possibilities for $f(x)$. If the planting is done perfectly at the midpoint between old rows, then the distance between the seed and the nearest old row will always be ½ s. But there will generally be some variation around the desired center point, both in the current and previous year's planting. We can approximate the distribution of planting around the midpoint with a triangular distribution. The probability density function for a symmetric triangle over values from j to k with midpoint m is (Evans *et al.,* 1993)

$$f(x) = 4(x - j)/(k - j)^2 \, I_{[j,m]} + 4(k - x)/(k - j)^2 \, I_{[m,k]}. \tag{2}$$

Adapting this to our scenario, we consider a triangular distribution over a range r produced by wobble in a planter so that, when planting is done with little enough wobble that the new row at least stays between the old rows ($0 < r \le s$) (Figure 2),

$$f(x) = 8(x - 1/2 \, (s - r))/r^2 \, I_{[1/2 \, (s-r), 1/2 \, s]}(x). \tag{3}$$

If the wobble of the planter is so great that the new row sometimes runs over and outside the old rows ($s < r \le 2s$), then

$$f(x) = 8(r - s)/r^2 \, I_{[0, 1/2 \, (r-s)]}(x) + 8(x + 1/2 \, (r - s))/r^2 \, I_{[1/2 \, (r-s), 1/2 \, s]}(x), \tag{4}$$

though this would be an unusual scenario with more precise planting equipment.

There may also be a bias in parallel planting. That is, planting may be systematically offset from the midpoint between the old rows. If the distance between the desired midpoint and the actual center of planting is b, then the distribution of x can again be calculated. We assume that the offset in planting is small enough that the midpoint between old rows is at least sometimes included in the planting ($b \le$ ½ r). If there is a bias, but no range, then x is a constant, ½ $s - b$. If there is also a range, or wobble, in planting ($r > 0$), the probability distribution of x is then (Figure 2)

$$
\begin{aligned}
f(x) = {} & 4(x - 1/2 \, (s - r) + b)/r^2 \, I_{[1/2 \, s - b - 1/2 \, r, \, 1/2 \, s - b]}(x) \\
& + 4(1/2 \, (s + r) - b - x)/r^2 \, I_{[1/2 \, s - b, \, 1/2 \, (s-r) + b]}(x) \\
& + 4(r - 2b)/r^2 \, I_{[1/2 \, (s-r) + b, \, 1/2 \, s]}(x).
\end{aligned}
\tag{5}
$$

Yield loss per plant as a result of exposure to inoculum at different
distances from seed

Kabbage and Bockus (2002) reported estimates of wheat yield loss as a function of distance of seed from inoculum. These estimates were based on yield loss in plants sown in a row parallel to and at a range of distances from a row of oat kernels infested with *Ggt*. They utilized both greenhouse and field studies, but here we use parameter estimates from only the field studies. Parameters were estimated in a linear regression analysis (Kabbage and Bockus, 2002). Yield loss was expressed in our current model as

$$y(x) = [\beta_0 + \beta_1 x + \beta_2 x^2] I_{[0, d*]}(x), \tag{6}$$

where $d*$ is the shortest distance away from the infected crown at which yield loss is equal to zero (Figure 3). For the first field study of Kabbage and Bockus (2002), the
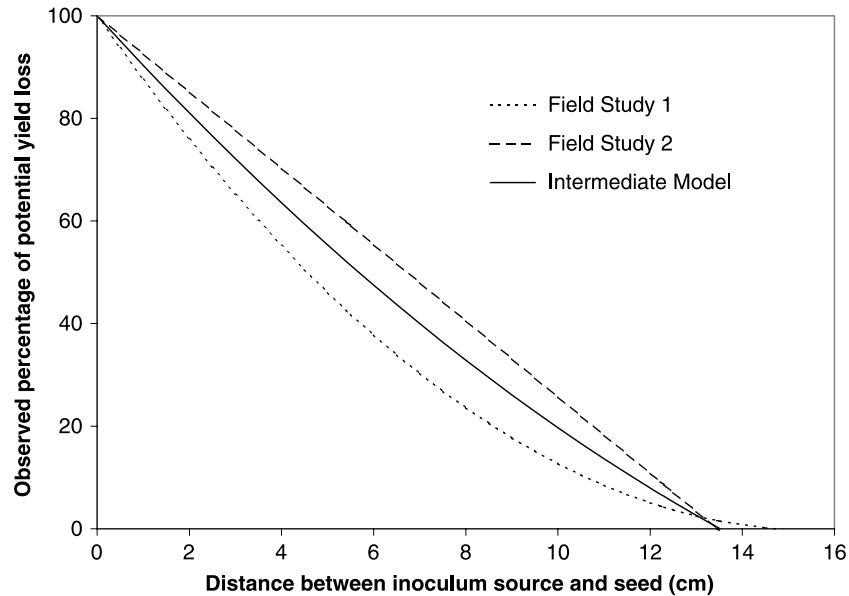
Figure 3. Illustration of yield loss to take-all as a function of distance of wheat seed from infected crowns from the previous planting season. Lines represent the results of two field experiments (Kabbage and Bockus, 2002) and a model intermediate between the results of the two experiments. Yield loss was scaled to express the percentage of the potential loss that would have been experienced if all seed were planted at the inoculum source.

model was fit as $y(x) = [61 - 7.82x + 0.25x^2]I_{[0,14.8]}(x)$; for the second field study, the model was fit as $y(x) = [76 - 5.65x]I_{[0,13.4]}(x)$. To simplify our analyses of planting patterns, in this study we have used a model intermediate between these two models and scaled it to express yield loss as the percentage of the potential loss experienced when the distance between the seed and the inoculum source is zero. The model we used in this study was

$$y(x) = [100 - 9.83x + 0.18x^2]I_{[0,13.5]}(x). \tag{7}$$

Predicted area yield loss for different planting patterns

Expected yield loss for areas with take-all inoculum was calculated by linking the models for yield loss in individual plants as a function of distance from inoculum, $y(x)$, and the probability density function for distance between seed and old crown, $f(x)$. The average value of a function y of a continuous random variable x, or the expected value of $y(x)$, is (Ross, 1997)

$$E[y(x)] = \int_{-\infty}^{\infty} y(x)f(x)\,dx. \tag{8}$$

For our application, this expectation was used to predict the mean yield loss for the different seeding scenarios. For example, for angled planting Eq. (1),

$$E[y(x)] = \int_0^{\min(13.5,1/2s)} [100 - 9.83x + 0.18x^2]2/s \, dx. \tag{9}$$

Maple analytical computation software (Waterloo Maple, Inc., 57 Erb St. West, Waterloo, ON N2L 6C2, Canada) was used to evaluate the integrals.

Results

Planting pattern to minimize yield loss

To make our results clear, we designated yield loss for seeds planted directly at the inoculum source as 100% of the potential yield loss, the loss that would have resulted if all seed had been planted directly at the old crowns (Figure 3). By comparison, all planting patterns give some reduction in predicted yield loss compared to the potential loss because seeds tend to be planted at some distance >0 from the previous year's rows (Figure 4). At the typical 15 cm row spacing, "perfect" parallel planting with attention to placement equidistant from the two old rows, with no wobble or offset in planting, gave the lowest yield loss in our model predictions. The predicted yield loss for angled planting ($0° < \theta \leq 90°$) was higher (Figure 4). A 2 cm crown diameter could be incorporated into this analysis by reducing the row spacing, s, by 2 cm.
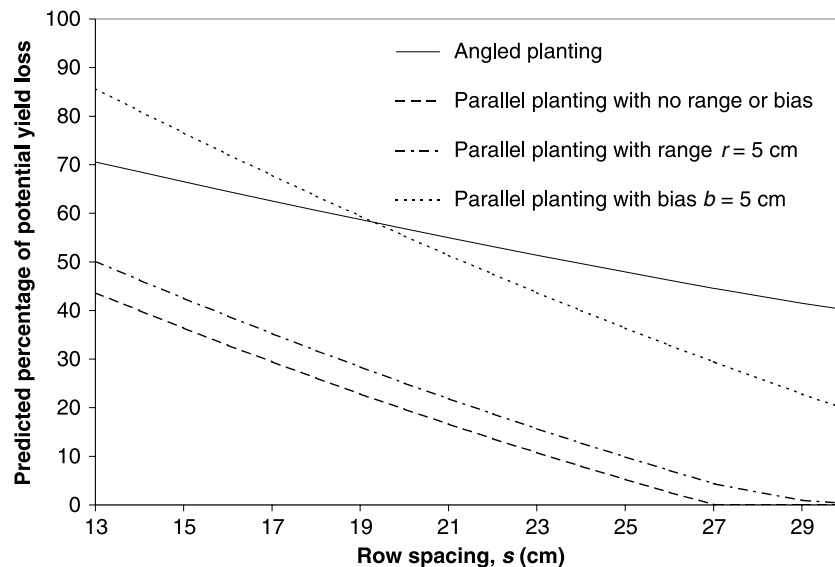

Figure 4. Predicted wheat yield loss to take-all as a function of row spacing for four different planting scenarios, including angled planting ($0° < \theta \leq 90°$) and parallel planting ($\theta = 0°$). Yield loss was scaled to express the percentage of the potential loss that would have been experienced if all seed were planted at the inoculum source.

Effects of bias and precision in planting and row spacing

For angled planting, predicted yield loss was less than 70% of the potential loss at a typical 15-cm row spacing and decreased gradually as the row spacing increased. For "perfect" parallel planting, with no wobble (range) or bias (offset), predicted yield loss is reduced to only 37% of the potential loss and decreases to 0% if the row spacing is doubled. If the parallel planting has a range of 5 cm, this changes the result compared to the "perfect" planting only slightly (Figure 4). But if a bias in the position of the parallel planting of 5 cm is added, this greatly increases the predicted yield loss, especially at the more typical row spacing of 15 cm. Changing the range of planting has only a modest effect on predicted yield loss even as the range is increased to equal the row spacing (Figure 5). But a bias in planting position has a much more important effect on yield loss, with the potential to increase predicted yield loss to 100% for an extreme bias that places the seed directly on top of the previous year's rows of crowns (Figure 6).

Magnitude of difference in yield loss

The most relevant comparison for realistically precise and accurate planting might be between angled planting and parallel planting with a small range and minimal bias. For this scenario, we predict that use of careful parallel planting will cut yield loss almost in half compared to angled planting or parallel planting without
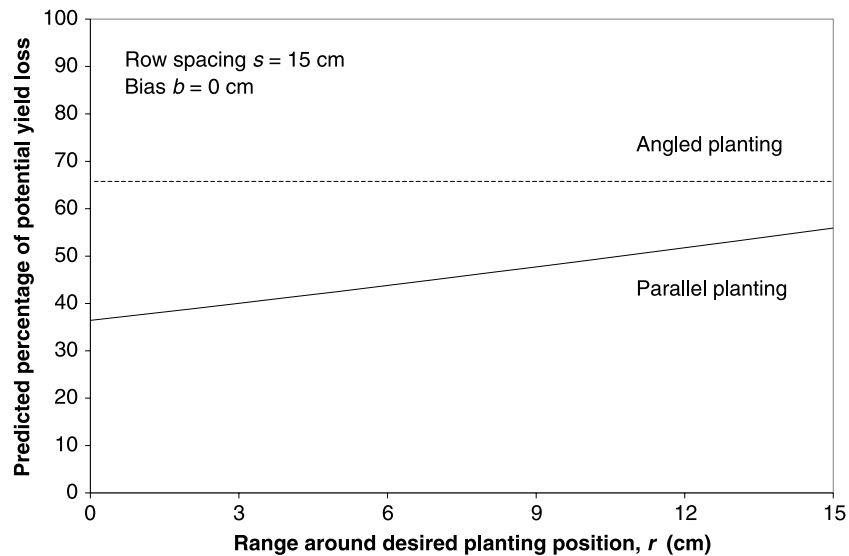

Figure 5. Predicted wheat yield loss to take-all as a function of the size of the planting wobble (range, r) for parallel planting ($\theta = 0°$). Yield loss was scaled to express the percentage of the potential loss that would have been experienced if all seed were planted at the inoculum source.
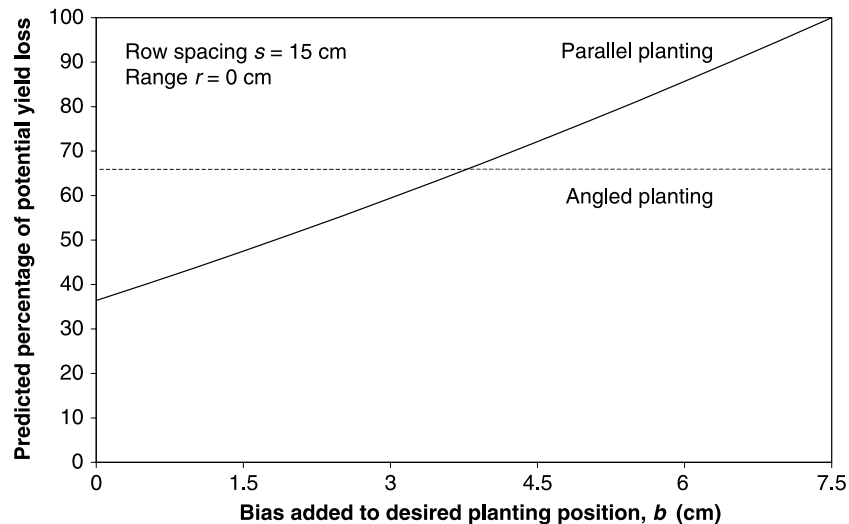
Figure 6. Predicted wheat yield loss to take-all as a function of the size of the bias in planting position (b) for parallel planting ($\theta = 0°$). The bias is the distance between the actual center of planting and the intended center of planting at the point equidistant between the old rows. Yield loss was scaled to express the percentage of the potential loss that would have been experienced if all seed were planted at the inoculum source.

attention to position relative to old rows (Figure 4). If planting cannot be done with only minimal bias, however, angled planting may be preferable (Figure 6).

Discussion

We have modeled the predicted yield loss due to take-all for different direct-drilled planting patterns as a function of how the planting patterns change the distance between new seedlings and infested crowns from the previous year. We predict that planting parallel to the previous year's rows would give the greatest advantage for reducing yield loss, even if there is a significant planting wobble, provided there is not a large planting bias, or offset. The difference in predicted yield loss between angled ($0° < \theta \leq 90°$) and parallel planting ($\theta = 0°$) for careful and efficient parallel planting was great enough to be a motivating factor in determining the pattern of wheat planting where take-all is important and rotation and tillage are not used. The potential precision of planting has recently been increased with the development of various guidance systems for tractors, including global positioning system-(GPS) based systems with accuracies below 2.5 cm. Planting accuracy and precision are likely to increase in the future.

We have not explicitly included the possible effects of compensation in our model, where neighboring healthy plants might offset the yield loss of diseased plants. If angled planting is used, a smaller angle θ would result in larger clumps of consecutive plants that are near the previous year's row than would occur for perpendicular

planting with $\theta = 90°$ (Figure 1); thus, the potential for compensation could be different for perpendicular planting compared to more shallow angles. But compensation may not be important in this consideration because plants with highly diseased neighbors will generally tend to be somewhat diseased themselves, and thus have less potential for compensation. Also, take-all usually kills plants later in the season when tillers have already used much of the available nutrients, space, and water, so that the potential for compensation is low. We have also not explicitly included the potential for secondary infection, but the experiment of Kabbage and Bockus (2002) from which we drew our model of yield loss (Eq. (7)) incorporates secondary infection under high inoculum pressure when seed is sown parallel to a row of inoculum source material. But it is also possible that the acuteness of the angle of planting could influence the rate of secondary infection and thus yield loss.

While our predictions should also be tested under commercial conditions, there is reason to expect that they will be robust. The oat-kernel inoculum used in the study of Kabbage and Bockus (2002) was very vigorous, probably more than would be inoculum in crowns in the field; for this reason, estimates of benefits to yield for wheat sown further from inoculum sources are probably conservative. Our model is also based on the assumption that the crowns are a much more important source of inoculum than senesced wheat roots, but this idea does seem well supported in the literature (Cotterill and Sivasithamparam, 1988; Moore and Cook, 1984; Wilkinson et al., 1985). We predict that yield loss to take-all for direct-drilled wheat following wheat can be significantly reduced by planting parallel to the previous year's rows, even when there is a sizeable planter wobble.

Acknowledgments

References

Bailey, D. J. and Gilligan, C. A. 1999. Dynamics of primary and secondary infection in take-all epidemics. Phytopathology 89, 84–91.

Bockus, W. W. 1983. Effects of fall infection by *Gaeumannomyces graminis* var. *tritici* and triadimenol seed treatment on severity of take-all in winter wheat. Phytopathology 73, 540–543.

Bockus, W. W., Davis, M. A. and Norman, B. L. 1994. Effect of soil shading by surface residues during summer fallow on take-all of winter wheat. Plant Disease 78, 50–54.

Butler, F. C. 1953. Saprophytic behaviour of some cereal root-rot fungi. I. Saprophytic colonization of wheat straw. Annals of Applied Biology 40, 284–297.

Colbach, N., Lucas, P. and Meynard, J.-M. 1997. Influence of crop management on take-all development and disease cycles on winter wheat. Phytopathology 87, 26–32.

Cook, R. J. 1981. The influence of rotation crops on take-all decline phenomenon. Phytopathology 71, 189–192.

Cotterill, P. J and Sivasithamparam, K. 1988. The effect of tillage practices on distribution, size, infectivity and propagule number of the take-all fungus, *Gaeumannomyces graminis* var. *tritici*. Soil Tillage Research **11**, 183–195.

Evans, M., Hastings, N. and Peacock, B. 1993. *Statistical Distributions* (Wiley, New York).

Garrett, S. D. 1940. Soil conditions and the take-all disease of wheat. V. Further experiments on the survival of *Ophiobolus graminis* in infected wheat stubble buried in the soil. Annals of Applied Biology **27**, 199–204.

Garrett, S. D. 1948. Soil conditions and the take-all disease of wheat. IX. Interaction between host plant nutrition, disease escape, and disease resistance. Annals of Applied Biology **35**, 14–17.

Hornby, D. 1975. Inoculum of the take-all fungus: Nature, measurement, distribution, and survival. EPPO Bulletin **5**, 319–333.

Kabbage, M. and Bockus, W. W. 2002. Effect of placement of inoculum of *Gaeumannomyces graminis* var. *tritici* on severity of take-all in winter wheat. Plant Disease **86**, 298–303.

Madden, L. V., Hughes, G. and Irwin, M. E. 2000. Coupling disease-progress-curve and time-of-infection functions for predicting yield loss of crops. Phytopathology **90**, 788–800.

Moore, K. J. and Cook, R. J. 1984. Increased take-all of wheat with direct drilling in the Pacific Northwest. Phytopathology **74**, 1044–1049.

Ross, S. M. 1997. *A First Course in Probability* (Prentice Hall).

Scott, P. R. 1969. Control of *Ophiobolus graminis* between consecutive crops of winter wheat. Annals of Applied Biology **63**, 47–53.

Whelan, B. M. and McBratney, A. B. 2000. The "null hypothesis" of precision agriculture management. Precision Agriculture **2**, 265–279.

Wilkinson, H. T., Cook, R. J. and Alldredge, J. R. 1985. Relation of inoculum size and concentration to infection of wheat roots by *Gaeumannomyces graminis* var. *tritici*. Phytopathology **75**, 98–103.