Growth, Development, Yield, and Seed Quality of Florunner Peanut Affected by Late Leaf Spot[1]

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ABSTRACT

Late leaf spot, induced by *Cercosporidium personatum* (Berk. & Curt.) Deighton, causes serious yield losses of peanut (*Arachis hypogaea* L.) in the southeastern United States. A two-year study was conducted to observe progress of late leaf spot and to evaluate subsequent effects of late leaf spot on accumulation of dry matter, leaf area index (LAI), and pod production of Florunner peanut in fungicide-treated and non-treated plots. Disease severity, which is an expression of both disease-induced defoliation and necrotic leaf area, was used as an indicator of disease progression in the field. The leaf dry weight, LAI, and the dry weight of the total biomass were significantly different at 93 days after planting (DAP) in 1986, and at 78 DAP in 1987 between fungicide-treated and non-treated plots. Late leaf spot reduced the potential yield (harvested and dropped pods) of Florunner peanut by 37% in 1986 and 46% in 1987. In non-treated plots, the abscission of pods was initiated later but progressed faster in 1986 than in 1987. The predictions of pod yield with the measures of healthy leaf area duration (HAD) and healthy area absorption (HAA) were adequate for fungicide-treated plots where pod losses were minimal. However, HAD and HAA were inadequate for predicting pod yield of a peanut crop severely infected by late leaf spot, primarily because this predictive approach does not account for losses of dropped pods.

Key Words: *Arachis hypogaea* L., *Cercosporidium personatum*, epidemiology, growth analysis, healthy leaf area duration, healthy area absorption, late leaf spot, peanut, pod losses, yield prediction.

Among all foliar diseases affecting peanut (*Arachis hypogaea* L.), early and late leaf spot, induced by *Cercospora arachidicola* Hori and *Cercosporidium personatum* (Berk. & Curt.) Deighton, respectively, are the most common and destructive diseases in the southeastern United States. They are, along with rust, the most serious disease problems on peanut worldwide. In Florida, late leaf spot is the predominant disease and can cause yield losses over 50% if fungicides are not used (13, 18, 21, 23). These losses in yield are primarily associated with a reduction in leaf area index (LAI) which causes a reduction in light interception (2, 24). Backman and Crawford (1) reported that for the cultivar Florunner, which has a yield potential of about 4400 kg ha^{-1}, yield was reduced by an average of 57 kg ha^{-1} for each percent of defoliation assessed two weeks before harvest. Defoliation caused by late leaf spot results in a reduction in canopy photosynthesis; therefore, less photosynthate is available for pod growth.

Waggoner and Berger (28) proposed the concept of healthy leaf area duration (HAD) and healthy area absorption (HAA) which can be used to predict the pod yield of a peanut crop affected by early and late leaf spot. HAD is defined as the healthy leaf area integrated during the growing season and HAA is defined as the energy (insolation) taken in during the growing season by the healthy leaf area. They concluded that yield was simply determined by HAD and was linearly related to HAA whether the crop was defoliated manually or by disease. However, they did not consider an important component of peanut yield losses, the abscission of pods close to harvest time. When the plants are pulled from the soil, some pegs break and the dropped pods can not be harvested with standard equipment (12, 18, 24, 25). Whether or not these losses are induced directly by *C. arachidicola* or *C. personatum* is not documented.

Early and late leaf spot can be first recognized as small necrotic flecks on the leaflets. Flecks enlarge and become necrotic lesions which are associated with loss of chlorophyll pigments (15). Differences in symptoms for early leaf spot and late leaf spot have been noted and positive identification can only be obtained by microscopic observation of the conidia (22). The major effect of leaf spot diseases is to increase leaflet abscission which reduces light interception and photosynthesis (5). The cause of this early defoliation is not fully understood. Associated with the presence of *Cercospora* spp., there are some reports of cercosporin production, a photosensitizing toxin activated by light (8,26), and an increase in production of ethylene, a growth regulator that induces abscission (11). In addition, the necrotic lesions themselves represent loss of photosynthetic area even though leaflets have not abscised.

The disease progresses from the lower part to the upper part of the peanut canopy. Plaut and Berger (19) divided the peanut canopy into three vertical semicircular leaf layers (bottom, middle, and top) to assess disease effects. Both necrotic area and defoliation must be estimated in a disease assessment program for peanut leaf spots. Necrotic area is usually assessed with the aid of an arbitrary scale, as the Horsfall-Barratt scale (10) or a pictorial key (20). The Horsfall-Barratt scale can also be used to assess percent defoliation, but the technique most commonly used is to count the number of missing leaflets on the main stem (20). Such an assessment assumes that leaflets are missing due to disease. Problems with the latter technique were observed early in the growing season due to natural leaf senescence at the lower nodes of the main stem. Pixley (16) reported a defoliation percentage of 20% at 50 days after planting (DAP) in plots treated with fungicide, whereas Shokes *et al.* (20) observed defoliation percentages of 10 to 20% in peanut which had excellent disease control. Pixley *et al.* (17) computed a measure of disease-induced defoliation by subtracting the defoliation estimated in the plots treated with fungicides from the one estimated in the non-treated plots. As a result, only 70% of the total defoliation at 131 DAP was

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found to be induced by the leaf spot disease.

To obtain a quantitative estimate of yield loss from disease severity, accurate assessments for both defoliation and necrotic area are needed. This experiment was undertaken to observe progress of late leaf spot and to evaluate subsequent effects of late leaf spot on accumulation of dry matter, LAI, and pod production of Florunner peanut. Data obtained from this experiment was used to develop and evaluate a simulation model for the progression of late leaf spot on Florunner peanut.

Materials and Methods

The experiment was conducted at the Agronomy Farm of the University of Florida in Gainesville. Florunner peanut was planted on 2 June during summers of 1986 and 1987 at a rate of 20 seeds m^{-1} in rows 0.91 m apart to achieve a population of 13 to 14 plant m^{-2}. Irrigation with overhead sprinklers provided water to the field (Fig. 1) to provide moisture for germination at seeding time and when wilting symptoms of the leaves were observed during the day. Weeds were controlled with a pre-plant application of benefin (Balan)[3] at a rate of 1.26 kg a.i. ha^{-1} (1986: 23 May; 1987: 26 May), and a pre-emergence application of alachlor (Lasso) at a rate of 2.26 kg a.i. ha^{-1} (1986 and 1987: 3 June). Escaped weeds were removed manually after plant emergence. The insecticides methomyl (Lannate) and acephate (Orthene) were applied as needed at a rate of 0.49 kg a.i. ha^{-1} (1986: 7 Aug., 21 Aug.; 1987: 24 Aug.) and 0.82 kg a.i. ha^{-1} (1986: 4 Sept., 15 Sept.; 1987: 31 July, 14 Aug.), respectively. Gypsum was applied at a rate of 1009 and 1345 kg ha^{-1} in 1986 and 1987, respectively, at the pegging stage which occurred 40 to 42 days after planting.

The experimental design was a randomized complete block with two treatments: 1) fungicide treated and 2) not treated, and four replications. The protectant fungicide chlorothalonil (Bravo 500) was used at a rate of 1.15 kg a.i. ha^{-1} and was applied with a CO_2-pressurized backpack system. Applications of fungicide began 32 and 23 days after planting in 1986 and 1987, respectively. Time between applications ranged from 8 to 12 days, and sprays were applied until the first week of October.

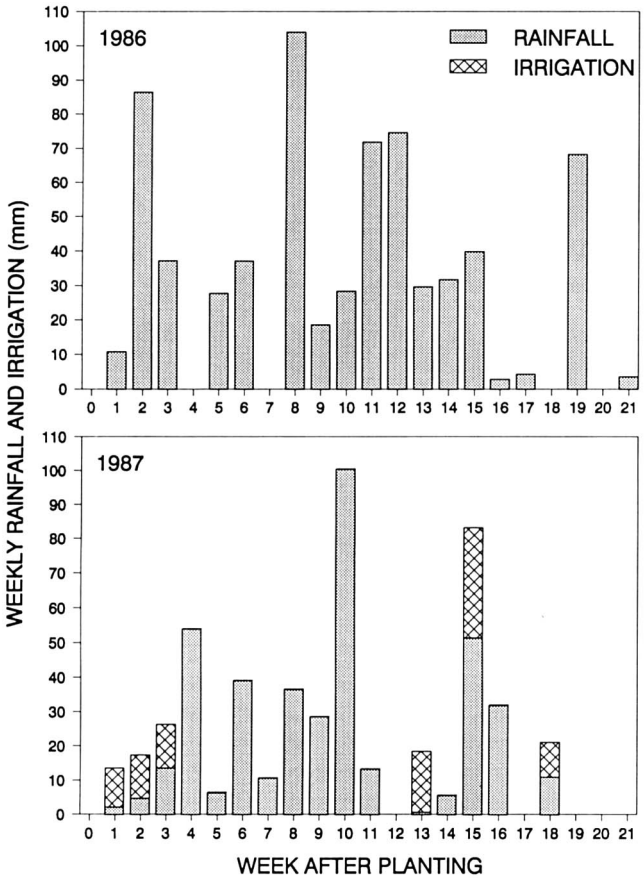

Fig. 1. Weekly rainfall and irrigation in field plots at Gainesville, Florida, during summers of 1986 and 1987.

Growth Analysis

Beginning three weeks after planting, one meter of row in each plot was systematically selected on a bi-weekly basis for measurements and analysis of growth. Percent light interception and absorption were determined using a line quantum sensor (LI-COR LI-191SA, Lincoln, Nebraska 68504). Reproductive and vegetative stages (4) were determined and the whole meter sample was harvested and the roots discarded. The soil in the harvested area was dug and sieved to find pods left in the soil due to the harvesting procedure or diseases that caused deterioration of the pegs. Pods abscised due to the handling of the plants could be easily distinguished from pods abscised due to diseases causing peg deterioration. With handling, the peg usually breaks at the attachment site of the pod or the plant stem. With disease, the peg generally breaks at sites other than these attachment sites, and rotting of the peg is evident. In the latter case, part of the peg is usually attached to the pod. Pods abscised due to handling were added to the whole biomass sample. An average representative plant was selected in each sample and separated into three plant components: 1) leaf blades, 2) pods, and 3) stems, pegs, petioles, and flowers. The area of the leaves was measured with a leaf area meter (LI-COR LI-3100). All samples were dried at 60°C until no changes in weight were observed, and the weight of dry matter was determined. Pods were subdivided into immature (shrunk after drying) and mature pods, and the number in each class was determined. Mature pods were shelled by hand to recover the seeds.Seed weight and number were also obtained.

Disease Assessment

Late leaf spot disease was assessed on each plant selected from the field sample. Defoliation was assessed by counting the number of missing leaflets on the main stem. This estimation was further corrected for defoliation due to natural senescence at the lower nodes of the main stem. The defoliation due to disease (d_t) was estimated with the following equation:

$$d_t = m_d / (f_t - \bar{m}_s) \qquad (m_d \geq 0)$$

where $m_d = m_t - \bar{m}_s$

The variables m_t, m_d, and f_t are the total number of missing leaflets, the number of missing leaflets due to disease, and the total possible number of leaflets on the main stem, respectively. The latter was estimated by counting the number of nodes on the main stem and multiplying by four leaflets per node. The node of the two cotyledonary branches is designated node "zero" because it is the site of seed leaves. The average number of missing leaflets in the fungicide-treated plots ($\bar{m}_s$) was used as the correction factor. In the fungicide-treated plots, defoliation was assumed to be caused by natural defoliation only.

Leaflets selected for the estimation of proportion of necrotic area were collected from the selected plant using a variation of the semicircular leaf layers approach (19). Twenty leaflets were randomly selected in each of the following semicircular areas: 1) 0 to 15 cm from the base of the plant, 2) 15 to 30 cm from the base, and 3) above 30 cm from the base. Necrotic leaf area was estimated by counting the number of lesions which were separated in the following classes: 1) lesion diameter of 1 mm and 2) lesion diameter of 4 mm (20), and by multiplying the number in each class by the corresponding circular area. The proportion of necrotic leaf area at the canopy level (n_t) was estimated with the following equation:

$$n_t = \frac{a_b n_b(1-d_b) + a_m n_m(1-d_m) + a_u n_u(1-d_u)}{(a_b + a_m + a_u) - (a_b d_b + a_m d_m + a_u d_u)} \qquad [0 \leq (d_b+d_m+d_u)<3]$$

where n_b, n_m, and n_u are the proportions of necrotic leaf area in the bottom, middle, and top canopy layers, respectively and d_b, d_m, and d_u, the proportions of defoliation due to disease in the corresponding canopy layers. The coefficients a_b, a_m, and a_u were used to weight the data from different canopy layers, and have values of 1, 3, and 5, respectively, and were determined from the respective semicircular areas described previously. Finally, the disease severity (s_v) which is a function of both disease-induced defoliation (d_t) and necrotic leaf area (n_t) was computed with the following equation (19):

$$s_v = n_t (1-d_t) + d_t$$

The first part of the equation evaluates the proportion of necrotic tissue on non-defoliated leaves, and the second part is the proportion defoliated. The disease severity was transformed with the linearized form of the

Gompertz function (3, 27):

$$-\ln(-\ln(y/y_{max})) = -\ln(B) + r_G t \qquad (0 < y < 1)$$

where: $B = -\ln(y_0)$

In this function, y is the disease severity, y_{max} the maximum disease severity, y_0 the disease severity when time (t) equals zero, and r_G the rate of disease progress. A y_{max} of 1 was assumed for the tranformations because complete defoliation ($d_t = s_v = 1$) occurred in both years. Transformed disease severity was regressed against, days after planting to estimate the intercept (-ln B) and the slope (r_G). Preliminary testings, which were based on the coefficient of determination and the analysis of the residuals, indicated that the Gompertz function was more appropriate than the logistic function to describe progress of late leaf spot of peanut.

Prediction of Pod Yield from HAD and HAA

The total pod yield (Y_t), defined as the sum of the yields of harvested pods (Y_H) and abscised pods, at 135 and 133 DAP in 1986 and 1987, respectively, were used to evaluate the prediction of pod yield (Yp) as a function of healthy leaf area duration (HAD) and healthy area absorption (HAA) given by Waggoner and Berger (28):

$$Y_{P(HAD)} = 735 \exp\{-3.15 \exp[-0.00821 (HAD - 93.71)]\}$$

$$Y_{P(HAA)} = -422.7 + (0.472\ HAA)$$

The following equations were used to compute HAD and HAA:

$$HAD = \Sigma \{[(1-n_{t(i)})L_i + (1-n_{t(i-1)})L_{i-1}] (t_i - t_{i-1})/2\}$$

$$HAA = \Sigma \{[I_i(1-n_{t(i)}) (1-\exp(-KL_i)) + I_{i-1}(1-n_{t(i-1)})(1-\exp(-KL_{i-1}))] (t_i - t_{i-1})/2\}$$

where $n_{t(i)}$, L_i, t_i, I_i are, respectively, the proportion of necrotic leaf area, the leaf area index, the time expressed in DAP, and the insolation (i.e. solar energy) that were obtained from sample i. The constant K is the coefficient for absorption of insolation and was estimated at 0.412 (28). The insolation was estimated at 73% of the insolation at the top of the atmosphere at 30° latitude (14) to obtain the variation from about 23 to 30 MJ m^{-2} d^{-1} that was reported by Waggoner and Berger (28).

Final Harvest and Peanut Quality

At the end of the growing season, two rows of 6.1 m were harvested in each plot. One row was harvested at approximately 125 DAP, and the other was harvested at approximately 140 DAP. Yields of pods, abscised pods, and seeds were obtained. A subsample of 500 g of pods was subjected to a standard analysis for peanut quality (9). Additional values obtained from this analysis were the shelling percentage, the number of seeds per pod, the average seed weight, the percentages of extra large kernels (ELK), and sound mature kernels (SMK).

Results and Discussion

Disease Progression

Late leaf spot was first observed at 51 DAP in 1986 and at 48 DAP in 1987, and was present in all non-treated plots at 70 DAP in 1986 and at 62 DAP in 1987. The experimental fields of 1986 and 1987 were last planted with peanut in 1976 and 1983, respectively. Since the planting date was the same in both years, possible reasons for earlier infection by the pathogen in 1987 are the proximity of the inoculum source and the amount of inoculum. In 1987, peanut was planted in the field adjacent to the experimental site of 1986. The percentage of necrotic leaf area never exceeded 10% for the whole canopy in either year (Fig. 2). Boote *et al.* (6) and Pixley (17), who both used the Horsfall-Barratt scale, reported necrotic percentages up to 30% and 20%, respectively, for the whole peanut canopy. Furthermore, a smooth increase in the percentage of necrotic leaf area was not observed as in previous work (17). This is consistent with the fact that defoliation of peanut leaflets occurred at low percentages of necrotic area and abscised leaflets are not included in the assessment of necrotic area. Therefore, abscission of diseased

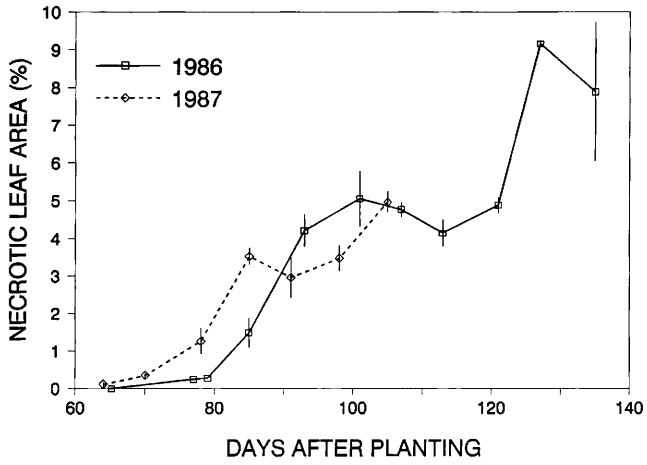

Fig. 2. Percentage of necrotic leaf area as a function of days after planting (DAP) in the non-treated plots. Observations in 1987 ceased earlier because the peanut canopy was completely defoliated at 112 DAP. Vertical lines are ± one standard error from the mean percentage of necrotic leaf area of four replications.

leaflets reduced the overall percentage of leaf area with lesions in the canopy.

Since leaf abscission was the major component of the effect of late leaf spot on peanut, disease severity, which included defoliation, was used as an indicator of disease progression in the field. As mentioned previously, late leaf spot occurred earlier in 1987 than in 1986 (Fig. 3). However, the rate of disease progress was similar in both years. With the Gompertz function, the disease severity (y) was estimated at 0.01 at 60 DAP in 1986, and at 48 DAP in 1987. The rate of disease progress (r_G) was slightly slower in 1987 (r_G=0.050 d^{-1}) than in 1986 (r_G=0.053 d^{-1}). The Gompertz function gave a coefficient of determination of 81% in 1986, and 82% in 1987.

Effect of Disease on Crop Traits

The effect of the disease was first observed on the leaves.

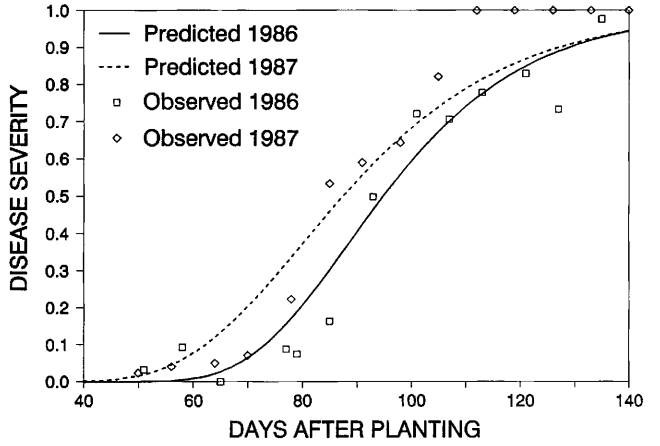

Fig. 3. Disease severity (necrotic leaf area plus defoliation) as a function of days after planting in non-treated plots. Parameters of the predicted lines were obtained from the linear regression of transformed disease severity against days after planting (1986: r_G=0.053, R^2=81%, s_{yx}=0.62; 1987: r_G=0.050, R^2=82%, s_{yx}=0.49). The disease severity was transformed with the linearized form of the Gompertz function: -ln (-ln y). Each point is the mean disease severity of four replications.

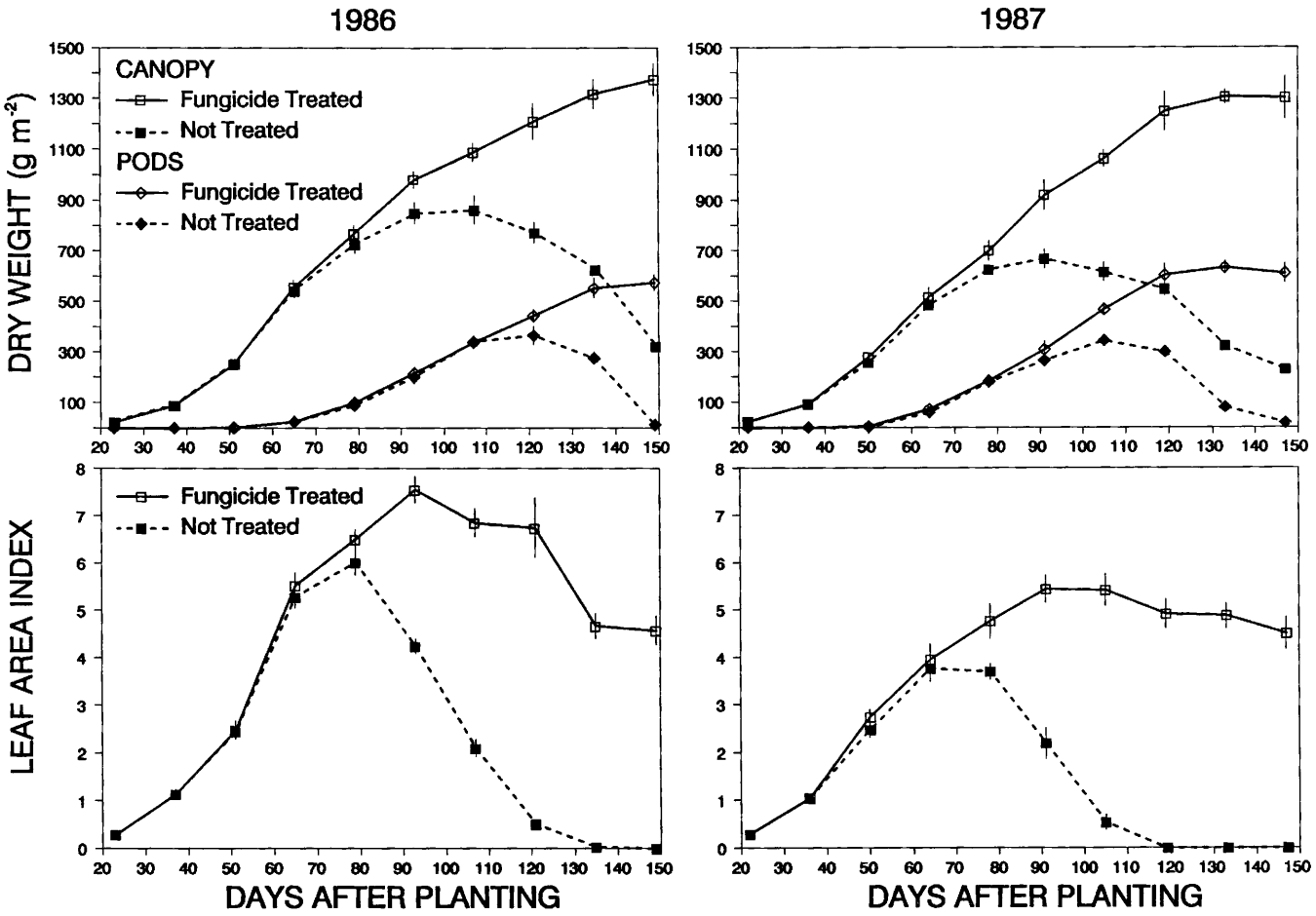

Fig. 4. Effect of late leaf spot on the dry weight of the total biomass, dry weight of the pods, and the leaf area index of Florunner peanut in 1986 and 1987. The two treatments were 1) fungicide treated and 2) not treated with fungicides. Vertical lines are ± one standard error from the mean dry weight and mean leaf area index of four replications.

The leaf dry weight, the leaf area index (LAI), and the dry weight of the total biomass were significantly higher in the fungicide-treated plots than in the non-treated plots at 93 DAP ($P \leq 0.01$) in 1986, and at 78 DAP ($P \leq 0.08$) in 1987 (Fig. 4, 5). Light interception at these dates was not significantly different ($P > 0.05$). In both years significant differences in light interception ($P \leq 0.01$) appeared two weeks after significant differences in LAI were observed. The light interception in the non-treated plots was reduced by approximately 10% and corresponded to a LAI of approximately 2 in the non-treated plots (7). The high values of light interception with such a low LAI may be due to the progressive defoliation of the peanut leaves from the bottom to the top of the canopy (2, 6). Since the top leaves of the canopy are usually the most efficient under high light intensities, it would be reasonable to assume that a large amount of carbohydrates are produced and translocated to the pods even when a diseased canopy has a LAI at or above 2. Up to this point, the significant effect on leaf dry weight, LAI, and dry weight of total biomass can be attributed primarily to leaflet abscission rather than reduced assimilation. The stem dry weight was higher in the fungicide-treated plots than in the non-treated plots at 121 DAP ($P \leq 0.13$) in 1986, and significantly higher at 91 DAP ($P \leq 0.05$) in 1987 (Fig. 5). This difference in stem dry weight is mainly due to a lack of dry matter gain after severe defoliation in the non-treated plots, and to losses in leaf petioles which were included in the stem fraction.

No significant differences ($P > 0.05$) between the two treatments were observed for the vegetative and reproductive stages, except at the end of the growing season for the reproductive stage. Pods in the non-treated plots reached physiological maturity (stage R8) earlier than the pods in the fungicide-treated plots. Furthermore, pods in the non-treated plots showed the characteristics of the R9 stage described by Boote (4) as the overmature stage. He reported that this occurrence resulted from poor late-season control of leaf spot, which caused a premature weakening of pegs and loss of pods for Florunner. Significant differences between fungicide-treated and non-treated plots for the number of pods and seeds, as well as their dry weights, first occurred at 135 DAP ($P \leq 0.01$) in 1986, and at 105 DAP ($P \leq 0.05$) in 1987 (Fig. 4). This difference of 30 days between 1986 and 1987 is probably due to earlier disease progress in 1987 (Fig. 3) and a higher LAI in the non-treated plot in 1986 (Fig. 4). The peanut canopy was almost completely defoliated ($LAI \leq 0.5$) in the non-treated plots at 121 DAP in 1986, and at 105 DAP in 1987 (Fig. 4).

Peg Deterioration and Pod Losses.

The necrotic area and the defoliation induced by late leaf

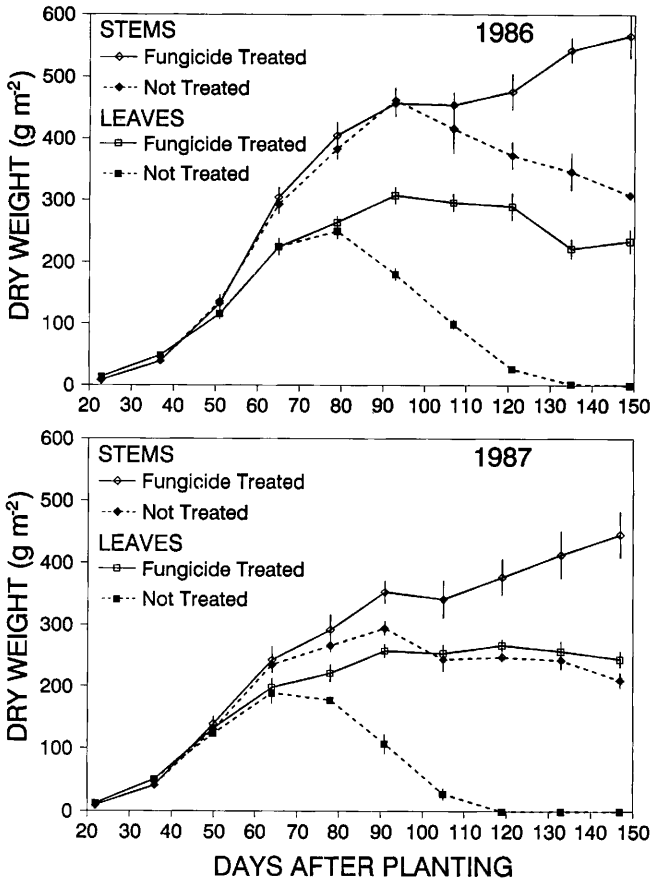

Fig. 5. Effect of late leaf spot on the dry weight of leaves and stems of Florunner peanut in 1986 and 1987. The two treatments were 1) fungicide treated and 2) not treated with fungicides. Vertical lines are ± one standard error from the mean dry weight of four replications.

spot reduced the potential yield of Florunner peanut by 37% (fungicide treated: 619 g m^{-2}; not treated: 387.6 g m^{-2}) in 1986 and 46% (fungicide treated: 640.6 g m^{-2}; not treated: 344 g m^{-2}) in 1987 (Table 1). The potential yield was defined as the highest mean pod yield observed in each treatment. However, much of this potential yield is lost with standard harvesting equipment because many of the pods remain in the soil when the peanut plants are harvested. These losses at harvest, commonly referred to as dropped pods, may be caused by the deterioration of the pegs. Some of this peg deterioration occurs naturally in fungicide-treated plots at the end of the growing season and seems to be related to natural aging. Peg deterioration is accelerated by high soil moisture and high soil temperature in the pegging zone (Boote, unpublished). Troeger *et al.* (23) observed a significant reduction in the peg attachment force with an increase in shelling percentage, an index of pod maturity. In non-treated plots, the peg deterioration was greatly accelerated soon after the peanut canopy was completely defoliated. Complete defoliation removes the source of photosynthates necessary to maintain the pegs, which then become more susceptible to infection by saprophytic microorganisms. Furthermore, defoliated leaves on the soil surface provide a good medium for microbial growth, which may contribute to peg deterioration, especially with high soil moisture and high soil temperature in the pegging zone.

Table 1. Yield of harvested and dropped pods for fungicide-treated and non-treated peanut treatments during summers of 1986 and 1987 in Gainesville, Florida.[a]

Days after Planting	Fungicide Treated			Not Treated		
	Harvested Pods	Dropped Pods	Total Pods	Harvested Pods	Dropped Pods	Total Pods
	g m^{-2}					
			1986			
65	24.7	0.0	24.7	23.5	0.0	23.5
79	99.0	0.0	99.0	89.4	0.0	89.4
93	216.2	0.0	216.2	201.5	0.0	201.5
107	338.1	0.0	338.1	341.2	0.0	341.2
121	444.0	1.0	445.0	366.1	5.6	371.7
135	552.7	15.9	568.6	276.6	111.0	387.6
149	573.9	45.1	619.0	13.6	240.2	253.8
			1987			
64	72.8	0.0	72.8	61.0	0.0	61.0
78	185.2	0.0	185.2	180.8	0.0	180.8
91	307.6	0.0	307.6	337.8	0.0	337.8
105	466.8	0.0	466.8	344.0	0.0	344.0
119	603.5	0.0	603.5	298.8	37.2	336.0
133	633.0	7.6	640.6	80.9	241.5	322.4
147	610.4	27.6	638.0	18.8	290.0	308.8

[a] Yield of pods was obtained from samples taken in a one meter section of the row (4 replications).

The Gompertz function was used to describe the time course of pod abscission for 1986 and 1987 in the non-treated plots. The abscission of pods was expressed as the fraction of abscised pod dry weight over the total pod dry weight (Table 1). A y_{max} of 1 was assumed. The coefficient of determination for the transformed values of pod abscission as a function of DAP was 86% in both years (Fig. 6). The abscission of pods progressed faster in 1986 (r_G=0.146 d^{-1}) than in 1987 (r_G=0.110 d^{-1}), and the percentage of abscised

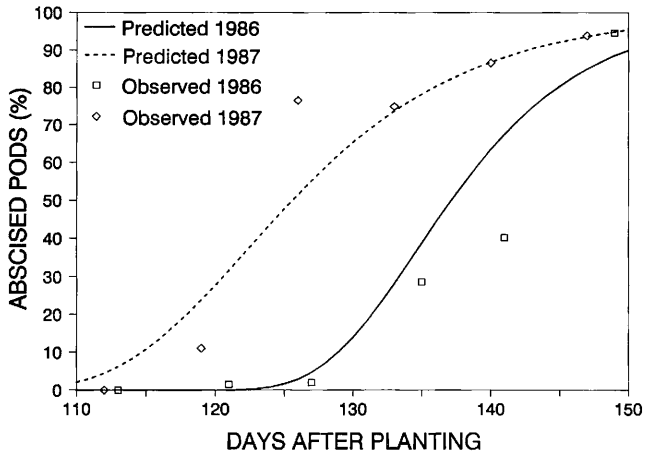

Fig. 6. Percentage of pods lost due to pod abscission for Florunner peanut in non-treated plots during the growing seasons of 1986 and 1987 in Gainesville, Florida. Parameters of the Gompertz lines were obtained from the linear regression of transformed abscised pods proportion against days after planting (1986: r_G=0.146, R^2=86%, s_{yx}=0.77; 1987: r_G=0.110, R^2=86%, s_{yx}=0.56). The proportion of abscised pods was transformed with the linearized form of the Gompertz function: -ln (-ln y). Each point is the mean abscised pods percentage of four replications.

pods reached 1% at 124 DAP in 1986 and at 107 DAP in 1987, when estimated with the Gompertz function. Similar trends in timing and rates were obtained with disease severity in the two years. Whether or not pod abscission was induced directly by late leaf spot or was a secondary consequence of the effects of late leaf spot was not determined.

Prediction of Pod Yield from HAD and HAA

The predictions of total pod yield (Y_T) and harvested pod yield (Y_H) with HAD ($Y_{P(HAD)}$) and HAA ($Y_{P(HAA)}$) were adequate in 1986 and 1987 for the fungicide-treated plots, except for $Y_{P(HAD)}$ in 1986. The LAI of 1986 was very high compared to other years (Table 2). However, a portion of this foliage does not contribute much due to shading. The inaccuracy introduced by this dense foliage is reduced by using HAA, which accounts for light interception. Under fungicide-treated conditions, pod losses are minimal, and the Y_T is almost equivalent to Y_H. When no fungicides are applied, complete defoliation occurs, and pod losses are very important. For the non-treated plots, the prediction of Y_H with HAD and HAA was overestimated in 1986 and 1987. However, the prediction of Y_T with HAD and HAA was adequate in 1986, but was underestimated in 1987 (Table 2). The concept of HAD and HAA is difficult to apply when pod losses occur after complete defoliation of the peanut canopy. HAD and HAA represent the photosynthetic potential of a canopy, and they both become constant after complete defoliation, while Y_H of peanut continues to decrease due to pod losses. Remaining relatively constant after complete defoliation of the canopy, Y_T is a better indicator of the cumulative photosynthetic potential of a peanut canopy that is defoliated by late leaf spot.

To further test the predictions with HAD and HAA, two other sets of data were used to evaluate $Y_{P(HAD)}$ and $Y_{P(HAA)}$: 1983 and 1985 (16, 18). In both 1983 and 1985, the prediction of Y_T and Y_H with HAD and HAA was adequate for fungicide-treated plots. In non-treated plots, the prediction of Y_H was overestimated in both years, and the prediction of Y_T was underestimated in both years (Table 2). However, the prediction of Y_T was close in 1985, but prior to 140 DAP, total pod yields of about 300 g m^{-2} were observed in these peanut fields. Such yields would cause a greater underestimation of Y_T in 1985. According to the results obtained in three out of four years, the concepts of HAD and HAA were not adequate to predict total pod yield of a peanut crop defoliated by late leaf spot and with necrotic lesions on the attached leaves.

Final Harvest and Peanut Quality

In the final harvests, pod and seed yields in the non-treated plots were significantly reduced ($P \leq 0.05$) at early (122-126 DAP) and late (136-140 DAP) harvests in both years (Table 3). Pod and seed numbers were also significantly reduced ($P \leq 0.01$) in all cases. In the non-treated plots, the shelling percentage was significantly higher ($P \leq 0.05$), the number of seeds per pod was significantly higher ($P \leq 0.05$), the average seed weight was significantly lower ($P \leq 0.05$). The lower shelling percentage obtained in treated plots is caused by continued adding of late, immature, and smaller pods which have smaller seeds and fewer seeds per pod. By contrast, this group of late and immature pods are not added on the diseased plants because of the shortage of assimilate. Bell (2) observed a significant reduction in kernel size at final harvest and no significant differences in shelling percentage

Table 2. Prediction of the pod yield with the healthy leaf area duration (HAD) and the healthy area absorption (HAA) (28) for peanut grown in 1983 (16,18), 1985 (16,18), 1986, and 1987.

	Fungicide Treated				Not Treated			
	1983	1985	1986	1987	1983	1985	1986	1987
	Field Observations[a]							
Days after Plant.	131	140	135	133	131	140	135	133
Maximum LAI	4.78	4.62	7.55	5.44	4.33	3.93	6.02	3.76
Total Yld (Y_T)	531.1	532.2	568.6	640.6	427.3	201.3	387.6	322.4
Harv. Yld (Y_H)	471.1	498.1	552.7	633.0	214.0	7.0	276.6	80.9
	Yield Prediction from HAD[b]							
HAD	367.1	382.6	551.7	428.6	237.0	183.4	304.3	190.8
$Y_{P(HAD)}$	526.3	547.8	683.0	600.8	278.2	162.6	420.2	177.8
Dev. from Y_T (%)	-0.9	+2.9	+20.1	-6.2	-34.9	-19.2	+8.4	-44.9
Dev. from Y_H (%)	+11.7	+10.0	+23.6	+5.1	+30.0	+2222.8	+51.9	+119.8
	Yield Prediction from HAA[c]							
HAA	2064.	1907.	2190.	2065.	1545.	1167.	1648.	1285.
$Y_{P(HAA)}$	551.3	477.5	611.2	552.0	306.7	128.1	355.4	184.0
Dev. from Y_T (%)	+3.8	-10.3	+7.5	-13.8	-28.2	-36.4	-8.3	-42.9
Dev. from Y_H (%)	+17.0	-4.1	+10.6	-12.8	+43.3	+1730.0	+28.5	+127.4

[a] Yields reported are pod yields in g m^{-2}. The total pod yield (Y_T) is the sum of the abscised pod yield and the harvested pod yield (Y_H). The maximum leaf area index (LAI) was assumed to be the highest LAI used in the calculations of HAA and HAD.

[b] $Y_{P(HAD)} = 735 \exp\{-3.15 \exp[-0.00821 (HAD - 93.71)]\}$. This equation was obtained from Waggoner and Berger (28). Deviations from Y_T and Y_H were calculated with the equations $(Y_{P(HAD)}-Y_T)/Y_T*100$ and $(Y_{P(HAD)}-Y_H)/Y_H*100$, respectively.

[c] $Y_{P(HAA)} = -422.7 + (0.472\ HAA)$. This equation was obtained from Waggoner and Berger (28). Deviations from Y_T and Y_H were calculated with the equations $(Y_{P(HAA)}-Y_T)/Y_T*100$ and $(Y_{P(HAA)}-Y_H)/Y_H*100$, respectively.

Table 3. Yield and quality analysis of the final harvests for fungicide-treated and non-treated Florunner peanut grown during summers of 1986 and 1987.

	Harvest 1[b]			Harvest 2		
Parameter[a]	Fungic. Treated	Not Treated	F	Fungic. Treated	Not Treated	F
	1986 (126 DAP[c])			1986 (140 DAP)		
Dropped Pod Yield	8	13	1.7	242	1353	31.7 *
Pod Yield	4981	3666	26.8 *	5249	2206	66.3 *
Seed Yield	3840	2990	22.3 *	4163	1832	52.6 *
Shelling Percent	77.1	81.5	64.3 **	79.3	83.0	49.7 **
Number of Pods	475	303	84.0 **	475	190	144.9 **
Number of Seeds	735	528	40.0 **	739	328	97.3 **
Seeds per Pod	1.55	1.74	18.1 *	1.56	1.72	13.5 *
Weight per Seed	607	574	13.7 *	610	597	0.4
ELK Percentage	32.6	31.5	0.1	42.0	38.0	0.6
SMK Percentage	71.3	77.5	63.2 **	74.6	79.1	45.0 **
	1987 (122 DAP)			1987 (136 DAP)		
Dropped Pod Yield	12	1406	157.6 **	27	2321	324.4 **
Pod Yield	5442	1674	225.0 **	5843	572	944.4 **
Seed Yield	4125	1319	230.7 **	4449	454	675.8 **
Shelling Percent	75.8	78.8	81.3 **	76.1	79.2	24.2 *
Number of Pods	485	144	678.7 **	501	60	975.0 **
Number of Seeds	752	249	509.6 **	778	97	1175.2 **
Seeds per Pod	1.55	1.73	61.1 **	1.56	1.62	4.1
Weight per Seed	652	563	266.1 **	655	529	22.7 *
ELK Percentage	43.0	25.2	32.5 **	39.8	22.9	23.0 *
SMK Percentage	68.7	73.4	32.9 **	69.4	70.9	0.8

[a] Yields are expressed in kg ha^{-1}, numbers are expressed in m^{-2}, and the weight per seed, expressed in mg, includes seeds from ELK (Extra Large Kernels) and SMK (Sound Mature Kernels).

[b] Significances at the 0.05 and 0.01 probability levels are denoted by * and **, respectively.

[c] DAP (Days After Planting)

due to the effect of foliar pathogens. The percentages of extra large kernels (ELK) were not significantly different for both harvests in 1986, but non-treated plots had a slightly lower ELK percentage. This same trend was observed in 1987, but the differences were significant ($P \leq 0.05$) between fungicide-treated and non-treated plots. This lower ELK percentage in the non-treated plots caused the lower weight per seed observed in the non-treated plots. The percentages of sound mature kernels (SMK) were significantly higher in the non-treated plots for all harvests in 1986, and for the first harvest in 1987.

Conclusions

Late leaf spot appears to have a significant effect on every part of the peanut plant. The fungus first attacks the leaves which subsequently defoliate at a very rapid rate. The loss of green photosynthetic leaf area causes significant reductions in production of carbohydrates available for stems and pods. Potential reproductive yield was reduced by 37% in 1986 and 46% in 1987. However, peg deterioration is also enhanced after complete defoliation. Further reproductive yield is lost if the crop is not harvested soon after complete defoliation. As discussed by Knauft *et al.* (1988), diseased peanut fields should be dug approximately two to three weeks earlier than the average 135 days after planting before important pod losses occur. Under high soil moisture and high temperature in the pegging zone, the peg deterioration seems to progress very rapidly.

To describe severity and peg deterioration for both 1986 and 1987, the Gompertz function was selected to fit the data for both years. The effect of environmental factors, such as relative humidity and air temperature, on the progress of late leaf spot disease needs to be investigated to forecast or predict initiation of disease and its rate of progress. Furthermore, the host plant plays an important role in disease progress. The presence of leaves is essential for the development of late leaf spot. The epidemic and resulting yield loss are a complex interaction between the disease, the crop, and the environment. With the use of simple disease-progress functions, the progression of a given disease can be described within a year, but this description may not be adequate to provide understanding of the complexity of a given pathosystem, and to predict disease progression in different years.

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Literature Cited

1. Backman, P. A., and M. A. Crawford. 1984. Relationship between yield loss and severity of early and late leafspot diseases of peanut. Phytopathology 74:1101-1103.
2. Bell, M. 1986. The effect of foliage pathogens on growth of peanuts (*Arachis hypogaea* L.) in tropical Northern Australia. Aust. J. Agric. Res. 37:31-42.
3. Berger, R. D. 1981. Comparison of the Gompertz and logistic equations to describe plant disease progress. Phytopathology 71:716-719.
4. Boote, K. J. 1982. Growth stages of peanut (*Arachis hypogaea* L.) Peanut Sci. 9:35-40.
5. Boote, K. J., J. W. Jones, J. W. Mishoe, and R. D. Berger. 1983. Coupling pest to crop growth simulators to predict yield reductions. Phytopathology 73:1581-1587.
6. Boote, K. J., J. W. Jones, G. H. Smerage, C. S. Barfield, and R. D. Berger. 1980. Photosynthesis of peanut canopies as affected by leafspot and artificial defoliation. Agron. J. 72:247-252.
7. Bourgeois, G. 1989. Interrelationships between late leafspot disease and Florunner peanut: a modeling approach. Ph.D. dissertation, Univ. of Florida, Gainesville. 219 pp.
8. Daub, M. E. 1982. Cercosporin, a photosensitizing toxin from *Cercospora* species. Phytopathology 72:370-374.
9. Davidson, J. I., Jr., T. B. Whitaker, and J. W. Dickens. 1982. Grading, cleaning, storage, shelling, and marketing of peanuts in the United States, pp. 571-623. *in* H. E. Pattee and C. T. Young (eds.), Peanut Science and Technology. Amer. Peanut Res. and Educ. Soc., Inc., Yoakum, TX.
10. Horsfall, J. G., and R. W. Barratt. 1945. Am improved grading system for measuring plant diseases. Pytopathology 35:655.
11. Ketring, D. L., and H. A. Melouk. 1982. Ethylene production and leaflet abscission of three peanut genotypes infected with *Cercospora arachidicola* Hori. Plant Physiol. 69:789-792.
12. Knauft, D. A., D. W. Gorbet, and A. J. Norden. 1988. Yield and market quality of seven peanut genotypes as affected by leafspot disease and harvest date. Peanut Sci. 15:9-13.
13. Knauft, D. A., A. J. Norden, and D. W. Gorbet 1986. The effect of three digging dates on oil quality, yield, and grade of five peanut genotypes grown without leafspot control. Peanut Sci. 13:82-86.
14. List, R. J. 1966. Meteorological Tables, 6th ed. Smithsonian Inst., Washington, DC.
15. Melouk, H. A. 1978. Determination of leaf necrosis caused by *Cercospora arachidicola* Hori in peanut as measured by loss in total chlorophyll. Peanut Sci. 5:17-18.
16. Pixley, K. V. 1985. Physiological and epidemiological characteristics of leafspot resistance in four genotypes. M. S. Thesis, Univ. of Florida, Gainesville. 138 pp.
17. Pixley, K. V., K. J. Boote, F. M. Shokes, and D. W. Gorbet. 1990. Disease progression and leaf area dynamics of four peanut genotypes differing in resistance to late leafspot. Crop Sci. 30:789-796.
18. Pixley, K. V., K. J. Boote, F. M. Shokes, and D. W. Gorbet. 1990. Growth and partitioning characteristics of four peanut genotypes differing in resistance to late leafspot. Crop Sci. 30:796-804.
19. Plaut, J. L., and R. D. Berger. 1980. Development of *Cercosporidium personatum* in three peanut canopy layers. Peanut Sci. 7:46-49.
20. Shokes, F. M., R. D. Berger, D. H. Smith, and J. M. Rasp. 1987. Reliability of disease assessment procedures: A case study with late leafspot of peanut. Oléagineux 42:245-251.
21. Shokes, F. M., D. W. Gorbet, and L. F. Jackson. 1983. Control of early and late leafspot on two peanut cultivars. Peanut Sci. 10:17-21.
22. Smith, D. H. 1984. Foliar diseases; early and late leaf spots, pp. 5-7. *in* D. M. Porter, D. H. Smith, and Rodríguez-Kábana (eds.), Compendium of Peanut Diseases. The American Phytopathological Society, St. Paul, MN.
23. Smith, D. H., and R. H. Littrell. 1980. Management of peanut foliar diseases with fungicides. Plant Dis. 64:356-361.
24. Teare, I. D., F. M. Shokes, D. W. Gorbet, and R. H. Littrell. 1984. Peanut growth responses to different levels of leafspot. Agron. J. 76:103-106.
25. Troeger, J. M., E. J. Williams, and J. L. Butler. 1976. Factors affecting peanut peg attachment force. Peanut Sci. 3:37-40.
26. Venkataramani, K. 1967. Isolation of cercosporin from *Cercospora personata*. Phytopathol. Z. 58:379-382.
27. Waggoner, P. E. 1986. Progress curves of foliar diseases: Their interpretation and use, pp. 3-37. *in*: K. J. Leonard and W. E. Fry (eds.), Plant Disease Epidemiology, Population Dynamics and Management, Volume 1. Macmillan Publishing Company, New-York.
28. Waggoner, P. E., and R. D. Berger. 1987. Defoliation, disease, and growth. Phytopathology 77:393-398.

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