EPIDEMIOLOGY OF POTATO EARLY BLIGHT IN COLORADO 1. INITIAL INFECTION, DISEASE DEVELOPMENT AND THE INFLUENCE OF ENVIRONMENTAL FACTORS[1]

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INTRODUCTION

Potato early blight, caused by *Alternaria solani* (Ellis and G. Martin) L. R. Jones and Grout, can be an important disease problem in the San Luis Valley of Colorado, particularly on the Russet Burbank variety. Improper timing of fungicidal applications has often resulted in unnecessary spraying or inadequate control of early blight in the San Luis Valley. For this reason, a field study was initiated in 1962 to attempt to determine the time and extent of primary infection and secondary development of inoculum; and the influence of environmental factors on the disease.

There is a general scarcity of published information on the epidemiology of potato early blight. Furthermore, epidemiological studies have never been reported in the arid areas of the Western United States. Rands (7) in 1917 reported a study in Wisconsin in which early blight was found to be most severe in years characterized by high moisture early in the season followed by high temperatures and sufficient moisture to promote abundant sporulation. He found that heavy dew lasting for approximately 12 hours on four consecutive nights was not sufficient to induce sporulation. Sporulation was, however, abundant following 0.9 inches of rainfall, from which he concluded that frequent rains associated with heavy dews provided the necessary moisture for sporulation in the field. Jones (3) in Vermont and Rolfs (8) in Florida had demonstrated earlier that early blight disease development in both potato and tomato was favored by warm, moist environmental conditions. Lutman (5) however, concluded from extensive studies prior to 1911 that early blight was most severe in drier seasons.

The spores of *Alternaria solani* are capable of surviving freezing temperatures on the soil surface or buried to depths of 2 to 8 inches (7). and may serve to produce primary infections in succeeding crops. The extent and severity of infections resulting from overwintered spores is obscure.

In laboratory studies (7) spore germination and mycelial growth of *A. solani* were shown to occur at temperatures between 1 C and 45 C with optimum temperatures of 26 C to 28 C.

Rowell (9) has demonstrated a temporary resistance to infection in young foliage of tomato and potato. Such resistance was further shown to retard fungus invasion and symptom development even though the foliage was infected. Age of plant and certain environmental factors were shown to influence this phenomenon to some extent. The majority of Rowell's experiments were performed in the laboratory and greenhouse, and the application of his findings to field conditions is not known.

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Wind is the principal means of dissemination of *A. solani* spores (6) and penetration may occur either directly through the leaf cuticle or through stomatal openings.

Materials and Methods

Field experiments were made during 1962, 1963 and 1964 at the San Luis Valley Branch Experiment Station near Center, Colorado, at an elevation of about 7600 ft. The studies were made in conjunction with tests to determine proper timing of fungicidal sprays for early blight control. The results of the spray timing tests will be reported in a separate paper.

In 1962 and 1963, Russet Burbank potatoes were planted during the second week of May (normal for the area) in a field where potatoes had been grown for at least two years prior to 1962. In 1964, Russet Burbank, Norland and Red McClure potatoes representing early, medium, and late maturing varieties were used in the test. The planting date was May 25 in the same field used in 1962 and 1963. The three potato varieties were located in the field so that prevailing winds blew from the late maturing varieties toward the early maturing varieties. This was done to reduce the possibility that earlier spore production on the early maturing varieties would influence the results in the later maturing varieties. The plots were sub-irrigated[3] in 1962 and row irrigated in 1963 and 1964.

A Bendix-Friez Model 594 Hygrothermograph was placed within a representative sub plot near the center and to the north side of the experimental field each year and was protected by a metal weather instrument shelter insulated with styrofoam sheets.[4] A Dew-Duration recorder manufactured by Hygrodynamics, Inc., Silver Spring, Md., was likewise placed in a representative plot each season except in 1963 when dew period data were not collected. Spores were trapped in 1962 using a spore trap developed by the authors and described elsewhere (4). This instrument measured the natural periodic sporeload of *Alternaria solani* during the growing season. Weather vane-type spore traps with vaseline coated glass microscope slides were used exclusively in 1963 and 1964. The slides were changed and spore counts were made three times a week. The height of the traps was adjusted periodically to keep the trapping surface approximately level with the tops of the plants. Three weather vane traps were used in 1963 and ten were used in 1964. Relative numbers of spores trapped were determined by examining ten or twenty low power microscopic fields per slide in 1963 and 1964 respectively. When the Periodic Spore Trap was used the vaseline from each one-inch segment of the bar surface representing a 6 hour trapping period was removed with a razor blade, placed on a microscopic slide, and examined as described elsewhere (4).

The incidence of initial leaf infections was determined by collecting random leaf samples from the top, middle and bottom portions of plants and isolating from them at 14 day intervals in 1962 and 1963 and at

[3]Water as applied in ditches separated by 70-80 ft. This raised the water table and wet the soil between the ditches.

[4]The metal instrument shelter was compared with comparable standard wood shelters. No difference was found in temperature or relative humidity readings between the two shelter types.

7 to 14 day intervals in 1964. Isolations were made from symptomless leaflets to determine the presence of *A. solani*. Leaflets for isolation were first washed thoroughly in running tap water then soaked 2 to 3 minutes in 0.1% mercuric chloride solution followed by a 1 minute soak in 1% sodium hypochlorite then rinsed in sterile water. The surface sterilized leaflets were then placed in sterile petri dishes and covered with potato dextrose agar cooled to approximately 45 C as described by Rowell (9) and incubated at 25 C to 30 C. Resulting fungus colonies were transferred to petri dishes containing 2% water agar as soon as they developed. These colonies were incubated for 7 to 10 days after which identifications were made by microscopic examination.

The plants in each plot were carefully examined at 7 to 14 day intervals to detect the appearance of initial symptoms. Disease readings were taken in the plots at regular intervals using the Horsfall-Barratt scale (2) to estimate the percentage of leaflets infected with one or more lesions. Top, middle and bottom leaves on randomly selected plants in each plot were examined and scored separately for early blight symptoms. The three readings were averaged to give an overall index of infection. Readings at each date were made by at least 2 individuals, and the independent readings were averaged to give a final score for each plot.

Results

Results of spore trappings, leaf isolations and disease readings are summarized in Tables 1 and 2 and Figs. 1, 2 and 3.

No *A. solani* spores were trapped until late July or early August in 1962 and 1963. The leaf isolation data in Tables 1 and 2, however, show that small numbers of infections occurred as early as June 28

TABLE 1.—*Summary of early blight disease readings and leaf isolations in the Russet Burbank variety — 1962 and 1963.*

1962 Sample date	Isolation from symptomless leaves[1]: Number of leaflets sampled	% Leaflets infected[2]	Visibly infected foliage: % Leaflets with Lesions[3]
June 28	144	4.2	0.0
July 13	144	3.5	Trace on lower leaves.
July 25	144	2.1	Trace on lower leaves.
Aug. 8	144	2.8	Lesions on many lower leaves. Trace on middle.
Aug. 21	144	25.7	1.4% of total leaf area infected. Severe Verticillium infection.
1963			Percent of leaflets with lesions
June 14	540	0.0	0.0
June 27	540	0.9	0.0
July 11	540	0.9	0.0
July 25	540	0.0	1.9
Aug. 10	540	6.7	2.7
Aug. 22	540	24.8	50.9

[1]No lesions visible to the unaided eye.
[2]Based on recovery of *A. solani*.
[3]Based on the Horsfall-Barratt rating system.

TABLE 2.—*Summary of early blight disease readings and leaf isolations in three potato varieties — 1964.*

Variety	Isolation from symptomless leaves[1] Date	No. leaflets sampled	% leaflets infected[2]	Visibly infected foliage Date	% leaflets with lesions[3]
Red McClure	June 29	225	1.8	June 29	0.0
	July 13	300	0.7	July 13	0.0
	Aug. 10	300	5.7	Aug. 11	7.5
				Aug. 18	13.0
				Aug. 25	21.0
Russet Burbank	June 29	801	0.9	June 29	0.0
	July 6	768	2.0	July 6	0.0
	July 13	300	1.0	July 13	0.0
	July 20	768	2.9	July 20	0.0
	July 27	300	4.3	July 29	1.4
	Aug. 3	768	13.2	—	—
	Aug. 10	300	8.0	Aug. 11	25.0
	Aug. 17	768	28.9	Aug. 18	25.0
	Aug. 21	768	37.4	Aug. 25	23.5
Norland	June 29	225	1.8	June 29	0.0
	July 13	300	1.7	July 13	0.0
	July 27	300	8.7	July 29	1.4
	Aug. 10	300	10.7	Aug. 11	46.0
				Aug. 18	52.0
				Aug. 25	59.5

[1]No lesions visible to the unaided eye.
[2]Based upon recovery of *A. solani.*
[3]Based on the Horsfall-Barratt rating system.

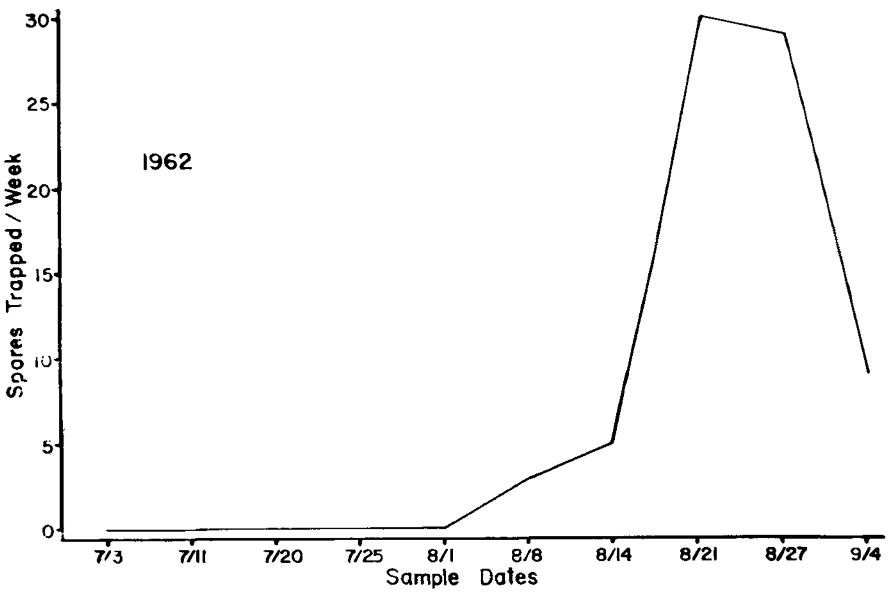

FIG. 1.—Results of spore trapping studies 1962 showing numbers of spores trapped at various periods during the growing season.

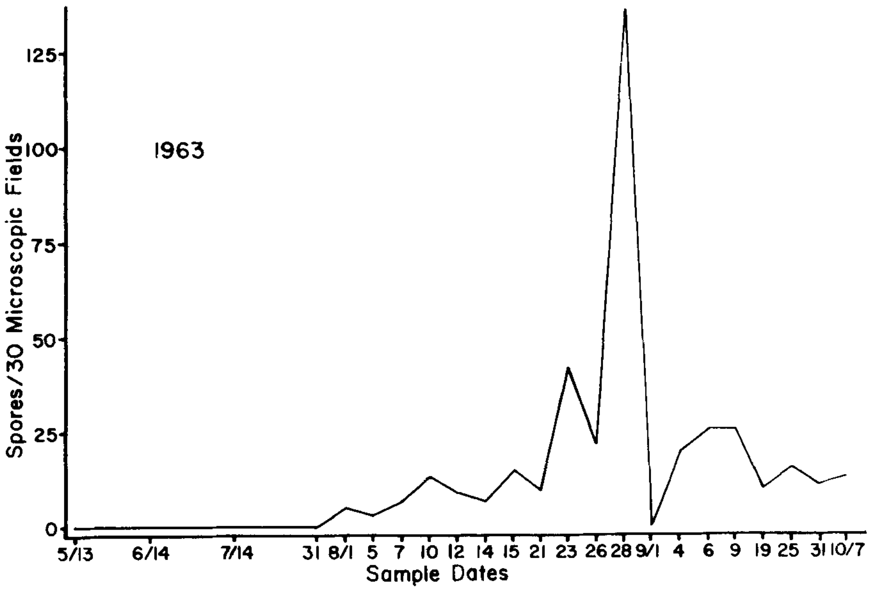

FIG. 2.—Results of spore trapping studies 1963 showing numbers of spores trapped at various periods during the growing season.

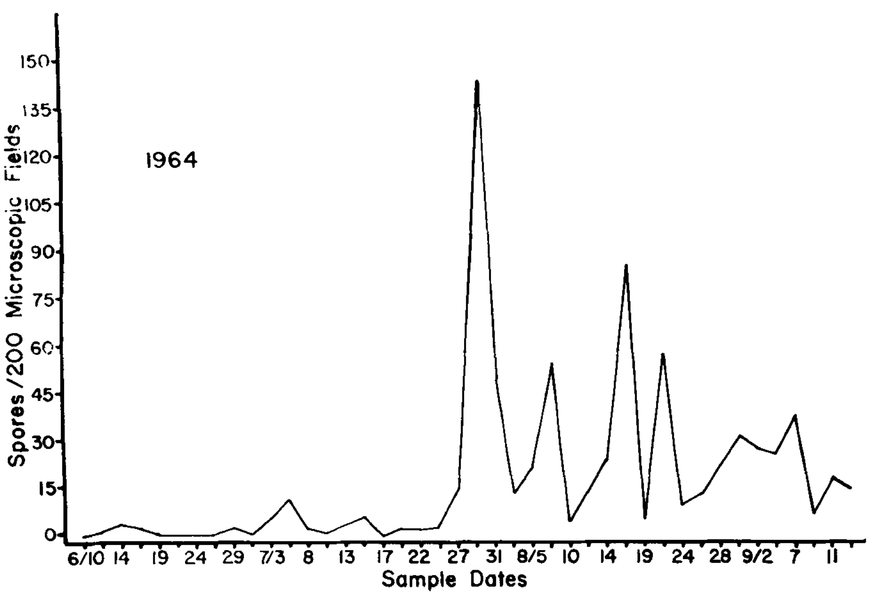

FIG. 3.—Results of spore trapping studies 1964 showing numbers of spores trapped at various periods during the growing season.

in all years and that it remained relatively constant until secondary spread began in 1962 but increased slowly but consistently in 1963 and 1964. The early season infections in 1964 were related ot the presence of small numbers of spores as detected by the spore traps. Early detection of spores in 1964 but not in 1962 and 1963 was probably due to the fact that ten spore traps were used in 1964 as compared to only three in 1963 and only one trap in 1962. Also, the traps were adjusted to a level slightly higher above the soil surface in 1964 thus reducing the amount of dirt collected that may have previously obscured some spores on the slides. Two hundred microscopic fields per sample date were examined in 1964 compared with only 30 in 1963. These factors all tended to increase the amount of air sampled and improve the probability of detecting small numbers of aid-borne spores present early in the season in 1964.

Figs. 1, 2 and 3 show that marked increases in spore numbers occurred each year in late July or early August regardless of planting date. Increased sporulation represented the beginning of secondary spread, and was closely related to the occurrence of the first early blight lesions in the plots (Tables 1 and 2). This was true in 1963 and 1964 but not in 1962 when secondary spread did not begin until about 2 weeks after the first lesions were observed (Table 2 and Fig. 1). Lesions invariably appeared first on the oldest lower leaves of the potato plants and then only after they became senescent due to natural maturity and/or Vericillium wilt infection. Symptoms of Verticillium wilt normally appeared about the same time secondary spread of early blight began in all 3 years. Wilt was more severe in 1962 than in 1963 or 1964 and greatly hindered early blight disease readings on the foliage. The percentage of leaflets which developed primary symptoms (lesions) was remarkably similar to the percentage of symptomless leaflets that yielded *A. solani* in isolation studies early in the season, particularly in 1963 and 1964 (Tables 1 and 2), indicating that the leaf isolations accurately measured the extent of primary infection.

Lesion development and percentage of symptomless infected leaflets following the occurrence increased sporulation activity (secondary spread) in late July or early August was closely related to the number of spores trapped. These results, common to all varieties in the study, indicate that the spore trap data were a good measure of fungus activity particularly after the beginning of secondary spread.

Indications of the relationship of plant maturity and variety to early blight development can also be seen in Table 2. Primary lesions appeared at the same time in all varieties and secondary spread as indicated by numbers of spores trapped and leaf isolations also began almost simultaneously in all varieties in the test. The early maturing Norland variety developed lesions more rapidly after secondary spread began than either the Red McClure or Russet Burbank varieties. The Russet Burbank variety also developed symptoms more rapidly than the Red McClure. The Red McClure variety has consistently shown a relatively low incidence of early blight infection in Colorado and may have some natural resistance or tolerance. The possibility of temporary resistance (9) associated with plant maturity should not be overlooked.

TABLE 3.—*The relationship between numbers of spores trapped and potato variety 1964.*

Period	Mean number of spores per 20 microscopic fields		
	Norland	Russet Burbank	Red McClure
June 9 - July 26[1]	0.3	0.3	0.4
July 26 - Sept. 14[2]	4.1	2.9	2.9

[1]Prior to beginning of secondary spread.
[2]Period of secondary spread.

TABLE 4.—*The relationship between time of day and relative numbers of A. Solani spores trapped — 1962.*

Time of day	Total spores trapped	Percent of total
3 a.m. - 9 a.m.	10	22.2
5 a.m. - 11 a.m.	13	16.9
9 a.m. - 3 p.m.	26	33.8
11 a.m. - 5 p.m.	10	13.0
3 p.m. - 9 p.m.	6	13.3
5 p.m. - 11 p.m.	6	7.8
11 p.m. - 5 a.m.	3	3.9
9 p.m. - 3 a.m.	3	3.9

Comparisons were made between the numbers of spores collected on spore traps located in Norland, Russet Burbank and Red McClure plots during comparable periods in 1964. The results presented in Table 3 show that the average number of *A. solani* spores trapped per 20 microscopic fields prior to the beginning of secondary spread (July 27 to 29) was essentially equal in all varieties. During the period from the beginning of secondary spread to the end of the season, however, greater numbers of spores were collected in Norland plots than in Burbank or Red McClure. This difference was generally related to the more rapid disease development and the resulting increase in the potential spore producing capabilities in the Norland variety.

Sporulation periods and the relationship of environment to sporulation

Data collected in 1962 through use of the Periodic Spore Trap described elsewhere (4) are presented in Table 4.

Sampling periods of 6 hours duration were varied during the season by starting the trapping period at 9:00 a.m. during one part of the season and at 11:00 a.m. during the remainder of the season.

The results shown in Table 4, even though they represent one year of sampling and relatively few total spores, indicate a strong tendency for most spores to be collected during the daylight hours. The most favorable time for spore dispersal appeared to be between the hours of 9:00 a.m. and 3:00 p.m. Spores trapped during this period represented 33.8% of the total spores collected. The periods 3:00 a.m. - 9:00 a.m. and 5:00 a.m. - 11:00 a.m. were also favorable for spore dissemination. These periods corresponded well with wind activity in the

San Luis Valley where winds generally rise shortly after sunrise, reach maximum velocities in the early afternoon, and generally diminish at sunset. This period also followed closely the dew periods which generally began about 9:00 p.m. and ended about 9:00 a.m. to 10:00 a.m. These results tend to substantiate Rands (7) data that spore production occurs during the moist period. The data also indicate that most spores are dispersed as the leaves dry and the winds increase in the morning and into the afternoon. Relatively few spores were trapped at night.

Air temperature, relative humidity and free moisture data collected during the 1962, 1963 and 1964 seasons are presented in Figs. 4, 5 and 6. Weekly means for 12-hour periods corresponding roughly to dew periods and non dew periods are presented and compared with numbers of *A. solani* spores collected on spore traps during corresponding periods.

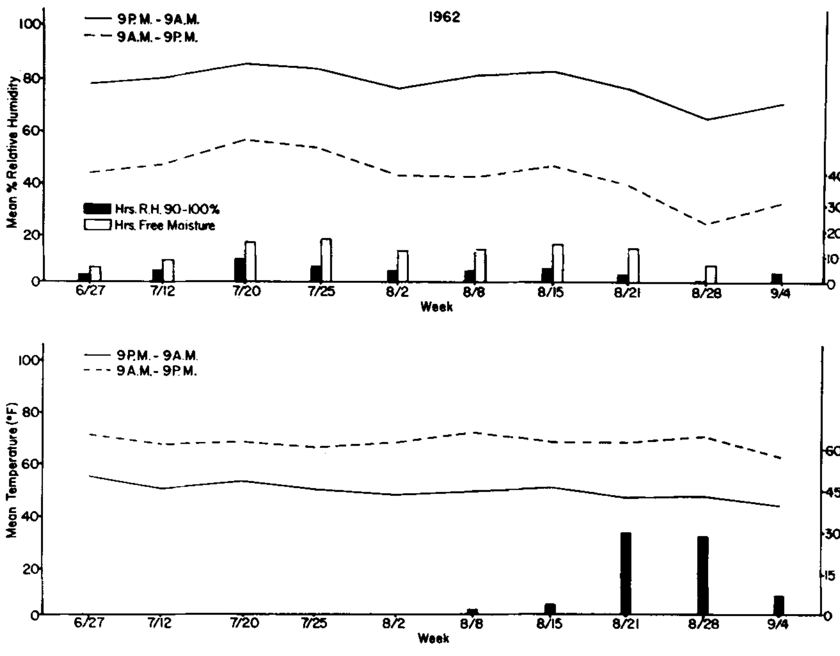

FIG. 4.—Temperature, relative humidity and free moisture data as related to total numbers of *A. solani* spores collected per weeks in 1962.

Large numbers of spores were trapped during periods in which the duration of free moisture ranged from 6.7 hrs. to 15.0 hrs. and in which the mean temperature during the dew period (Approx. 9:00 p.m. - 9:00 a.m.) ranged from 47.0 F to 58.3 F. There was a marked tendency for spore numbers to decrease drastically as relative humidities decreased and dew-periods became shorter.. This is particularly evident when the data from July 27 through September 9 are examined in Fig. 6.

During the period from the beginning of secondary spread to the end of the growing season (late July to early September) an average of 0.91 *A. solani* spores per microscopic field were detected on spore trap

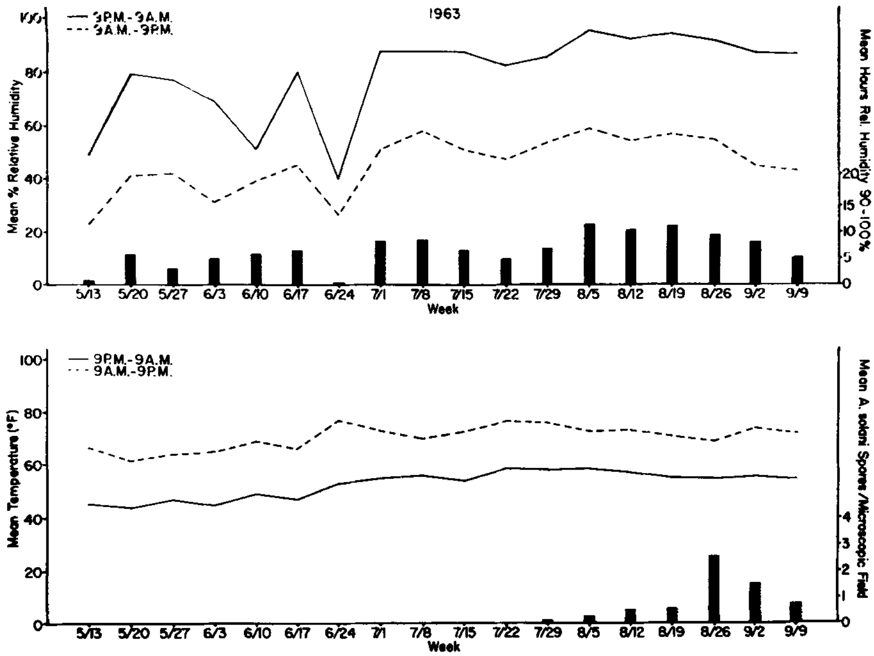

FIG. 5.—Temperature and relative humidity data as related to numbers of *A. solani* spores trapped in 1963.

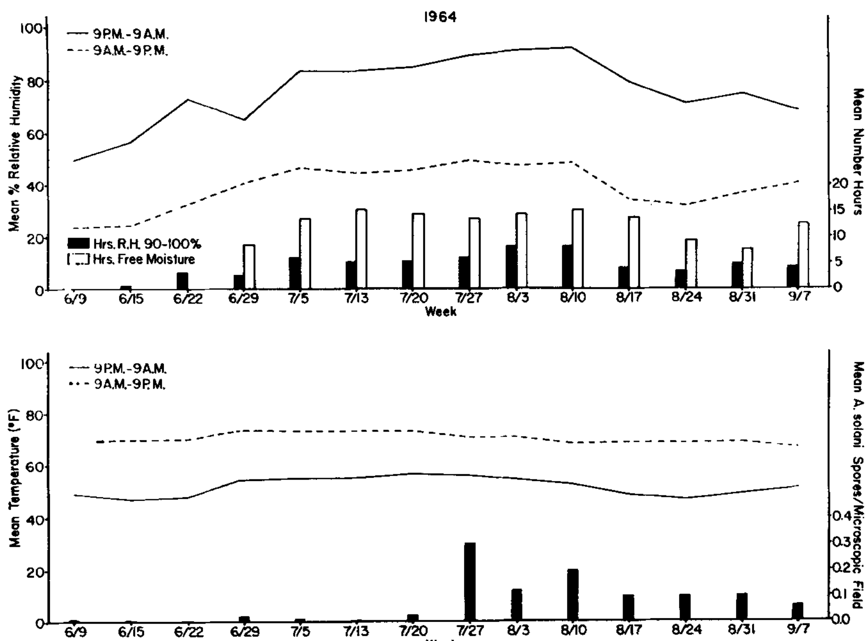

FIG. 6.—Temperature, relative humidity and free moisture data as related to numbers of *A. solani* spores trapped in 1964.

slides in 1963 compared with an average of only 0.16 spores per field in 1964. In 1963 the mean dew period temperature was 56.1 F compared with 51.2 F during a comparable period in 1964. The mean relative humidity during the dew period was 90.6% in 1963 and 81.3% in 1964. The corresponding durations of dew periods were 9.1 hours and 5.7 hours respectively. These results agree closely with those of other workers (3, 7, 8) who have found the disease to be favored by warmer more moist conditions.

Regardless of the fact that fewer spores were collected in 1964, disease severity (see Tables 2 and 3) was as great in 1964 as in 1963; apparently sufficient sporulation and infection occurred even under the cooler, drier season of 1964 to result in relatively heavy infections.

Relatively light late developing infection was observed in 1962 compared to the 1963 and 1964 seasons. This appeared to be related to the lower temperatures and relative humidities recorded in 1962. Mean temperatures were 3 to 6 F lower in 1962 than in 1963 or 1964.

Large numbers of *A. solani* spores were trapped during periods when the mean hours of free moisture per day ranged from 9 to 15 hours (Fig. 6). These results are somewhat different from those of Rands (7) who showed that up to 0.9 inches of rain in addition to approximately 12 hours of dew were necessary for spore production by *A. solani* in Wisconsin.

Discussion

The results of these studies clearly demonstrate that initial infection of potato plants by *Alternaria solani* in the San Luis Valley of Colorado occurs very early in the season. This infection apparently results from overwintered spores or from new spores possibly produced on plant debris in or on the soil as suggested by Rands (7). The degree of infection resulting from primary spread was small in these studies yet, the importance of the primary infections cannot be minimized, in that the few lesions resulting from such infections are probably the basic source of secondary sporulation responsible for heavy infections observed late in the season.

Whether high moisture early in the season would increase the numbers of spores present and also increase the efficiency of this inoculum to the point where control of primary infections would become important is unknown. The answer to this problem may depend on whether primary infection is the result of wind blown spores produced the previous season or whether infected plant debris from a previous infected crop is capable of producing crops of new spores under proper conditions. The data presented here fail to answer this question.

The data presented in Tables 1 and 2 show that even though leaflet infection occurred early in the growing season symptom expression was delayed at least one month in 1963 and 1964. This suggests that the phenomenon of temporary resistance and/or tolerance (between initial infection and the appearance of first lesions) characteristic of young foliage described by Rowell (9) is operating under field conditions. Also, the first lesions noted invariably developed on senescent lower leaves even though leaf isolations showed that middle and top leaves were as frequently infected early in the season as the bottom ones. Symptom development following the beginning of secondary spread when plants were reaching senescence was not retarded to the degree that primary infections were (see Table 2).

The data in Table 4 showing heavier spore production on the early maturing Norland variety following the beginning of secondary spread in 1963 demonstrate the relationship of plant maturity to disease development, and points out the possible role of early maturing varieties as sources of inoculum for later maturing varieties in areas where early and late varieties are planted in close association. This is a common practice in Colorado. This relationship has been observed repeatedly under field conditions.

It was postulated that initial symptom development and secondary sporulation would also occur earlier in the early maturing Norland variety if senesence were the most important factor in determining when first lesions appeared. Such *was not* the case; initial lesions did not occur appreciably earlier in the Norland variety than in Russet Burbank or Red McClure nor did secondary spread begin earlier based on spore trap data. It is also of great interest to note that first lesion development and secondary spore production occurred on almost the same date in the three consecutive years this study was conducted in spite of the fact that the planting date in 1964 was a least two-three weeks later than in previous years. Other factors such as temperature, moisture, light intensity and day length, may play important roles in breaking temporary plant resistance and allowing initial lesions to develop thus either hastening or delaying the onset of secondary spread of early blight. Rowell (9) has shown that some of these factors are involved. If this is true, early primary lesion development and associated early secondary blight spread could conceivably occur in certain areas. This appears to be the case in western Idaho[5] where, primary lesion development and secondary spread begin earlier and result in serious losses and high costs of control.

Temperatures and relative humidities during the dew periods as related to spore production indicate that spores are produced over a relatively wide range of conditions. Mean temperatures during the study periods were considerably below the 26-28 C optimum temperature for spore production reported by Rands (7) but results were consistent with his observation that spores are produced to some extent over a wide temperature range. When temperature and relative humidity data for 1963 and 1964 (Figs. 5 and 6) are compared and related to sporulation data it is evident that the higher temperatures and more moist conditions of 1963 were conducive to greater spore production.

The report of Rands (7) that rainfall in addition to extended periods of heavy dew was required for spore production by *A. solani* were not borne out by this study. Rainfall during the growing season under Colorado conditions is rare. Even though unusual afternoon showers occurred frequently in 1964 the number of spores trapped and the degree of plant infection was not increased over 1963. An early frost in August 1964

[5]Personal communication from Mr. R. E. Thornton, Extension Agricultural Agent, University of Idaho, Caldwell, Idaho.

undoubtedly eliminated some late season blight development. Examinations of data for comparable periods in 1963 and 1964, however, indicate that there was actually more disease development in 1963 than in 1964.

It should be pointed out that the meteorological measurements reported in this paper do not reflect the microclimatic conditions existing in a potato field particularly after a dense foliar canopy has formed over the soil. Hirst (1) has pointed out that temperaures and relative humidities are markedly changed when this occurs and that this change is closely related to initial outbreaks of potato late blight. This may also be an important factor in the development of early blight in Colorado.

In light of Hirst's findings and the results of our studies in Colorado, it seems particularly important that the microclimatic conditions existing within potato fields in the western United States where vine growth is often very heavy be investigated with regard to their influences on the epidemiology of potato early blight.

Summary

The dissemination of primary inoculum of *Alternaria solani* and the infection of potato plants in the field was shown to occur early in the season under Colorado conditions. Secondary spore dispersal was easily detected by spore traps. The use of such measurements may serve as a basis for timing initial spray applications.

Temporary resistance of young potato foliage and the relationship of plant senescence and other factors to primary symptom development and secondary spread of *A. solani* under field conditions were explored. These phenomena are important factors in the epidemiology of the disease in certain areas and may have direct bearings on control practices.

Early primary symptom development and secondary spread was initiated simultaneously in early, medium and late-maturing potato varieties; symptom development was, however, more rapid and more spores were produced following the beginning of secondary spread in the early maturing varieties than in the later maturing ones. Early varieties planted near later varieties may contribute inoculum to the latter and increase plant infection.

Low temperatures and relatively dry conditions in Colorado appeared to influence the extent of losses due to early blight. More spores per unit area were trapped in 1963 than in 1964. This was closely related to lower temperatures and relative humidities which prevailed in 1964.

SUMARIO EN ESPAÑOL

La diseminación del inóculum primario de *Alternaria solani* y la infección de la planta de patata se demostró que ocurre al principio de temporada bajo las condiciones de clima de Colorado. La difusión secundaria de esporos fué fácilmente determinada con el uso de la trampa de capturar esporos.

La resistencia temporal de la hoja de la planta joven y la relación de la evolución de la planta y otros factores relacionados con el desarrollo de los sintomas primarios y difusión secundaria del *A. solani* fueron explorados bajo las condiciones del campo. Estos fenómenos son factores importantes en la epidemiología de la enfermedad en ciertas zonas y tienen infiuencia directa en las prácticas de control. El uso de tales medidas

puede servir de base para la elección del debido tiempo del tratamiento inicial.

El desarrollo de los síntomas primarios y difusión secundaria fué iniciado simultáneamente en variedades de patatas temprana, media y tardía; el sesarrollo de síntomas fué mas rápido y se produjeron mas esporos seguido de la iniciación de la difusión secundaria en las variadades de patata temprana que en las variedades tardías. Variedades tempranas sembradas junto a variedades mas tardias pueden contribuir a la contaminación e incremento de la infección de las plantas.

Temperaturas bajas y condiciones atmosféricas relativamente secas parecen influenciar la extensión de las pérdidas debidas al tizón temprano en Colorado. En 1963 se atraparon mas esporos por unidad de zona que en 1964. Esto se consideró relacionado con las temperaturas mas bajas y humedades relativas existentes en 1964.

Acknowledgments

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