Factors Affecting the Development of Head Smut Caused by *Sphacelotheca reiliana* on Corn

Carl A. Matyac and Thor Kommedahl

Department of Plant Pathology, University of Minnesota, St. Paul 55108.

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ABSTRACT

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Silty and sandy loam soils containing spores of *Sphacelotheca reiliana* were allowed to dry to matric potentials of −0.1, −0.5, or −1.5 bar before resaturation and were held at 25, 20, 15 or 10 C in flats. A greater percentage of corn seedlings were diseased at high soil temperatures and low matric potentials than at low temperatures and high matric potentials. Teliospores on agar, adjusted with NaCl to decrease the osmotic potential, germinated at rates of 22% at solute potentials of −22 bars and 78% at solute potentials close to zero. Field plots that received irrigation water had 22% smutted plants which was significantly less than that in the dry soil plots which had 30% diseased plants. In microplots, clay loam soils maintained higher matric potentials than silty or sandy loam soils and had 10% fewer smutted plants. Applications of urea, ammonium sulfate, and triple superphosphate significantly reduced the frequency of disease in field plots, whereas the addition of calcium nitrate caused slight but nonsignificant increases. There was no difference in the frequency of smutted plants when seed was planted at depths of 2.5 or 8.0 cm.

Head smut is a systemic disease caused in corn (*Zea mays* L.) by *Sphacelotheca reiliana* (Kühn) Clint. [*Sporisorium reiliana* Kühn Langdon and Fullerton]. Seedlings are infected by soilborne teliospores during or after emergence. Soil moisture and temperature, soil fertility, depth of planting, and soil type can affect disease development; however, there are contradictory reports concerning the influence of these factors on head smut.

Several reports have addressed the effects of soil moisture and temperature on head smut development (3,7,9,14,21). The greatest amount of infection occurred with soil temperatures of 23–30 C, which corresponds with the optimum temperature for germination of spores on agar (20). More diseased plants occurred in dry than in wet soils. In these studies, however, soil moisture was reported as percentage moisture on a dry weight basis, percentage water holding capacity, percentage field capacity, or as a relative amount of irrigation water applied. These units can only be used to compare treatments on one particular soil type and thus prevent valid comparisons between different investigations. Futhermore, most of these studies assume that it is possible to hold a soil at a given moisture content for extended periods of time by partially rewetting soil as it dries. The direct influence of water potential on germination of teliospores has not been investigated.

Fertility levels have been reported to increase, decrease, or have no effect on the frequency and development of head smut. Head smut incidence decreased when ammonium nitrate, superphosphate, potassium chloride, or calcium nitrate was applied (19); smut incidence increased with the application of ammonium sulfate, ammonium nitrate, superphosphate, and potassium chloride (3,8). Authors of one of the above studies also reported that ammonium sulfate in agar stimulated the germination of teliospores (8).

Factors such as soil type and depth of planting may affect disease incidence. Reports indicate that some soil types reduce smut incidence (9); yet disease has occurred in a variety of soils from sandy loam to muck soils (16,23). Finally, Mack et al (17) reported that fewer diseased plants resulted from shallow than deep planting.

The purpose of this study was to determine the effects of soil water potential and temperature, soil type, fertility and depth of planting on the incidence of head smut in corn.

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MATERIALS AND METHODS

Soil water potential, temperature, and soil type interactions. Head smut sori were collected from a corn field on the Staples Area Vocational Technical Institute (AVTI) farm at Staples, MN, and stored in an unheated building through the winter. Teliospores were removed from sori, passed through a No. 16, 1.8-mm soil sieve, and mixed with screened field soil at a ratio of 1:1000 (v/v). This was equivalent to 0.35 g of spores per liter of soil and 3.0×10^5 spores per gram soil. The soils used in this experiment were a Waukegan silt loam typic haplydolls collected from the Minnesota Agricultural Experiment Station (MAES) at St. Paul and a vernale sandy loam udic agriboroll soil collected from the AVTI farm, at Staples, MN. Some of the physical and chemical characteristics of these soils are listed in Table 1. Soils were stored in bins and screened before use. Seeds of a susceptible corn hybrid, P 3978 (Pioneer Hi-Bred International, Inc., Des Moines, IA), were planted with the coleorhizal end down in four rows per flat, 15 seeds per row at a depth of 5 cm in 50 x 35 x 9-cm galvanized steel flats. This same genotype was used in all the experiments reported in this paper. Tensiometers, (Irrometer Moisture Meters; Irrometer Co., Riverside, CA) or soil psychrometers (Wescor, Inc., Logan, UT) and gypsum blocks calibrated with a soil psychrometer were installed. A split-split plot design was used with temperature being the main plot treatment, water potential being the subplot treatment, and soil type being the sub-subplot treatment. Flats were placed in greenhouses set at 10, 15, 20, or 25 ± 2.5 C. Hygrothermographs were used to monitor air temperature, and mercury thermometers were placed in soil and read daily. Supplemental light was provided by 2.4 x 0.8-m banks of fluorescent lamps on an 18 hr/day schedule. Soil was saturated at the time of planting and allowed to dry to −0.1 and −0.5 bars as measured by tensiometers, or approximately −1.5 bars as measured by an HR-33T Dew Point Microvoltmeter (Wescor Inc., Logan, UT) when isothermal conditions existed or a KS1 Moisture Meter (Delmhorst Instrument Co., Boonton, NJ) when nonisothermal conditions existed, before being resaturated. Seedlings were grown under these conditions until the fourth or fifth leaf emerged at which time disease frequencies were determined by using the chlorotic fleck as an indicator of infection (10,18). The experiment was conducted four times. Data were analyzed using a Statistical

Analysis System Program for split-split plot designs (11) on an IBM 4341 computer.

Effects of osmotic potential on teliospore germination. The osmotic potential of water agar was adjusted by using solutions of sodium chloride as suggested by Lang (15). After autoclaving the agar, sterile distilled water was added to compensate for any losses in volume during autoclaving. Ten milliliters of the adjusted agar was poured into each petri plate. The total water potential of the agar was then verified with thermocouple psychrometry. Teliospores were dusted on the agar surface, and the plates were sealed with Parafilm® and incubated at 25 C for 5 days. After incubation, agar plugs were removed, placed on glass slides, and stained with dilute acid fuchsin in lactophenol; 100 spores were counted and the percent germination was determined.

Soil moisture in the field. Field plots were established on the AVTI farm at Staples in a randomized complete block design. Treatments consisted of low and high soil matric potentials and controls. Tensiometers were installed 75-mm deep in each plot and read at midday three times per week for 5 wk after planting. Plots assigned the low moisture treatment were tilled before planting to enhance drying and were covered with black plastic during rain before emergence. Mercury and YSI model 42SC Telethermometers (Yellow Springs Instrument Co., Inc., Yellow Springs, OH) were used to monitor maximum soil temperature when tarps were over the plots. The average soil matric potential in these plots was −0.30 bar (range, −0.13 to −0.35 bars). High-moisture plots were irrigated after planting and averaged −0.1 bar (range, 0 to −0.20 bars). Soil moisture in control plots was not modified before planting or during seedling development and averaged −0.15 bar (range, 0.0 to −0.24). About 120 cc of a 1:200 (v/v) spore to soil mixture was placed over each kernel after it was placed in a jab planter (24). Border rows were planted mechanically. Plots consisted of eight rows 6 m in length with 76 cm between rows and 3 m of border on all sides. Plant height of twenty randomly chosen seedlings from each treatment were assessed at the four-leaf stage to determine the effects of various treatments on seedling growth.

Soil type in microplots. A Webster clay loam typic haplaquolls collected from Waseca, MN (Table 1), in addition to the two soils mentioned earlier, were used in this experiment. Soils were stored, screened, and mixed with teliospores as described above. Microplots consisted of 3.75 × 1.5 × 0.15-m greenhouse benches, placed adjacent to greenhouses on the St. Paul farm. Benches were divided into 1.25-m sections; each section was filled with a different soil type, and six rows with nine seeds per row were planted in each section. A randomized complete block design was followed with each block being one of three planting dates and each soil type being a treatment. Tensiometers and mercury thermometers were installed at the time of planting and read daily. Rain was the only moisture these plots received. Plants were allowed to develop to the four- to five-leaf stage and then transplanted to field plots at the AVTI farm and allowed to mature.

Fertility. Field plots were established on the AVTI farm in 1982 and 1983 with one planting date per year. A randomized complete block design was used for each of three experiments with each planting date being a block and three replicates of each treatment were included in each block. Each plot consisted of five 3.8-m-long rows, with 0.76 m between rows. Two border rows on the sides of each plot were planted mechanically. Corn seed was hand planted and inoculated by using methods described earlier (24). For trials evaluating the effects of individual elements, rows were sidedressed with the total amount of fertilizers immediately after planting. For the trials evaluating the effects of various combinations of elements, rows were sidedressed with the total application of phosphorus and potassium after planting and the nitrogen application was split at dosages of one-sixth after planting, one-sixth at the eight-leaf stage, one-half at the 12- to 16-leaf stage, and one-sixth at tasseling. Maximum rates and split application of nitrogen were based on recommendations made by the Department of Soil Science at the University of Minnesota, St. Paul (22).

Depth of planting. Teliospores were mixed with greenhouse soil mix at a ratio of 1:1,000 (v/v) as described above. Greenhouse soil mix consisted of 7 parts of silt loam, 3 parts of sand, 2 parts of manure, and 1 part of peat. Seeds were planted 2.5 or 8 cm deep in four rows per flat, 15 seeds per row in galvanized steel flats. A randomized complete block design was followed with each block being one of three planting dates.

Plots were established in a field with naturally occurring inoculum at the AVTI farm, and the depth of a mechanical planter was adjusted to approximately 2.5 or 8 cm. A completely randomized design was followed with four replicates per treatment. Each plot consisted of one row approximately 91.5 m long.

RESULTS

Effects of soil water potential, temperature, and soil type on disease incidence. Soil water potential, temperature, and the water potential × temperature interaction had significant effects on disease development. The response surfaces generated by plotting these variables versus disease development are illustrated in Fig. 1. Corn plantings in dry soils and at high temperatures consistently had a higher incidence of smut than those in wet soils and at low temperatures. However, data from plots with either of these soil conditions generated similar response surfaces and analysis of variance indicated that this variable did not have a significant effect on disease incidence. Temperature had a greater effect on disease incidence than did soil moisture as indicated by the low disease frequencies at 10 C at all soil moisture levels. Conversely, disease incidence at each moisture level was greatest at 25 C. The F values from the analyses of variance were 180.6 (3 df), 49.4 (2 df), and 13.2 (6 df) for soil temperature, soil moisture, and the temperature × water potential interaction, respectively, which indicated that temperature had a greater influence on disease incidence than did either soil moisture or the indicated interaction.

Effect of osmotic potential on teliospore germination. The highest level of germination (78%) occurred on agar unamended with salt and that had a water potential close to zero (Fig. 2), and the lowest germination (20%) occurred at the lowest osmotic potential (−22.8 bar).

TABLE 1. Characteristics of three Minnesota soils and incidence of head smut of corn in microplots

Soil	Moisture at three points on a desorption curve (%)[w]			pH[x]	Cation exchange capacity (meq/100 g)	Organic matter (%)	Disease incidence in microplots[y] (%)
	−0.1 bar	−0.3 bar	−15 bar				
Staples sandy loam	17.7	10.5	4.9	5.4	8.67	1.3	39.8 a
Waukegan silt loam	35.0	30.0	12.7	6.2	21.1	3.8	39.7 a
Webster[z] clay loam	32.4	28.9	20.4	6.2	33.8	1.9	28.4 b

[w] Desorption curves were run on the sandy loam and the silt loam using a 15-bar ceramic plate extractor.

[x] Analysis for pH, cation exchange capacity, and organic matter on the sandy loam and silt loam was performed by the University of Minnesota, Department of Soil Science, Research Analytical Lab.

[y] Mean of three planting dates with 54 plants per date. Mean disease frequency followed by the same letter were not significantly different according to Duncan's multiple range test at $P = 0.05$.

[z] All data on the clay loam soil was obtained from Arneman et al (2).

Effects of soil moisture in the field. Irrigated field plots had 22% diseased plants while controls and plots with low soil moisture had 28 and 30% diseased plants, respectively. Neither treatment was significantly different from the control, but means for the wet treatment were significantly different from those for the dry treatment according to Duncan's multiple range test, $P = 0.05$. Average soil temperatures for high and low water potential treatments and controls were 18.0 (range, 14.3–21.5), 19.4 (range, 16.0–23.0), and 19.6 C (range, 16.6–23.0), respectively. Treatments did not result in any significant difference in plant height at the four-leaf stage.

Effect of soil type in microplots on disease. Plots with clay loam soil had fewer diseased plants each planting date and over the three planting dates disease incidence averaged 10% less than that in the sandy loam or silt loam soils. These differences were significant according to Duncan's multiple range test $P = 0.05$ (Table 1). Temperatures were similar for each soil, but the matric potential of the clay loam was consistently greater than that of the two other soils (Fig. 3).

Effect of soil fertility on disease incidence. Application of ammonium sulfate at 120 and 240 kg/ha resulted in 34.4 and 31.9% fewer diseased plants, respectively, than in control plots (Table 2). However, when the applications were split and applied in combination with phosphorus and potassium, this effect was diminished and only resulted in 4.2 and 0.2% less disease than in the controls (Table 2). Urea at 240 and 120 kg/ha resulted in 14.9 and 9.1%, respectively, fewer diseased plants than in the controls. Calcium nitrate at the same rates caused a slight, but nonsignificant, increase in disease incidence in both experiments. Application of superphosphate resulted in 7.8% fewer diseased plants than in controls at 224 kg/ha (Table 2). Other phosphorus or potassium treatments resulted in a slight numerical, but statistically insignificant, reduction in disease incidence according to Duncan's multiple range test $P = 0.05$.

Depth of planting. Variation in planting depth did not affect the incidence of plants with head smut in field plots or greenhouse experiments.

DISCUSSION

The effects of soil temperature on head smut development observed in this study confirm earlier reports that temperatures of 23–30 C are optimum for infection of corn or sorghum by teliospores of *S. reiliana* (2,3,9,13). These are consistent with Potter's observation (19) that the maximum germination of teliospores on agar occurred at 27 C.

In previous studies of the effect of soil moisture on disease incidence, other units (percent moisture, percent water holding capacity, or percent field capacity) were used to measure soil moisture; these do not allow valid comparisons among different investigations. Numerous articles and reviews dealing with the measurement of soil moisture unequivocally agree with the need to report soil moisture as soil water potential in units of bars or pascals which measure the energy status of the water in the soil and not merely mass-volume relationships. Furthermore, earlier workers attempted to control soil moisture by replacing evaporated and transpired water so that a prescribed level of stress would be maintained. However, this technique is not valid because small volumes of water added to a dry soil do not equilibrate with the total soil mass. It has been suggested that drying cycles are the only appropriate method for simulating the natural water stress condition of the field environment (12). Nevertheless, the conclusions from these previous studies, that more plants became infected in dry than in wet soils were confirmed here. In this study, an average of 32% infected plants occurred at −1.5 bar across all

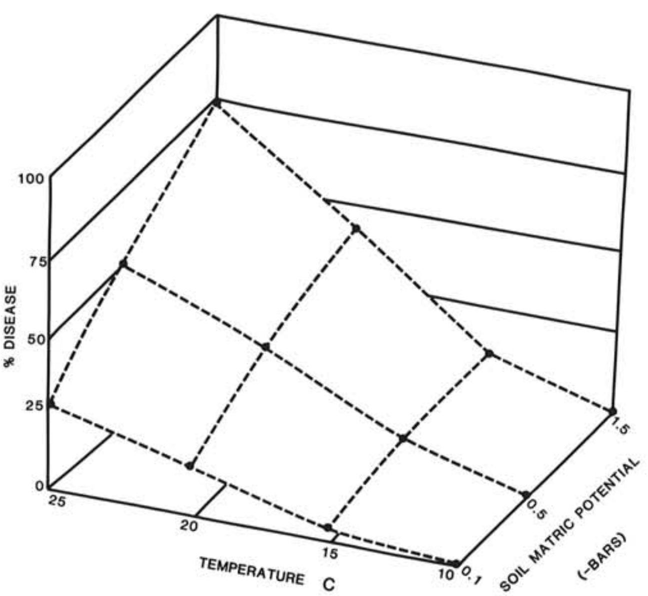

Fig. 1. The effect of soil temperature and water potential on the incidence of head smut caused in corn seedlings by *Sphacelotheca reiliana*. Each point represents an average based on 480 plants representing four planting dates and two soil types.

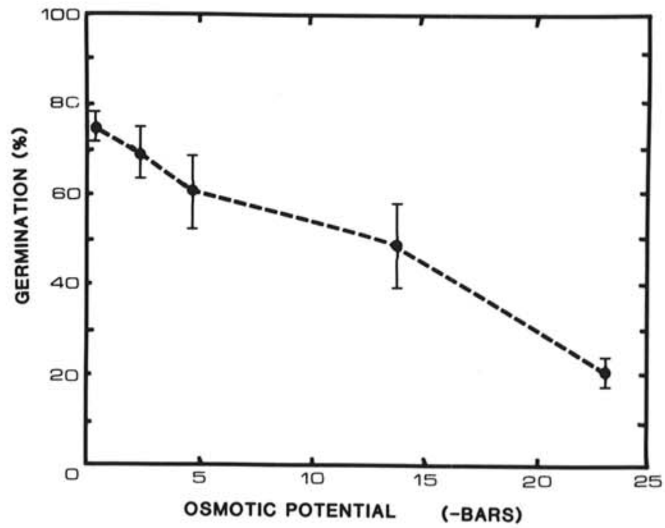

Fig. 2. Percent germination of teliospores of *Sphacelotheca reiliana* on water agar osmotically adjusted with NaCl. Each point represents the mean of three replicates of an experiment that was repeated twice. Germination frequencies were determined after 5 days of incubation at 27 C.

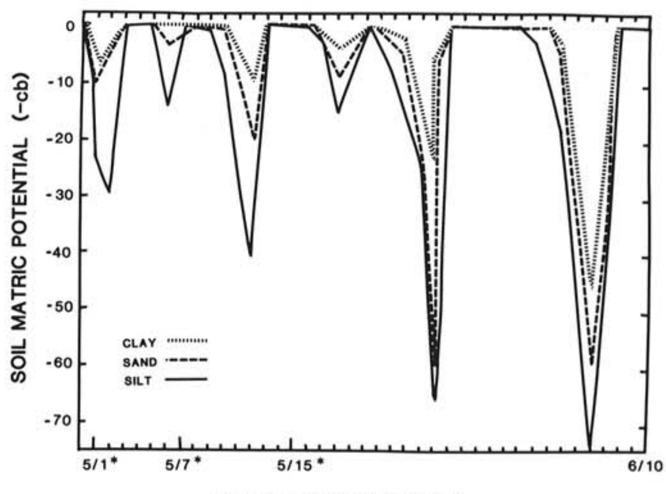

Fig. 3. Soil matric potentials in microplots of three loam soils measured daily from 1 May to 10 June 1983. Asterisks indicate planting dates, and cb = centibar.

temperatures tested, and this decreased to 25 and 13% at −0.5 and −0.1 bar, respectively. The greatest germination of teliospores on agar occurred at 0 bar and decreased to 20% at −23.8 bar; thus, teliospore germination appears to be inhibited by low moisture. We recognize that germination may vary depending on the osmoticum used or that a differential sensitivity to matric potential may exist. Nevertheless, the data still indicate that teliospores can germinate at water potentials far below those required to support the growth of corn seedlings. Plant water potentials of the seedlings in this experiment were not measured, but Brunini and Thurell (5) reported that plants grown under greenhouse conditions in soils at matric potentials of −1 to −2 bars will develop water potentials as low as −9 bars during exposure to light. Water potentials of this magnitude have been shown to inhibit numerous physiological processes (1,4,5,12,25). These data suggest that low soil matric potentials affect disease development through low-moisture stress on corn seedlings and probably have no effect on teliospore germination. As determined here, this increased susceptibility is maximally expressed between 20 and 25 C which is a range favorable for teliospore germination.

Although the effects of controlled soil moisture in the greenhouse were striking, abundant spring rains in Minnesota made it impossible to measure the effect of large differences in soil moisture in the field. Irrigation during seedling development resulted in a significant reduction of 8% disease incidence compared to plots with the low water potentials.

TABLE 2. Incidence of head smut of corn in field plots that received various applications of nitrogen, phosphorus, and potassium

Element and form of application	Treatment	Rate (kg/ha)	Disease incidence[w] (%)
Nitrogen			
Single application	Calcium nitrate	240	56.5 a
	Calcium nitrate	120	55.9 a
	Positive control[x]	0	51.1 a
	Urea	240	41.9 b
	Urea	120	36.2 bc
	Ammonium sulfate	240	29.2 cd
	Ammonium sulfate	120	26.7 d
	Negative control[y]	0	12.4 e
	Negative control plus urea	240	11.5 e
Split application[z]	Calcium nitrate	202	45.7 a
	Positive control[x]	0	38.6 ab
	Ammonium sulfate	101	38.4 ab
	Calcium nitrate	101	37.4 ab
	Ammonium sulfate	202	34.2 b
	Negative control[y]	0	11.3 c
	Negative control plus urea	202	8.9 c
Potassium and phosphorus	Positive control[x]	0	49.0 a
	Muriate of potash	112	48.8 a
	Triple superphosphate	112	47.6 ab
	Potassium magnesium sulfate	112	46.0 ab
	Potassium magnesium sulfate	224	43.9 ab
	Muriate of potash	224	43.2 ab
	Triple superphosphate	224	41.2 b
	Negative control[y]	0	14.1 c
	Negative control plus potash and triple superphosphate	112	13.5 c

[w] Mean of three replications at two planting dates with 30 seed per replication. Within each element and form of application, mean disease frequencies followed by the same letter were not significantly different according to Duncan's multiple range test, $P = 0.05$.

[x] Inoculated, no fertilizer applied.

[y] Not inoculated, no fertilizer applied.

[z] Superphosphate was applied at 120 kg P/ha and potash was applied at 288 kg K/ha.

Plots with the low soil moisture treatment were periodically tarped and thus had slightly higher temperatures than high soil moisture plots, but they had the same temperature as the control plots which were not tarped. The temperature reduction was likely due to the increased soil moisture content and the interaction of these factors may have contributed to a decreased incidence of disease.

Even though the moisture characteristics of the sandy loam and silt loam were vastly different, an equivalent amount of moisture stress in greenhouse studies resulted in similar disease frequencies. However, the same amount of rain on the three soils in microplots resulted in consistently higher water potentials in the clay loam with a resulting 10% decrease in disease incidence over the three planting dates. Even though susceptible hybrids are grown throughout the state, head smut has not spread beyond the four-county region in central Minnesota in which it was first discovered. Sandy soils are prevalent in these counties, while heavier clay soils are the predominant soil type in the main corn-growing region of the state. Thus, soil type may have had a role in restricting the distribution of this disease.

Some fertilizers significantly reduced the incidence of head smut of corn grown in the sandy loam soil on the Staples farm. The greatest reduction in disease was obtained when ammonium sulfate was applied at 120 kg/ha. The texture of these soils requires split application of nitrogen to prevent ground water contamination. This approach diminished the effect of ammonium sulfate on head smut development. In both experiments, calcium nitrate increased the occurrence of smut. Only one phosphorus or potassium treatment resulted in a significant reduction in disease. Superphosphate might reduce the occurrence of head smut, but presently infested soils are normally high in phosphorus and low rates are recommended. Thus, the economic feasibility of phosphorus application would be questionable. Effects of fertilizers on head smut development have been contradictory as reported throughout the literature. These differences in response might be due to the variety of soil types used in the various investigations.

LITERATURE CITED

1. Acevedo, E., Hsiao, T., and Henderson, D. W. 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. Plant Physiol. 48:631-636.
2. Arneman, H. F., Erickson, R. A., and Rust, R. H. 1973. Soil Survey of the Southern Experiment Station, Soil Series 106. University of Minnesota, St. Paul. 8 pp.
3. Baier, W., and Krüger, W. 1962. *Sphacelotheca reiliana* on Maize. II. Field studies on the effect of soil conditions. S. Afr. J. Agric. Sci. 5:183-202.
4. Bardzik, J. M., Marsh, H. V., and Harvis, J. R. 1971. Effects of water stress on the activities of three enzymes in maize seedlings. Plant Physiol. 47:828-831.
5. Boyer, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol. 46:233-235.
6. Brunini, O., and Thurell, G. W. 1982. Thermocouple hygrometer for in-situ measurements of soil water potential. Soil Sci. Soc. Am. J. 46:900-904.
7. Christensen, J. J. 1926. The relation of soil temperature and soil moisture to the development of head smut of sorghum. Phytopathology 16:353-357.
8. Farag, I. S. 1975. Host-pathogen relationship of corn and *Sphacelotheca reiliana* (Kühn) Clinton. Ph.D. dissertation, University of Idaho, Moscow. 127 pp.
9. Foster, J. H. 1979. Study of the etiology and inheritance of resistance to maize head smut. MS thesis, Texas A & M University, College Station. 58 pp.
10. Foster, J. H., and Frederiksen, R. A. 1977. Evaluation of maize for resistance to head smut. (Abstr.) Proc. Am. Phytopathol. Soc. 4:142.
11. Freund, R. J., and Littell, R. C. 1981. SAS for linear models. A guide to the ANOVA and GLM procedure. SAS Institute, Inc., Cary, NC.
12. Hsiao, T. C. 1973. Plant response to water stress. Annu. Rev. Plant Physiol. 24:519-570.
13. Kaufman, M. R. 1979. Watering: Critique I. Pages 291-300 in:

Controlled Environmental Guidelines for Plant Research. T. W. Tibbitts and T. T. Kozlowski, eds., Academic Press, New York. 413 pp.
14. Krüger, W. 1962. *Sphacelotheca reiliana* on maize. I. Infection and control studies. S. Afr. J. Agric. Sci. 5:43-56.
15. Lang, A. R. G. 1967. Osmotic coefficients and water potentials of sodium chloride solutions from 0 to 40 C. Aust. J. Chem. 20:2017-2023.
16. Lynch, K. V., Edington, L. V., and Busch, L. V. 1980. Head smut: A new disease of corn in Ontario. Can. J. Plant Pathol. 2:176-178.
17. Mack, H. J., Bagett, J. R., and Koepsell, P. A. 1980. Cultural practices affecting corn smut. Oregon Veg. Digest 29:1-2.
18. Matyac, C. A., and Kommedahl, T. 1985. Occurrence of chlorotic spots on corn seedlings infected with *Sphacelotheca reiliana* (head smut) and their use in evaluation of head smut resistance. Plant Dis. 69:251-254.
19. Popov, A. 1968. *Sphacelotheca reiliana* infection on maize grown in monoculture. Rev. Appl. Mycol. 47:623 (original not read).
20. Potter, A. 1914. Head smut of sorghum and maize. J. Agric. Res. 2:339-372.
21. Reed, G.M., Swabey, M., and Kolk, L. A. 1927. Experimental studies on head smut of corn and sorghum. Bull. Torrey Bot. Club 54:295-310.
22. Schoper, R. P., Caldwell, A. C., Swan, J. B., and Malzer, G. L. 1978. Corn fertilization on irrigated sandy soils. Soils Fact Sheet 31, Agricultural Extension Service, University of Minnesota, St. Paul. 2 pp.
23. Stromberg, E. L. 1981. Head smut of maize: A new disease in Minnesota (Abstr.). Phytopathology 71:906.
24. Stromberg, E. L., Stienstra, W. C., Kommedahl, T., Matyac, C. A., Windels, C. E., and Geadelmann, J. L. 1984. Smut expression and resistance of corn to *Sphacelotheca reiliana* in Minnesota. Plant Dis. 68:880-884.
25. Virgin, H. I. 1965. Chlorophyll formation and water deficits. 1965. Plant Physiol. 18:994-1000.