

The Role of Plant Stresses in Development of Corn Stalk Rots

Stalk rots of corn cause problems for farmers somewhere every year. Potential grain yields are lost because kernels on rotted plants are lightweight and ears are missed during harvest. Furthermore, lodging resulting from corn stalk rot causes difficult, slow machine harvesting in the U.S. corn belt at a time when farmers are concerned about finishing before winter.

The distribution of stalk rot of maize is frequently difficult to explain or predict. A cultivar may have acceptable stalk quality one year and be badly lodged in the same field the next year. Performance in adjacent fields may differ, with nearly all plants lodging in one area but standing in another. Often, a stalk-rotted plant is next to a genetically identical but healthy plant.

A concept unifying host, pathogen, and environment interactions is presented to explain the distribution of maize stalk rot. This discussion of the role of plant stresses is intended not only to lead to improved stalk rot control but also to stimulate investigation of the mechanisms of resistance to weak, facultative parasites.

The Stalk Rot Syndrome

This discussion concerns the deterioration of lower stalk tissue after flowering and includes *Fusarium*, *Diplodia*, *Gibberella*, anthracnose, and charcoal stalk rots; bacterial and *Pythium* stalk rots are excluded. Disease pattern is the same for each stalk rot, although specific environments apparently favor one fungus over others.

Typically, the first sign of stalk rot is permanent wilting of the plant (Fig. 1). Within a day, all leaves become gray and the leaves and ear droop. The outer rind of the lower stalk is yellow-green, turning yellow-brown within a week. At this point, pith tissue in the lowest internode is rotted and pulls away from the rind, greatly weakening the stalk, whose structure is changing from a solid rod to a tube.

Stalk rot develops in every plant with wilt symptoms. Wilting also stops all

Table 1. Results of stalk inoculation treatments^a

Treatment	Percent plants wilted, dead, or rotten on:			
	Sept. 15	Sept. 22	Oct. 4	Oct. 23
<i>Gibberella zeae</i> , toothpick	11	18	31	59
<i>G. zeae</i> , spore suspension	4	21	36	63
<i>Colletotrichum graminicola</i> , toothpick	2	7	32	62
<i>C. graminicola</i> , spore suspension	7	23	53 ^b	67
<i>Diplodia maydis</i> , toothpick	14	21	41	53
<i>D. maydis</i> , spore suspension	13	21	43	56
Soil	13	20	36	66
Hole only	9	24	30	60
Toothpick only	6	16	35	55
Control (not inoculated)	11	26	30	63

^aFrom Dodd (3).

^bSignificantly greater than control at 0.05 level.

Table 2. Number of kernels on plants with rotted stalks compared with number on adjacent plants with healthy stalks^a

Year	Hybrids (no.)	Pairs (no.)	Number of kernels on:		
			Rotted stalks	Healthy stalks	Diff. ^b
1976	40	112	561.9	459.0	66.9
1978	30	65	647.6	586.8	60.8

^aFrom Dodd (5).

^bSignificance level of $P = 0.001$ using Student's t test.

translocation to grain, and kernels are lighter if normal grain filling is not complete. Symptoms do not occur uniformly within a field but are scattered, with wilted plants adjacent to healthy ones (Fig. 2). Rot generally begins at the lowest internodes, and development probably increases with rising temperatures. Affected plants usually have rotted roots and are easily pulled from the ground. Whether an affected plant will lodge is determined by strength dynamics, including weight and height of the ear, amount of stalk deterioration, rind strength, and wind force.

Dynamics of the Disease Triangle

The interactions of host, pathogen, and environment greatly influence corn stalk rots. Fortunately, the many investigations of each part of the disease triangle allow development of a general concept

elucidating the dynamics of their interactions.

The pathogen. All fungi associated with corn stalk rots are ubiquitous, although some apparently are favored by certain temperature, humidity, and soil moisture regimens. With the exception of *Colletotrichum graminicola* (Ces.) Wils. on a few genotypes, no fungus appears able to damage healthy, vigorous cell tissue. In other words, as long as cells remain vigorous, most host genotypes have genetic components for resistance to potential pathogens.

Rarely is only a single fungal species present in a rotted stalk. Although *Gibberella zeae* (Schw.) Petch perithecia are visible on the outer rind, species of *Fusarium*, *Penicillium*, *Aspergillus*, and *Trichoderma* may be isolated from the same rotted tissue. Obviously, many fungal species are able to receive

nourishment from cellulose and lignin in dead stalk tissue. Identifying the fungi rarely contributes to controlling the disease; the host-environment interactions are the pertinent variables. For example, inoculating three pathogens into the lower stalk of five genotypes did not increase the number of plants that developed stalk rot (Table 1).

The host. Genotypes (hybrids or cultivars) vary in tendency toward stalk rot but all probably are predisposed to the disease. Cultivars that develop stalk rot most often in a particular environment and individual plants that become affected have several characteristics in common. One of these is cellular senescence. Senescence or cell death of pith tissue precedes stalk rot, apparently beginning at the top of the plant and progressing downward. Living pith tissue

resists pathogens, but dead tissue does not. Apparently, synthesis of cellular resistance substances decreases with senescence (2). The ability of several fungi to rot pith tissue correlates positively with the percentage of cell death in that tissue.

Although no nutritional basis for pith cell death has been established and the results of some studies are contradictory, lowered concentrations of reducing and total sugars are associated with increases in stalk rot development (6). Under normal culture conditions, the sugar content is higher in the lower stalks of "resistant" hybrids than of "susceptible" hybrids. Treatments that predispose plants to stalk rot, such as high plant density and leaf removal, reduce sugar content in lower stalk tissue. Prevention of kernel development and low plant density are associated with higher stalk

sugar content and increased stalk rot resistance (6).

That carbohydrate nutrition influences resistance is supported by findings that stalk-rotted plants have 10–19% more kernels than adjacent healthy, genetically identical plants with no obvious differences in stresses (Table 2) (5). Apparently, translocation of a disproportionate amount of available sugar to the kernels in the rotted plants results in starvation of other tissues.

Root rot generally precedes stalk rot in corn (9). Roots are in a milieu of high fungal populations for much of the season and some tissues are invaded by *Fusarium* spp., but only the roots of stalk-rotted plants are completely rotted by harvest time. Several factors point to lack of soluble carbohydrate as the reason for lowered resistance in these root tissues.

The environment. Several field environmental stresses have been associated with occurrence of stalk rot (3). Stress influences the ability of plants to produce carbohydrates. When disease, artificial cutting, or second-brood corn borers destroy leaf area, critical photosynthetic capabilities are removed. Photosynthesis is also reduced when soil moisture is below the minimum level and when light intensity is decreased by cloudy weather or high plant density.

Environment can favor one potential pathogen. Exceptionally dry soil favors *Macrophomina phaseoli* (Mauhl.) Ashby, the incitant for charcoal rot, over *Fusarium* spp. In the U.S. corn belt, *G. zae* is more prevalent in the humid eastern areas than in the drier western regions. Regardless of the pathogen, however, stalk rot does not occur unless the host is adversely affected. The environment-host interaction is most important in determining whether stalk rot develops in a plant or becomes prevalent in a field.

The PS-TB Concept

A concrete explanation of the myriad factors in each component of the stalk rot disease triangle seems to be lacking at first. The confusing differences in disease occurrence in adjacent plants, areas in a field, or fields can be frustrating to the field pathologist, the agronomist, and the farmer. However, a central theme called the photosynthetic stress-translocation balance (PS-TB) concept of predisposition of corn to stalk rot has been proposed to explain the field distribution of the disease and the host-pathogen-environment interactions (3). According to the concept, root and lower stalk tissues are decayed by several microorganisms as the tissues lose their metabolically dependent defense system because of an increase in cellular senescence caused by carbohydrate deficiency. This deficiency is due to the



Fig. 1. Wilting of plant is first sign of stalk rot; plant roots are deteriorated. Adjacent healthy plants are genetically identical to wilted plant.



Fig. 2. Brown stalk of rotted plant next to green stalk of healthy, genetically identical plant. Stalks turn brown within 1–3 weeks after plant wilts.

Table 3. Effect of northern leaf blight on stalk rot^a

Genotype ^b	Phenotype	Treatment ^c	Percent plants with:		Kernels/plant (no.)	Kernel weight (gm)	Bushels/acre	Quintals/hectare
			Stalk rot	Stalk lodging				
HtHt	Resistant	Inoculated	3.3	0.0	425.3	0.365	149.7	94.0
Htht	Resistant	Inoculated	0.0	0.0	462.7	0.335	146.1	91.7
htht	Susceptible	Inoculated	93.2	38.3	496.1	0.273	127.7	80.2
htht	Susceptible	Not inoculated	0.0	0.0	472.3	0.359	159.9	100.4

^aFrom Dodd (*unpublished*).

^bIsogenic types of Cargill hybrid 19379.

^cSpore suspension of *Exserohilum turcicum* placed in whorls at seven-leaf stage.

combination of insufficient photosynthesis and competition with translocation to grain. Root tissue suffers when the plant becomes more "committed" to grain fill than photosynthesis can provide. Root rot then develops, the plant wilts because of insufficient water uptake, and stalk-rotting organisms decay stalk tissue. Although some organisms, eg, *Fusarium* spp., may already be in these stalks, active decay of tissue apparently does not begin until cellular senescence.

Every plant requires a specific amount of carbohydrate to fill kernels and maintain root growth. These requirements are not static, however. Genetic and

preflowering environment interactions determine the number of kernels a plant establishes. The major influences on kernel establishment, which begins about 25 days after germination, are moisture, fertilizer, and temperature. The rate that carbohydrate moves to each kernel, on the other hand, is fairly constant for 10–50 days after pollination. The daily rate per kernel varies with the genotype, but environment, with the possible exception of nitrogen deficiency (8), has little effect. Kernel number, therefore, is the main variable among genetically identical plants that affects total translocation to grain.

Not much is known of the energy

requirements for cellular maintenance in roots. The requirements probably increase with heat, as they do with the whole plant (7).

Environmental Influences on Photosynthesis Rate

Photosynthesis before and after flowering provides carbohydrate for storage in grain and cellular maintenance in plants. Although much preflowering energy is spent on growth and cellular maintenance, up to 20% of grain weight comes from carbohydrate stored in stalks. Because photosynthesis after pollination provides most of the ability to meet grain and plant

energy requirements, environment during this period is of major importance. Light intensity, effective leaf area, moisture availability, and minerals interact with inherited characteristics of the plant to determine the rate of photosynthesis.

Light intensity. In maize, the rate of photosynthesis increases with light intensity. The rate in a top leaf exposed to full sunlight (10,000 ft-c of light intensity) is 20 times that in the same leaf on a dark, cloudy (500 ft-c) day. The rate in leaf tissue shaded by another leaf is one-tenth that of a fully exposed leaf. Thus, cloudy weather and plant density greatly affect the rate a plant synthesizes carbohydrate. A plant density resulting in good yield and acceptable stands for a hybrid in a field one season may be too high for the same hybrid in the same field during a cloudy season.

Effective leaf area. Although genotypes differ in basic leaf area, effective leaf area can be reduced by certain environmental stresses. For example, artificially removing the upper leaves increases the probability of stalk rot, as shown in an experiment in which stalks were cut at different nodes below and above the ear. Stalk rot developed in plants cut one node above the ear but not in those cut immediately below the ear (Fig. 3). The fewer leaves removed, the lower the incidence of stalk rot. Plants whose leaf area is removed by hail, corn borers, or disease produce less carbohydrate. Hail damage after pollination usually results in an increased incidence of stalk rot. Second-brood corn borers that cause plants to break above the ear are also often associated with stalk rot; stalks broken below the ear remain green, even though the ear may be on the ground.

Such leaf diseases as northern leaf blight [*Exserohilum turcicum* (Pass.) Leonard and Suggs (= *Helminthosporium turcicum*)] and southern corn leaf blight (*Helminthosporium maydis* Nisi. and Miy.) can be major contributors to stalk rot. With these blights, yield reductions are associated more closely with kernel weight loss due to premature wilting than with gradual loss of leaves. A plant that stays alive until the black layer forms sustains little yield loss. The incidence of stalk rot was studied in a hybrid very susceptible to *E. turcicum*; the incidence was 93% in plants inoculated with *E. turcicum*, 3.3% in inoculated plants protected with the Ht gene, and 0% in noninoculated plants. A yield loss of 15–21% in the unprotected inoculated plants was mostly attributable to reduced kernel weight (Table 3).

Moisture availability. Photosynthesis rates in maize are not directly correlated with moisture content after a certain minimum turgidity is maintained. The rate drops drastically when the leaf water potential is less than -11 bars (1). The amount of rainfall and/or irrigation needed to maintain optimal photosynthesis depends greatly on transpiration rates and soil types. Plant density also is an important determinant of water requirements.

Abundant moisture before flowering promotes good ear development and high kernel numbers; if the postflowering environment is dry, stalk rot is likely to occur. If, on the other hand, an early drought inhibits pollination and later rains promote photosynthesis, stalk rot is less likely to occur. The timing of irrigations can influence the incidence of stalk rot by affecting the availability of

water before and for 55 days after pollination.

Minerals. Fertilizers high in nitrogen and low in potassium often are associated with an increased incidence of stalk rot. The role of these minerals in the PS-TB concept is not as clear as that of the other plant stress components. Nitrogen promotes growth of leaf and stalk tissue, helps establish high kernel numbers, and interacts in the translocation of carbohydrate to grain. Potassium is involved in many metabolic processes, including stomatal function. The photosynthesis rate is lower in plants deficient in potassium than in those high in potassium. Perhaps high nitrogen promotes a large grain "sink" and more energy-expensive plant tissue to maintain, whereas low potassium reduces the plant's ability to meet these energy demands.

Efforts to Control Stalk Rot

The PS-TB concept apparently applies to all maize genotypes. If a grain sink is established, sufficient stress can be applied to predispose the plant to stalk rot. Aspects of the concept vary according to genotype, however. Inherited differences include size of the grain sink, utilization of minerals, resistance to leaf diseases, photosynthesis rate per unit area of leaf, total leaf area, resistance to drought, and efficiency of energy use. That the inheritance of stalk rot resistance is regarded as complex is therefore not surprising. The environment in which a hybrid is grown must be considered when characterizing a genotype as susceptible or resistant. A more accurate way to predict a genotype's vulnerability to stalk rot is to expose the hybrid to specific stresses. Breeding efforts must concentrate on selecting genotypes with consistently high grain yields and low percentages of stalk-rotted plants in field environments.

Certain cultural methods help reduce vulnerability to stalk rot. Fertilizer balance, with equal amounts of nitrogen and potassium, is important. Mineral analysis of leaf tissue at pollination is the best way to assure adequate potash application; several tests have shown proper amounts of potash decrease the incidence of stalk rot. Because of light and water stresses, plant density is very influential. Optimal density is determined by weather conditions, soil type, kind and amount of fertilizer, and genotype. Unfortunately, what is optimal density during a sunny season with adequate moisture will not be satisfactory during a cloudy or dry season.

Timely irrigations control water stresses somewhat. The amount of moisture available before pollination greatly influences grain sink size, yield potential, and vulnerability to stalk rot. Avoiding water stress during the grain filling period (about 55 days) after

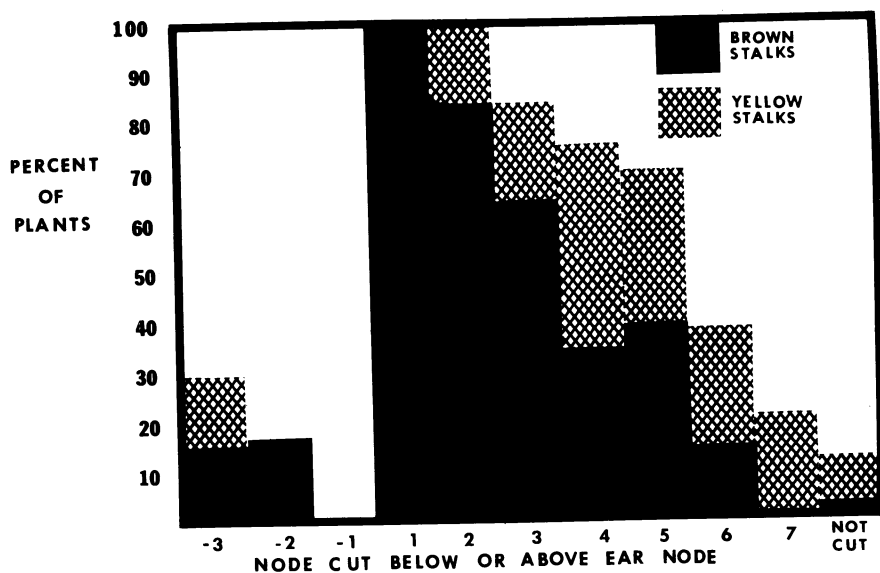


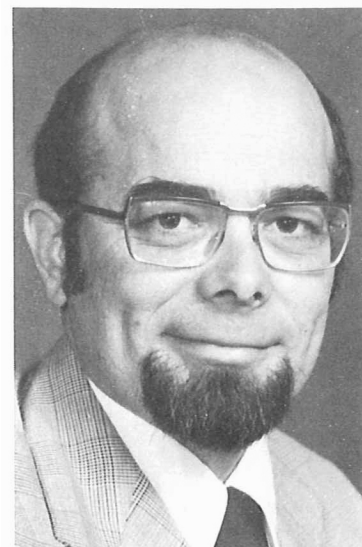
Fig. 3. Relationship between artificial removal of leaves and development of stalk rot. Stalks were cut at various nodes (nodes below ear node are indicated by minus signs) approximately 3 weeks after silking, and stalk condition was recorded 8 weeks later. Brown stalks began rotting before yellow ones, but both were regarded as rotten. Unshaded areas represent green, healthy stalks.

pollination lowers the incidence of stalk rot.

Although the PS-TB concept appears to be consistent with what is known about maize stalk rot, several questions concerning the mechanisms of resistance remain unanswered. What is the biochemistry involved in host-interactions to "weak" pathogens such as *G. zae* or *F. moniliforme*? Do roots deteriorate gradually during the whole season? Is root degeneration initiated by carbohydrate nutrition or are other metabolites more important? What determines the size and duration of the root carbohydrate sink? The PS-TB concept is also consistent with host-pathogen-environment interactions involved in stalk rots of sorghum (4) and in common root rot of wheat. Does root tissue "vigor" influence these and other postflowering root rots? These and other questions should be answered by further studies, but that total plant biology integrates closely with environmental stresses and pathogen biology in the development of maize stalk rots is clear.

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James L. Dodd

Dr. Dodd is a plant pathologist for the Seed Division of Cargill, Inc. His main responsibility is improving disease resistance in maize through efforts by company plant breeders. His primary research concerns developing and applying efficient techniques for evaluating disease resistance. He received his Ph.D. from the University of Tennessee in 1970.