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Integrated Control of Verticillium Wilt of Cotton

Verticillium wilt, caused by the soil-inhabiting fungus *Verticillium dahliae* Kleb., is one of the most important diseases of cotton and causes great economic losses. Verticillium wilt in commercial cotton was first discovered in Tennessee by Sherbakoff (29) in 1927 and in California by Shapovalov and Rudolph (28) in 1930. Since then, the disease has been reported almost simultaneously in Arkansas and Texas and from other major cotton-growing areas of the world. The disease is now a major problem in the irrigated areas of the northern Mississippi Delta and in the western and southwestern regions of the United States. Verticillium wilt is particularly severe in the United States, the Soviet Union, Peru, and Uganda, where cotton is grown under relatively cool conditions. The fungus is now recognized as one of the most widely distributed and destructive pathogens in agricultural soils. Average yearly crop loss for the cotton-producing states in the United States during 1952–1981 was estimated at 2.37% and ranged from 1.01% in 1954 to 4.4% in 1967 (17). In California, the yearly loss ranged from 2.0% in 1970 to 7.6% in 1977. Several workers (3,4,11,24,26,31) have presented detailed reviews of Verticillium wilt.

This article concerns the epidemiology of Verticillium wilt and how the disease affects plant phenology, yield, and quality and also presents a conceptual model for an integrated crop management system (ICMS). Frisbie and I (8) defined an ICMS as: "A system whereby all interacting crop production and pest control tactics aimed at maintaining and protecting plant health are harmonized in the appropriate sequence to achieve optimum crop yield and quality and maximum net profit, in addition to stability in the agroecosystem, benefiting society and mankind." The main objective of an ICMS is to maintain the plant's health throughout the growing season. "Plant health" means relative freedom from biotic and abiotic stresses that limit the plant's productivity in both quantity and quality from its maximum genetic potential. The conceptual model for Verticillium wilt (Fig. 1) integrates and links our knowledge of system components (host resistance, genetic potential, fruit set, other pests in the system, pathotypes and inoculum density of the pathogen, disease progress, temperature and moisture, and rhizoplane and phylloplane environment) to plant health, yield, and quality. The system adjusts biological activities to environment and management tactics.

Cotton Growth and Development

An understanding of cotton phenology is essential to achieving optimum cotton production. Under normal growing conditions, the cotton plant follows an orderly and predictable calendar and physiological pattern. Figure 2 shows the development of cotton (Acala SJ-2) in the San Joaquin Valley of California. Seedlings emerge 5–15 days after planting, and the plant establishes its basic framework—root, vegetative and fruiting branches, and partial canopy—in 45 to 55 days.

Cotton, which has an indeterminate growth habit, produces squares, flowers (blooms), and bolls over 2.5–3.5 months. The effective flowering period in the San Joaquin Valley occurs from late June through mid-August, and about 60% of the flowers are produced within 110 days of planting (8,10). Conversion of flowers to bolls that will be retained is more effective in the early part of the season. The plant normally sets 80% of its bolls in the first 6 weeks of the bloom period (10). Shedding of some squares, flowers, and small bolls is natural and is increased by such factors as deficient or, in some cases, excessive soil moisture, inadequate number of fertilized ovules, insufficient nutrient supply, excessive heat or cold, and damage from insects and diseases (8,15). Fruit shed also results when the demand by the various plant parts for photosynthates exceeds the supply. This is common when several bolls per plant reach maximum size.

The period of boll growth begins when the plants are about 100 days old and continues until the last boll opens about 190–210 days after planting in the San Joaquin Valley (Fig. 2). In the Texas High Plains, the boll growth period occurs 73–140 days after planting. The plant normally attains its boll-carrying capacity during this period. Under favorable conditions in the San Joaquin Valley, this period occurs from early June to early August (8,10). Rapid accumulation of dry matter in fruits coincides with the peak of square formation, the beginning of flowering and boll production (15,16).

The cotton plant has a primary taproot with many laterals. Root growth shows a typical sigmoidal curve, with exponential growth in the early part of the season when the root system is unaffected by soil conditions such as compaction and

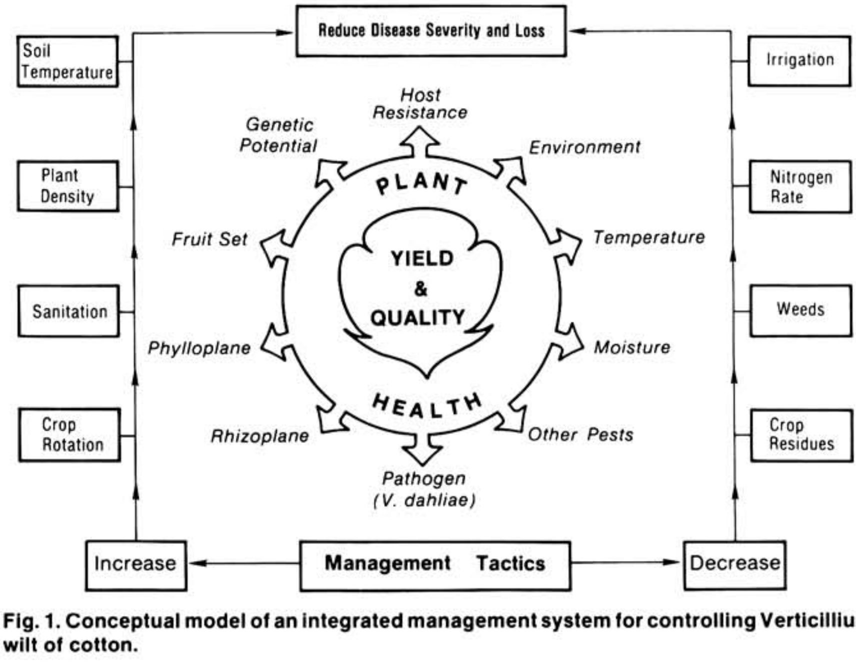

Fig. 1. Conceptual model of an integrated management system for controlling Verticillium wilt of cotton.

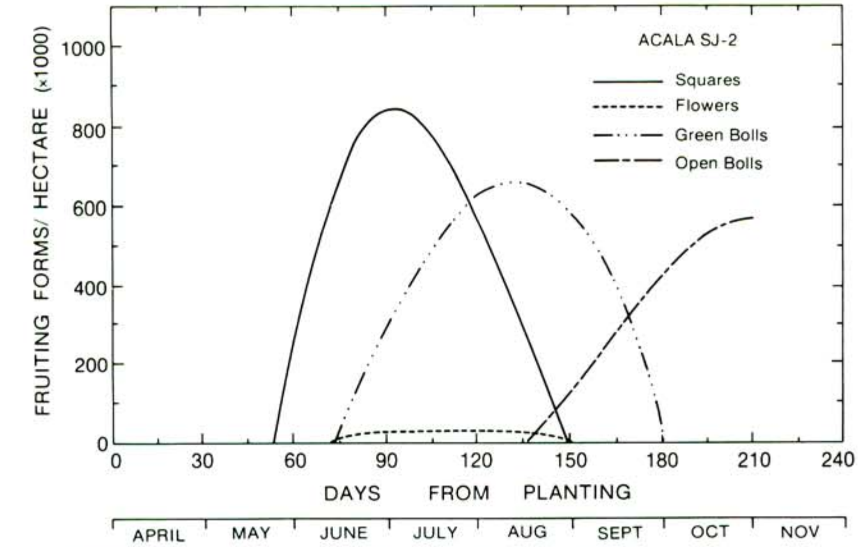

Fig. 2. Seasonal development of Acala SJ-2 cotton fruiting forms in the San Joaquin Valley of California.

Fig. 3. Microsclerotia and germinating propagules of *Verticillium dahliae* and growing infectious hyphae.

Fig. 4. Chlorotic and necrotic mottling between the main veins and on margins of a cotton leaf.

hardpans. With little or no growth restriction, the taproot grows rapidly downward, 2.5 cm per day, for several weeks after planting. A significant decrease in growth rate normally occurs at the onset of flowering. Toward the end of the season, a sharp drop in root densities is common. Root death during the growing season often involves a major portion of the root biomass. The causes of root death are varied and may involve both biotic and abiotic factors. Soil moisture is a major factor affecting root growth rates and distribution (13); other variables are temperature, soil compaction, lack of oxygen in waterlogged soils, soil pH, and nutrient (i.e., nitrogen) supply and availability.

As roots continue to grow and explore more soil, they should make increasingly more contacts with fungal propagules within the rhizoplane. The extent of root growth and of propagule mobililty, along with germ tube growth, would be expected to influence the number of root-propagule contacts (18). Studies of root colonization by *V. dahliae* relative to soil inoculum density revealed a sphere of influence of approximately 100–300 μm (18). This suggests that mobility of the fungus is negligible compared with the extensive growth of the root system. Huisman (18) suggested that disease incidence (corrected for random multiple infection) as a function of time need not necessarily parallel root growth. In addition to root growth, pathogen behavior and/or host resistance affect disease incidence. Whenever a fluctuating environmental variable has a major impact on disease incidence (e.g., effects on propagule germination, germ tube survival in soil, establishment on the host), the relationship between root growth and disease development may not be simple and direct. Some environmental variables (e.g., water or fruiting stress on the host) could conceivably favor systemic invasion by epiphytic colonies (18). Root damage from cultivation or nematodes may also favor invasion. If any of these occurs, there would be a sudden increase in disease incidence far in excess of that expected from root growth rate alone.

Epidemiology

Factors important in the epidemiology of Verticillium wilt of cotton are inoculum density and pathotype (defoliating and nondefoliating) of *V. dahliae* in soil, plant age, host resistance and its genetic potential, air and soil temperature, soil moisture, plant density, and potassium and nitrogen availability to growing plants.

Causal organism. *V. dahliae* has a wide host range of more than 160 plant species in 40 different families (26,27). The fungus includes several strains; some are rather host-specific and others attack many plant species. At least five strains are known to attack American Upland (*Gossypium hirsutum* L.) cotton cultivars (26). Two major strains or pathotypes of *V. dahliae* (defoliating and nondefoliating) differ in virulence. Both cause common symptoms of Verticillium wilt, but the defoliating strain is extremely virulent and can cause complete leaf defoliation and shedding of small bolls of infected plants (27).

Disease cycle. The life cycle of *V. dahliae* can be divided into dormant, parasitic, and saprophytic stages (26). Some propagules that initiate infection, including melanized microsclerotia (Fig. 3), hyaline microsclerotia, and various types of hyaline hyphae, can survive adverse environmental conditions and remain dormant in the soil or undecomposed plant material for several years. Extended dormancy could account for the extreme longevity of this pathogen. Microsclerotia are distributed mainly in the upper 45 cm of field soils, with the greatest concentrations in soil zones mixed with crop debris. Propagules in the rhizosphere are usually dormant and are stimulated to germinate by root exudates. Infectious hyphae (Fig. 3) emerging from microsclerotia about 16 hours after incubation begin direct penetration of roots, mainly in the areas of differentiation and in the root hair zone and probably in epidermal tissues ruptured by the emergence of lateral roots. Only propagules in the vicinity of such an infection site would have an opportunity to germinate, penetrate, and infect. The infective hyphae grow intercellularly and intracellularly through the root cortex and the endodermis to the xylem tissues. In the xylem, mycelia continue to colonize the vessels and produce conidia that move rapidly in the transpiration stream to aboveground parts of the plant. Infected xylem vessels become plugged by the combined formation of gels, gums, and tylosis. About 14 days elapse between root infection and detection of systemic infection by symptom expression in leaves.

After the affected tissues have died, new resting structures form when the tissue is moistened by rain or irrigation or is turned into moist soil (26). New propagules are then available to infect plants in succeeding crops and to accumulate for later years. A single infected cotton plant may contain more than 25×10^4 *V. dahliae* microsclerotia. Cultivation distributes the propagules in the soil, where they may germinate, sporulate, or produce secondary microsclerotia several times in the vicinity of organic matter or the rhizosphere of nonhost plants. Infectious propagules normally are not formed until plant tissues are dead or near death. Thus, a single cycle of production of overwintering infectious propagules occurs each year. Based on Vanderplank's (30) concepts, Verticillium wilt of cotton is a monocyclic disease. Disease severity is therefore directly proportional to inoculum density in the soil at the start of the growing season.

Symptoms. The first noticeable symptoms of Verticillium wilt are reduced plant growth rate, slight to moderate epinasty, and a change in leaf color. Irregular chlorotic areas develop on infected leaves between the main veins and along the margins. These gradually become larger and paler, resulting in a mottled appearance (Fig. 4). Chlorotic and necrotic mottling are especially apparent on the older leaves and less severe on younger ones. Considerable stunting may accompany leaf mottling.

Light to dark brown vascular discoloration is prominent in the main stem, branches, and petioles of diseased plants (Fig. 5). The pathogen colonizes the xylem vessels and may occlude the vascular system, inhibit the rate of nutrient flow to growing plant parts, and reduce photosynthetic productivity in leaves.

Invasion of a susceptible cultivar by a virulent pathotype of *V. dahliae* causes the leaves to wilt and abscise, resulting in partial defoliation. Severely affected plants shed all their leaves (Fig. 6). Defoliation of cotton is a severe expression of the disease and causes substantial reduction in yield. Terminal dieback and regrowth of leaves from lower nodes often occurs after defoliation if the plant is not killed.

The stage of plant development when foliar symptoms of Verticillium wilt occur has a direct effect on cotton lint yield (2,9,16,23) and quality (9). If the disease occurs early, about 60 days after planting, it reduces total dry matter accumulation, internode elongation, and fruiting branch development; increases shedding of squares and small bolls; and inhibits further square production. Large bolls usually remain attached to the infected plant and eventually open, even after defoliation.

Rapid pathogenesis occurs at the onset of flowering about 80 days after planting (Fig. 2), which is directly related to the diversion of a portion of photosynthate to reproductive structures (squares and bolls). After flowering, carbohydrate and nitrogenous compounds stored in plant tissues are translocated to the developing bolls. Lint yield reductions are small when foliar symptoms appear after mid-August.

Inoculum density and disease progress and severity. The severity and rapidity with which disease symptoms progress depend primarily on the cultivar, pathotype of *V. dahliae*, inoculum density, host growth stage, fruit load, and soil moisture and temperature (Fig. 1). Increasing virulence or inoculum density of the pathogen can offset effects of host resistance (3,4). Pathogen density and virulence levels for specific sites and fields can be estimated, especially when the history of the disease is known. The number of microsclerotia of *V. dahliae* can be quantitatively determined with the modified Anderson sampler technique (5) or the wet sieve method (19). The number of microsclerotia recovered by the Anderson method averages 2.8 times higher than that recovered by wet sieving (5).

The effect of initial inoculum densities of 5, 20, 40, and 60 *V. dahliae* propagules per gram (p/g) of soil on foliar disease symptoms and on disease progress with time is presented in Figure 7 (22). An increase in inoculum density from 5 to 60 p/g resulted in an increase in the percentage of infected plants as the season progressed, with 15% of the plants with foliar symptoms at 5 p/g and 95% at 60 p/g. The fungal population density required for 50% disease is approximately 22 p/g. Also, with 60 p/g, symptoms appear early, about 50–60 days after

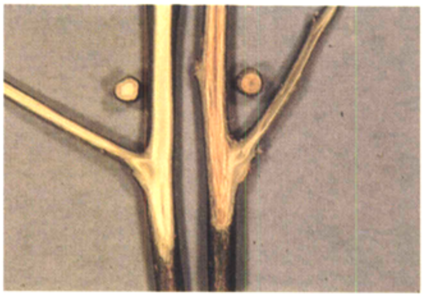

Fig. 5. (Right) Light to dark brown vascular discoloration in the main stem and branches of a diseased cotton plant; (left) healthy stem.

Fig. 6. (Left) Severe defoliation of a cotton cultivar susceptible to Verticillium wilt; (right) resistant cultivar.

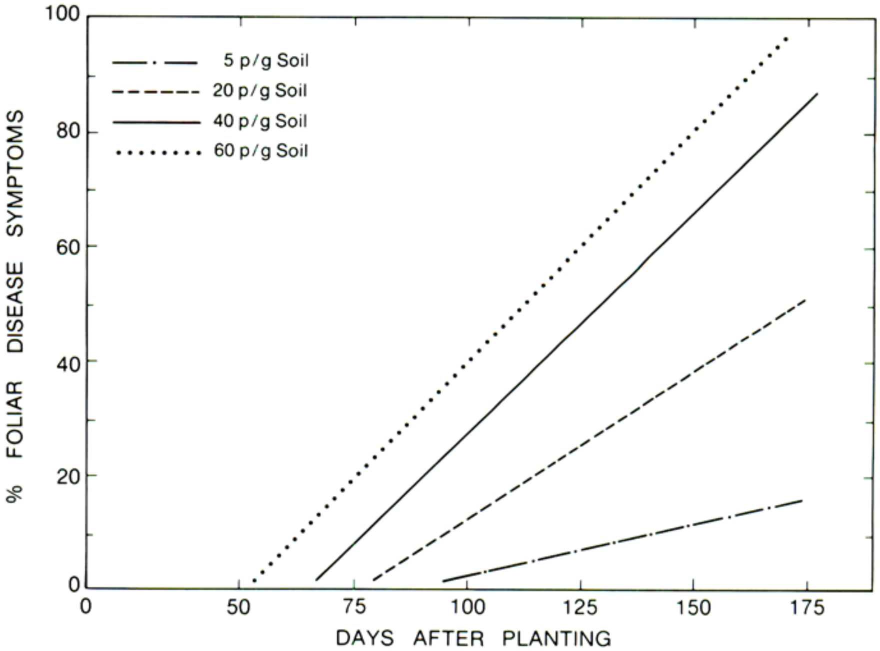

Fig. 7. Relationship of initial inoculum density of *Verticillium dahliae* at 5, 20, 40, and 60 propagules per gram of soil to foliar Verticillium wilt symptoms of cotton with time. (Adapted after Pullman and DeVay [22] and El-Zik [*unpublished*]).

planting, compared with 90 days with 5 p/g (Fig. 7). Ashworth et al (1) obtained similar results using the wet sieve method to assay for inoculum density as microsclerotia per gram (m/g) of soil. In the 24 fields assayed, disease incidence was 100% in soil containing 3.5 m/g or more and 20–50% in soil containing 0.3–1.0 m/g. The quantitative effect of inoculum density on defoliation and yield varied from year to year among different fields (1,22). Additional studies are needed to determine the minimum number of propagules required for the initiation of systemic infection and disease incidence. This number may vary with fungal pathotype, cropping history, cultivar, soil moisture, and environmental conditions, especially temperature.

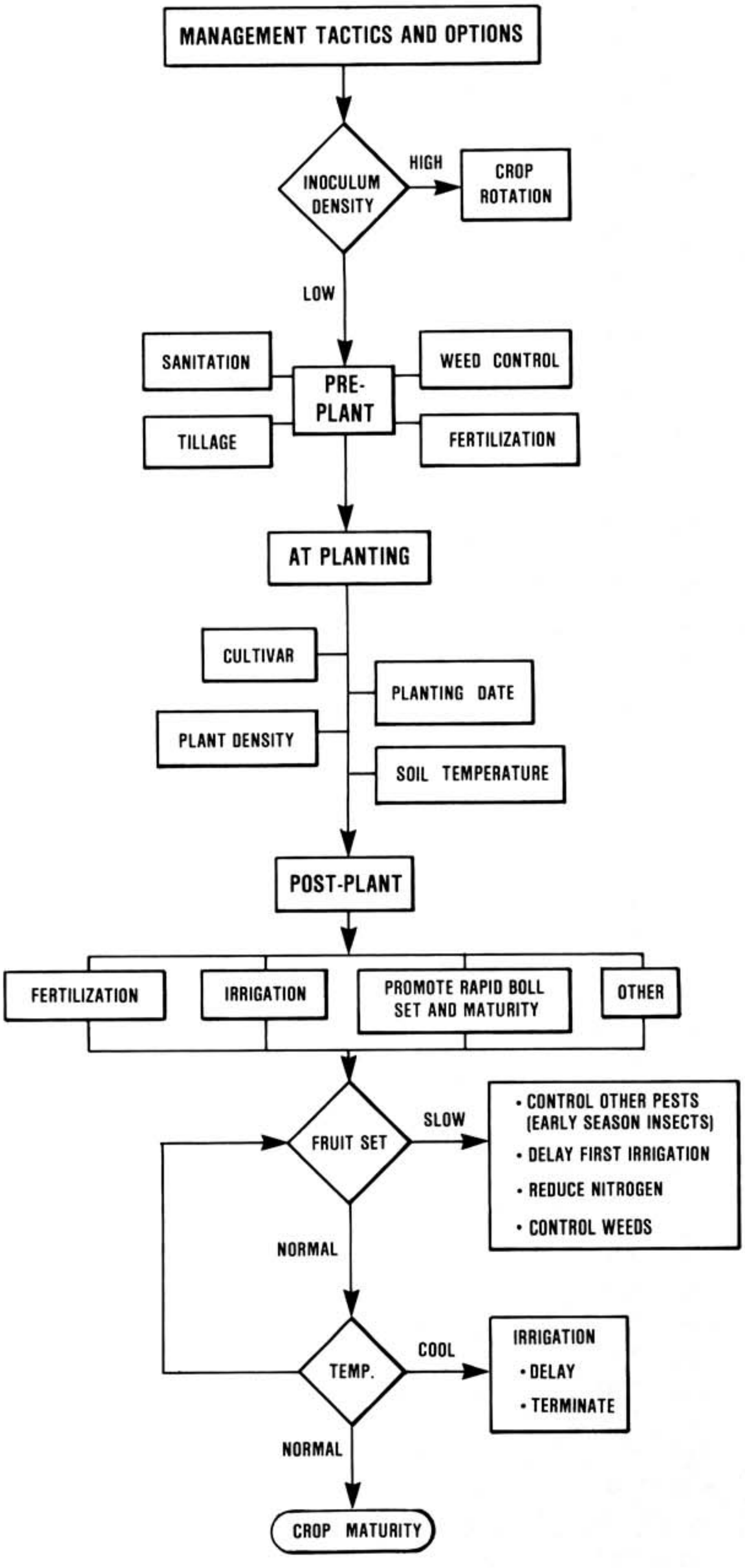

Fig. 8. Integrated seasonal management tactics and options to control Verticillium wilt of cotton.

Temperature effects. Cool air and soil temperatures favor Verticillium wilt of cotton. Optimum temperatures for disease development are between 22 and 25 C (3,12). Low night temperatures trigger early-season disease development, provided the maximum day temperatures do not exceed 30 C. Symptom severity and fungal colonization decrease rapidly as temperature increases from 22 to 28 C. High air temperatures (⩾28 C) decrease the susceptibility of cotton to wilt (3,4,12) and restrict in vivo growth of the fungus. *V. dahliae* pathotypes also differ in optimum temperatures for growth. The nondefoliating SS-4 strain from cotton has an optimum of 24 C, whereas the defoliating T-1 strain has an optimum of 27 C (26). Germination and growth of *V. dahliae* are inhibited at temperatures above 30–33 C, and fungus structures die at temperatures above 36 C.

Control Measures

Only an integrated management system (Fig. 1) can effectively control Verticillium wilt. The most effective control is achieved by growing adapted resistant cultivars and using cultural and management practices known to reduce disease severity (6,8). The benefits derived from different control measures depend largely on the pathotype of the causal fungus and the amount of inoculum in the soil. Disease development and symptom expression are influenced profoundly by environment, including temperature and light, soil moisture, major elements (nitrogen, phosphorus, potassium), minor elements, soil texture and organic content, rhizosphere-rhizoplane flora and fauna, and chemicals (8).

The rate at which epidemics of plant diseases progress depends on the magnitude of four fundamental variables: the initial inoculum density, the infection rate, time, and the stage of growth and development of the host. Each of the four variables may act as a limiting factor. If either initial inoculum density or infection rate is zero, there can be no epidemic. If time is short, as when an early-maturing cultivar sets its potential yield before infection progresses, the disease progress curve would never reach its theoretical stationary stage. Control tactics, each affecting a different factor among the four, may produce a synergistic and additive effect. Control methods to prevent a disease epidemic should be aimed at reducing the initial inoculum density, the survival and dispersal of the inoculum, the rate of infection, and the time the crop is exposed to infection.

Figure 8 illustrates an ICMS for cotton and control of Verticillium wilt. The system, as with all production systems, is dynamic in that it can vary according to the production region and environmental conditions. This ICMS can be used as a production model and as a checklist of key disease control tactics and options that should be considered throughout the season.

Control measures may be implemented before, at, or after planting, depending on the amount of inoculum in the soil (6). If the initial inoculum density is high, control measures may not lower the number of infective propagules enough to reduce disease severity and maintain yield. If inoculum density is 22 p/g or higher, the main option is crop rotation. If inoculum density is 5–20 p/g, several preplanting, at-planting, and postplanting practices are available.

Crop rotation. In planning a crop rotation system, consideration should be given to effects on the target pest and microbial balance in soil, other pests in the ecosystem, preserving the physical condition of the soil, practicality, and economics. Both short and long rotations are used as control tactics, but growers are often reluctant to utilize rotations longer than 1–3 years. A particular crop rotation system may be effective and practical in one area of the cotton belt, whereas an entirely different crop and rotation cycle may be most practical and economical in another area. Rotation crops must be chosen with care; even nonhosts of the pathogen may enable the pathogen to multiply and persist in the soil.

In cotton, rotation sequences such as cotton/sorghum/cotton, cotton/grain/cotton, and cotton/sorghum/grain aid in reducing propagules of soilborne pathogens. Barley straw has proved to be effective in reducing inoculum of many soilborne pathogens, including *V. dahliae*. Other rotation sequences of cotton with grasses, corn, sweet clover, alfalfa, or soybeans and weedfree fallowing may reduce losses from Verticillium wilt. Summer fallow and aeration reduce the amount of *V. dahliae* mycelia and conidia, but resistant microsclerotia are capable of surviving for many years in clean-fallowed fields. Paddy rice for a single year has given substantial increases in cotton yields and marked reductions in the amount of pathogen inoculum (21). Flooding alone reduces Verticillium wilt but not as effectively as paddy rice.

Preplanting practices. *Sanitation.* Sanitation is important in preventing the introduction of the fungus into wiltfree fields and in reducing losses from wilt in infected fields. Field application of plant residues infested with the pathogen, such as gin trash, often is a source of inoculum and can spread *V. dahliae* to disease-free fields. Composting trash eliminates some of the inoculum, and early plowdown to allow thorough rotting before planting further reduces inoculum in trash. Thus, stalk shredding, plowing under, and proper disposal of infected plant parts and debris that may harbor the pathogen can reduce the spread and severity of the disease. Implements and equipment used to prepare the soil for planting, cultivation, or other operations should always be cleaned and free from pest organisms.

Tillage. Verticillium wilt has been reported to be severe in sandy loam, loam and clay soils, and soils high in organic matter. The disease causes the most striking damage on clay soils. For years, Verticillium wilt was believed to be a problem only in alkaline soils; however, the disease is known to occur in neutral to acid soils in the Mississippi Delta and in Oklahoma.

Propagules of *V. dahliae* are most prevalent in the plant bed and top 30 cm of soil. Deep plowing, particularly where the soil is completely inverted, can be effective in reducing disease losses. Deep cultivation and root pruning in the presence of the pathogen increase disease severity and should be avoided during the growing season.

Weed control. Several weed species growing in and around cotton fields may serve as alternate hosts for *V. dahliae*. Development of microsclerotia in senescent tissues of infected weeds could raise the inoculum levels in the soil and thus neutralize any disease control obtained by rotation with a nonsusceptible crop. Susceptible weed species of economic importance in cotton production include pigweed, annual morningglory, prickly sida, common purslane, Carolina horsenettle, and silverleaf nightshade. An effective weed control program helps reduce the incidence of Verticillium wilt.

Row spacing. In the United States, cotton traditionally has been grown in rows spaced 102 cm apart and requires about 150–190 days to produce a crop. Attention in recent years has focused on the use of narrow-row spacings in a short-season production system as a means of controlling late-season pests and reducing production costs. Several row spacings and patterns have been studied. My colleagues and I (7) established that the 76-cm row spacing in the San Joaquin Valley of California increased lint yield 19% over that with the conventional 102-cm spacing. This increase represented 173 kg/ha for the Acala cultivars. In addition to higher yields, the percentage of plants showing foliar symptoms of Verticillium wilt was lower in cotton grown in narrow rows (51 and 76 cm) than in that grown in conventional 102-cm rows (9). Minton et al (20) reported that the percentage of wilt was decreased slightly in double-row patterns and significantly in single-row patterns by close row spacings (13, 25, and 51 cm) in Texas. Growers are

Table 1. Effect of irrigation treatments and cultivar on cotton lint yield and percentage of Verticillium wilt symptoms

Irrigation treatments				Percentage of Verticillium wilt	
Date of first irrigation	Number of irrigations	Water amount (cm)	Lint yield (kg/ha)	Foliar	Vascular
June 12	4	55.9	1,359 a[y]	50.8 a	76.6 a
June 28	3	43.2	1,537 b	26.8 b	52.2 b
July 6	2	30.0	1,518 b	24.4 b	52.1 b
Cultivar					
Acala SJ-2			1,406**[z]	44.8**	58.1*
Acala SJ-5			1,536	23.2	62.4
Mean			1,471	34.0	60.3

[y] Means within a column with the same letter are not significantly different ($P = 0.05$) according to Duncan's multiple range test.

[z] Significant at the * = 0.05 and ** = 0.01 probability level.

adopting the 76-cm row spacing and the short-season cotton production systems.

Fertilization. A balanced nutrition of the major elements (nitrogen, phosphorus, potassium) and the minor elements is very important in minimizing plant stress and susceptibility to pests. The amount, form, and time of application of fertilizers used in cotton production have a bearing on the incidence and severity of the disease and its control. Excessive use of nitrogen induces rank growth and delays maturity, often increases disease incidence and yield loss, and enhances insect problems. Research has established that Verticillium wilt severity is correlated positively with the availability of nitrogen and negatively with the availability of potassium. Ammonium increases Verticillium wilt more than does nitrate or urea (24). Thus, nitrogen fertilization should be limited to levels for optimum yield. Potassium deficiency or unavailability greatly increases disease severity. The effects of phosphorus and micronutrients are variable and depend on nitrogen and potassium levels (24). However, manganese and zinc were reported to be the micronutrients that most frequently reduced disease severity.

Chemicals. Chemical control, including therapeutic control with systemic chemicals, has been reviewed (11). Fumigants, such as the general biocides methyl bromide and mixtures of methyl bromide and chloropicrin, are effective in eradicating *Verticillium* in soils. Effective treatments, however, frequently require tarping of the soil with polyethylene sheeting and deep placement of large doses of the chemical; these procedures are expensive. Chemical fumigants also may have undesirable effects on beneficial organisms, such as mycorrhizal fungi, in the rhizosphere. Several plant growth regulators have been reported to reduce disease severity and increase cotton yield (11).

At-planting practices. *Soil temperature.* Management tactics and practices that raise soil temperature, such as planting on beds, skip-row planting, and alternate furrow irrigation, reduce disease severity and crop loss.

Planting date. It is important to plant as early as possible to escape the effects of Verticillium wilt late in the season. Serious damage usually occurs during the latter third of the growing season, especially when soil temperature is below 28 C. Economic loss may be minimized when a high percentage of the crop is set and matured during the first two-thirds of the growing season. My associates and I (*unpublished*) concluded that the optimum time to plant cotton in the San Joaquin Valley is during the last week of March through April. Yield and fiber quality of cotton planted in May were significantly reduced and crop maturity delayed, compared with cotton planted during April.

Plant density. Several studies (8,20,24) have shown that increasing plant populations to about 120,000–150,000 plants per hectare increased yield and reduced the incidence of Verticillium wilt. Increasing the seeding rate, however, requires a positive control of the seedling disease complex.

Cultivars. The choice of cultivar is probably the single most important decision the grower makes in an integrated crop management system. The cultivar sets the framework for the level of susceptibility to pests, the tactics applied to manage the crop, and production costs. Differences in the resistance of *Gossypium* species and cultivars and sources of resistance to Verticillium wilt have been reviewed (2–4,31). All cottons are resistant to *V. dahliae* pathotypes when temperatures are above 30 C. High levels of resistance have been obtained from *G. barbadense* and *G. darwinii.* Only low levels of resistance to defoliating pathotypes of *V. dahliae* are available, and considerable loss may occur in the most resistant cultivars when temperatures are cool for extended periods. Although progress has been made during the past 25 years in developing cultivars resistant or tolerant to *V. dahliae*, higher levels of resistance are still needed. Examples of resistant American Upland (*G. hirsutum*) cultivars are Acala SJ-5, Acala C-1, Acala 1517V, and Paymaster 266. In the Soviet Union, the Tashkent cultivars show resistance to the pathogen.

Postplanting practices. Fertilization, irrigation, and promotion of rapid boll set and early maturity are the main postplant options for disease control (Fig. 8). Soil moisture, in the form of irrigation or rainfall, can influence both the host and the soil microflora and fauna. Irrigation practices that reduce soil temperature increase disease losses. Excessive moisture and nitrogen fertilization encourage rank growth, delay fruit set and maturity, and increase incidence of Verticillium wilt.

Fertilization. A split application of nitrogen can reduce disease severity and increase yield. Multiple application avoids excessive levels of nitrogen early in the growing season. If the need to correct nitrogen deficiency arises as the season progresses, nitrogen can be easily side-dressed or applied as a foliar fertilizer or in irrigation water.

Irrigation. Water management is an effective tool to manipulate cotton growth and development and to control pests (13). This can be achieved by regulating the amount and the schedule of irrigations. Other water management tactics involve reducing excessive soil moisture by using raised beds and drains and by selecting soils with good internal drainage. Earlier research on the effect of irrigation in Verticillium wilt has been reviewed (24).

The effects of irrigation and cultivar on the incidence of Verticillium wilt and cotton yield were studied during 1976, 1978, and 1979 on panoche clay loam soil at the University of California West Side Field Station. Field inoculum density ranged from 15.6 to 40.8 p/g of soil. The percentage of wilt was reduced significantly by decreasing the amount and frequency of irrigations (Table 1). The lower postplant irrigation treatments (30 and 43.2 cm) gave similar lint yields (1,518 and 1,537 kg/ha, respectively). The highest irrigation treatment (55.9 cm), however, reduced yield significantly (1,359 kg/ha). The percentage of both foliar and vascular wilt symptoms was significantly increased when irrigation was increased from 30 to 55.9 cm (Table 1). When the first irrigation was applied early, on June 12, the percentage of wilt symptoms was significantly higher than when the first irrigation was delayed until June 28 or July 6 (Table 1). Grimes and Huisman (14) reported similar results. Outbreaks of Verticillium wilt often follow irrigation late in the growing season, particularly when irrigation lowers soil temperature. Thus, irrigation should be kept to a minimum once mean temperatures begin to decrease appreciably late in the growing season. Cultivar differences were highly significant; the percentage of foliar wilt symptoms was lower and the amount of lint yield was higher with Acala SJ-5, a resistant cultivar, than with Acala SJ-2 (Table 1).

Promoting rapid boll set and maturity. Serious damage to plants and yield loss usually occur during the latter third of the growing season when the days are shorter, plant growth shades the soil more, and night temperatures are lower. Economic loss may be minimized by managing the crop for rapid boll set and maturity.

Protection of early fruiting forms (squares and flowers) is vital to reducing loss due to Verticillium wilt. When excessive early fruit forms are lost because of insect damage, the consequence is delayed fruit set, which extends the crop into periods when pathogen infection is more severe and damaging to production. Effective early-season insect detection and control based on economic thresholds are needed to avoid delayed fruiting and to prevent shedding of early forms. Care should be exercised in the selection of insecticides, however. The use of some organic phosphate insecticides before the first fruiting branch is initiated can delay fruiting and maturity (25).

Relationship of Wilt Symptoms with Yield and Fiber Quality

Verticillium wilt affects fiber properties as well as lint yield. Correlation coefficients and linear regressions were computed between the percentage of foliar and vascular wilt symptoms and the corresponding yield, gin turnout, percentage of lint, and fiber properties. The correlation between percentage of foliar symptoms and percentage of vascular symptoms was positive and highly significant (Table 2). However, foliar symptoms are generally recognized as a better indicator of adverse yield effects than vascular discoloration (2,9,22).

A highly significant linear correlation between cotton lint yield and percentage of foliar wilt symptoms was obtained. As the percentage of plants with foliar symptoms increased, lint yield decreased. This relationship can be expressed by the regression model ($R^2 = 0.421$),

$$RY = 1{,}419.2 - 3.886 \times (FS),$$

that expresses relative yield (RY) for Acala SJ-2 in the San Joaquin Valley, grown on panoche clay loam soil, as a function of the percentage of plants with foliar symptoms (FS) of Verticillium wilt.

A significant negative correlation was obtained between foliar and vascular wilt symptoms and fiber length (2.5% SL) and strength, and a positive correlation was obtained between wilt symptoms and fiber uniformity index. A negative relationship existed between foliar symptoms and percentage of lint, and a positive one existed between vascular symptoms and fiber elongation. Verticillium wilt did not influence gin turnout, fiber length (50% SL), or fiber fineness (micronaire value).

Integrating the Components

One must not tie his ship to a single anchor, nor his life to a single hope.—Epictetus

Verticillium wilt of cotton exemplifies the integrated crop management system. An ICMS must consider the biology and phenology of the crop, phenologies and dynamics of pests, rhizoplane and phylloplane microorganisms, soil characteristics, cultural and management practices, and environment (Fig. 1).

Various factors and components originating outside the specific plant-pathogen interactions influence the course of an epidemic or pathosystem dynamics. The formulation of economic thresholds, although a complicated process, is a key to the success of an ICMS. Predictive models for crops and pests will allow growers to determine and more accurately project economic thresholds and to predetermine the components of an ICMS that should be maximized for effective disease control. Models will facilitate the development of economic decision rules for the integrated management of the crop and pests, which may in turn reduce production costs and increase yields.

Table 2. Correlation coefficients (*r*) of cotton lint yield, gin turnout, and fiber properties with percentage of Verticillium wilt symptoms

Parameter	Percentage of Verticillium wilt	
	Foliar	Vascular
Foliar symptoms(%)	...	0.805**[a]
Lint yield (kg/ha)	−0.545**	−0.364**
Gin turnout	−0.085	0.077
Lint percentage	−0.245*	−0.054
Fiber length, 2.5% SL (in.)	−0.322**	−0.337**
Fiber length, 50% SL (in.)	0.093	0.193
Fiber uniformity index	0.327**	0.421**
Fiber strength (g/tex)	−0.611**	−0.609**
Fiber elongation (El)	0.157	0.288*
Fiber fineness (micronaire value)	−0.172	−0.048

[a] Significant at the * = 0.05 and ** = 0.01 probability level.

Three important precepts arise from the integral relationship between crop production and disease development. The first is that the integration of control practices must be based on the realization that individual pest species are single components of a complex agroecosystem. The second precept is that disease management is more successful if considered during all phases of crop production. A management system implies an orderly and planned approach involving two or more major components. Effective disease management may require the use of several approaches, at several

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times during a crop cycle, and integrated into the overall crop production system. The third precept is that changes in crop production affect disease management and control. For example, replacement of tillage by herbicide application is likely to alter the activities of several microorganisms in the rhizosphere; some may become more prevalent, others less so. Other pests in the system and pesticides may directly or indirectly influence host susceptibility to the pathogen and crop productivity. The Verticillium wilt conceptual model summarizes and links the interrelated factors conducive to disease development with the ICMS. Efforts to control Verticillium wilt of cotton that involve several options and tactics will be more stable and effective than those relying on a single option.

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