Effect of Planting Date and Host Genotype on the Root-Knot Nematode-Fusarium Wilt Disease Complex of Cotton

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ABSTRACT

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Four cotton (*Gossypium hirsutum*) genotypes and three biweekly planting dates, beginning during late March, were examined for 3 yr in a split-plot field design to determine effects on Fusarium wilt development. Cotton genotypes included Acala SJ-2, susceptible to *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita*; Acala SJC-1, tolerant of *F. o. vasinfectum* and susceptible to *M. incognita*; N6072, susceptible to *F. o. vasinfectum* and resistant to *M. incognita*; and N8577, tolerant of *F. o. vasinfectum* and resistant to *M. incognita*. Fusarium wilt disease was low, moderate, and severe, for 3 yr, respectively. A planting-date effect of more Fusarium wilt in earlier plantings was found and was most evident in Acala SJ-2. This effect was indicated by a higher percentage of plant death, total foliar and plant-death symptoms, root discoloration, and yield suppression in earlier compared to later plantings. Analyses of planting-date main effects indicated significant ($P = 0.05$–0.001) linear trends in these variables. In the moderate- and severe-wilt years, Acala SJ-2 final plant-death values were 62–75 in the first and 23–28% in the third planting, and yield was suppressed by 55–75% in the first compared to the third planting date. Adult female and total *M. incognita* numbers in Acala SJ-2 roots early in the season were higher in the first compared to the later plantings during the severe-wilt year, and during 2 yr, significant ($P = 0.05$–0.001) linear trends of higher post-harvest nematode root-infection levels in earlier plantings were found in Acala SJ-2 and Acala SJC-1. Acala SJ-2 was colonized most extensively by *F. o. vasinfectum*, followed by N6072; Acala SJC-1 and N8577 had limited stem colonization. Compared to Acala SJC-1, plant death in N6072 caused by Fusarium wilt was similar at low but greater at high *M. incognita* initial densities. N6072 had healthier root systems and higher yield than had Acala SJC-1, indicating nematode resistance was more effective than wilt tolerance in protecting plants from the disease complex, whereas combined nematode and wilt resistance in N8577 was most effective. Delayed planting of cotton has important potential as a Fusarium wilt disease-management tactic.

Fusarium wilt of cotton (*Gossypium* spp.) was first described by Atkinson in Alabama in 1892 (2). In upland cotton (*Gossypium hirsutum* L.), a disease complex involving *Fusarium oxysporum* Schlechtend.:Fr. f. sp. *vasinfectum* (Atk.) W.C. Snyder & H.N. Hans. and the root-knot nematode *Meloidogyne incognita* (Kofoid & White) Chitwood occurs. In the presence of the nematode, the incidence and severity of Fusarium wilt generally are increased (2,13). In California, Fusarium wilt symptoms typically are associated with the presence of *M. incognita*, although in many *M. incognita*-infested cotton fields *F. o. vasinfectum* apparently is absent (11). *M. incognita* has not been shown to predispose *G. barbadense* L. or *G. arboreum* L. to Fusarium wilt under field conditions.

Soil fumigation to control *M. incognita* has been effective in reducing Fusarium wilt disease in *G. hirsutum* (24), although this can be expensive and the long-term availability of widely used fumigants such as 1,3-dichloropropene is uncertain. Resistance in cotton to both *F. o. vasinfectum* and *M. incognita* has been described, and many cultivars are tolerant of or resistant to one or both of these pathogens (25,26,36–38,41). No commercially suitable *M. incognita*-resistant cotton cultivars are available for the San Joaquin Valley of California, where losses from *M. incognita* and Fusarium wilt are often important in lint and seed production (9,11,19); however, two breeding lines (N8577 and N6072) have been developed with *M. incognita* resistance and are adapted for the San Joaquin Valley (the USDA, SEA, and Calif. Agric. Exp. Stn., Univ. Calif. released four root-knot nematode resistant cottons of noncommercial breeding stock [N9281, N9308, N9311, and N6072] in 1978).

Few studies have reported on the influence of planting date on Fusarium wilt severity in cotton, although in other crops, soil temperature influences root infection and wilt severity (4,8, 27,28). *G. barbadense* grown at 15 C prior to inoculation with *F. o. vasinfectum* was more susceptible to Fusarium wilt than was cotton grown at higher temperatures (1). Temperatures favorable for root infection by *F. o. vasinfectum* and those optimal for wilt development may differ (10). A soil temperature of 30.5 C was optimal for disease development in *G. hirsutum* inoculated with *F. o. vasinfectum* in the absence of *M. incognita*. Below this temperature, little wilt developed (45). However, Fusarium wilt developed at 23–25 C (day) and 17–19 C (night) temperatures when both *F. o. vasinfectum* and *M. incognita* were present (13).

Temperature influences the dynamics of *Meloidogyne* populations by affecting egg development and hatch (14,43), second-stage juvenile (J2) activity in the soil and during root penetration (14,31,32,34,44), and growth, development, and reproduction once a feeding site has been established within the root (32,34,44). Hatch occurs between 10 and 35.5 C (14), but J2 motility and root penetration have a lower threshold temperature (18 C) (14, 31,32,34). Once a feeding site is established, nematode development proceeds between 10 and 35 C (6,43). Development of *M. arenaria* (Neal) Chitwood in grape roots has been expressed in degree days above the threshold temperature of 10 C (DD10), and 440 DD10 is required to reach reproductive maturity after inoculation with infective J2 (12). In the absence of host root tissue, 90% of *M. incognita* J2 became nonmotile by 500 DD10 (14). *Meloidogyne* J2 are responsive to minute temperature changes and migrate in a thermal gradient of 10^{-3} C/cm (30); the importance of this thermal sensitivity is not known. The impact of *Meloidogyne* infection on root development and plant growth is influenced by the plant's developmental stage at the time of infection; soil temperature influences the duration of increased susceptibility of the root tissue early in seedling development (35). Adjustments in planting date of host crops, such as carrot and wheat, affect root infection and seasonal multiplication rates of

M. incognita and have important potential for nematode-management programs (32,34).

The objectives of this study were to evaluate the influence of cotton genotype, planting date, and initial population densities of *F. o. vasinfectum* and *M. incognita* on Fusarium wilt development in *G. hirsutum* under field conditions. Preliminary reports have been published (20–22).

MATERIALS AND METHODS

During 1984–1986, field-plot studies were conducted at the USDA Cotton Research Station near Shafter, CA, on a site infested by *M. incognita* race 3 and *F. o. vasinfectum*. The soil type was a Wasco sandy loam (77% sand, 11% silt, and 12% clay) with pH 7.3–7.8. A split-plot design with four replications was used. Main-plot treatments were three planting dates, and subplot treatments were cotton genotypes. Subplots were four rows wide by 18-m long, with 1-m row spacing. Three planting dates were spaced 2 wk apart, beginning at the end of March. Cotton genotypes were chosen based on different reactions to *F. o. vasinfectum* and *M. incognita*: cv. Acala SJ-2, susceptible to both *F. o. vasinfectum* and *M. incognita*; cv. Acala SJC-1, tolerant of *F. o. vasinfectum* and susceptible to *M. incognita*; breeding line N6072, susceptible to *F. o. vasinfectum* and moderately resistant to *M. incognita*; and breeding line N8577, tolerant of *F. o. vasinfectum* and more resistant to *M. incognita* than is N6072. The portion of the field site used in 1985 was planted to okra (*Hibiscus esculentus* L.) in 1984 to increase both *F. o. vasinfectum* and *M. incognita* soil-population densities. The same portion was replanted in 1986 after the cotton genotypes were randomly reassigned to the subplots within the planting dates.

Preplant soil-inoculum determinations. Two composite soil samples, each consisting of 12 cores (2 × 35 cm), were taken from the center two rows of each subplot prior to planting to determine the initial *F. o. vasinfectum*- and *M. incognita*-population densities. *M. incognita* J2 were extracted from a 250-cm^3 subsample of soil by the wet sieve-Baermann funnel mist extraction method (32). The values presented are the means of two soil samples but are not corrected for total numbers, based on an extraction efficiency of approximately 20% (11). Only one of the bulked soil samples was used to determine *F. o. vasinfectum* propagule density. A 5-g air-dried soil subsample was dilution-plated on five plates of peptone pentachloronitrobenzene (P-PCNB) medium (29). Putative *F. oxysporum* colonies (based on physical appearance) were transferred to potato-dextrose agar plates and incubated at 22 C for 4 days prior to identification. All putative *F. o. vasinfectum* colonies were tested for pathogenicity in greenhouse tests on 1-wk-old cotton Acala SJ-2 seed-

TABLE 1. Preplant soil populations of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* and effects of planting date and cotton genotype on end-of-season disease and nematode ratings and yield for 1984

Main effects and interactions	*F. o. vasinfectum* (p/g soil)[s]	*M. incognita* (J2/250 cm^3 soil)[s]	Vascular discoloration (%)[t,u]	Root-system discoloration (%)[t,v]	Weighted nematode rating (%)[u,w]	Yield (kg/ha)
Planting date						
1	331	0	48.9	24.9	15.2	1,361
2	305	0.4	37.7	15.9	7.3	1,396
3	248	0	40.8	16.4	5.0	1,301
Linear[x]	NS	NS	NS	*	**	NS
Nonlinear	NS	NS	NS	NS	NS	NS
Genotype	320 a	0.5 a	51.1 b[y]	27.7 a	20.4 a	1,396 a
Acala SJ-2	300 a	< 0.1 a	74.9 a	23.9 a	13.3 a	1,294 b
Acala SJC-1	288 a	0 a	30.1 c	14.2 b	2.5 b	1,294 b
N6072	270 a	0 a	13.7 d	10.5 b	0.5 b	1,426 a
N8577						
Genotype × Planting date						
Linear	NS	NS	NS	NS	**	NS
Nonlinear	NS	NS	NS	NS	NS	NS
Acala SJ-2 × 1	320	nd[z]	60.0	35.2	22.2	1,433
Acala SJ-2 × 2	300	nd	45.8	22.8	11.8	1,438
Acala SJ-2 × 3	280	nd	47.5	25.2	5.8	1,318
Linear	NS	...	NS	*	**	NS
Nonlinear	NS	...	NS	NS	NS	NS
Acala SJC-1 × 1	325	nd	79.0	29.0	36.4	1,292
Acala SJC-1 × 2	320	0.1	70.2	21.5	17.0	1,288
Acala SJC-1 × 3	220	nd	75.5	21.2	7.8	1,301
Linear	NS	NS	NS	NS	***	NS
Nonlinear	NS	NS	NS	NS	NS	NS
N6072 × 1	320	nd	20.5	22.0	1.2	1,273
N6072 × 2	330	nd	11.0	11.5	0	1,350
N6072 × 3	310	nd	9.5	9.0	6.4	1,260
Linear	NS	...	NS	*	NS	NS
Nonlinear	NS	...	NS	NS	NS	NS
N8577 × 1	360	nd	36.0	13.2	1.1	1,447
N8577 × 2	270	1.4	23.8	8.0	0.4	1,508
N8577 × 3	180	nd	30.5	10.2	0	1,323
Linear	NS	NS	NS	NS	NS	NS
Nonlinear	NS	NS	NS	NS	NS	NS

[s] Preplant.
[t] Postharvest.
[u] Percentage of plants with vascular discoloration.
[v] Percent root discoloration (100% based on all plants with maximum score on index of 0–4).
[w] Percent weighted nematode rating (100% based on all plants with maximum root-gall score on index of 0–4).
[x] Probability levels for main effects and interactions are $P \leq 0.05$(*), 0.01 (**), and 0.001(***); NS = not significant.
[y] Means with no letters in common are significantly different ($P \leq 0.05$) on Fisher's protected LSD test.
[z] Not detected.

lings. Each fungal colony was dispersed in 15 ml of water to prepare conidial suspensions. The lower third of taproots from three seedlings was excised, and the cut ends of the seedlings were placed in a conidial suspension (approx. 3.5×10^5 total conidia per colony) for a minimum of 3 min and were planted in UC-soil mix (3). The plants were incubated at 27–32 C (day) and 21–27 C (night) temperatures for 2–3 wk, at which time the plants were rated for foliar wilt symptoms and vascular discoloration. The lower hypocotyl of each seedling was cut transversely and given a plus or minus vascular discoloration rating. The density of *F. o. vasinfectum* propagules/g of soil was calculated by multiplying the number of colonies producing vascular discoloration by the total-dilution denominator (propagules per 5 g of soil) and dividing by five.

Data collection after planting. Soil temperatures were recorded continuously with a Foxboro thermograph (Foxboro Company, Foxboro, MA.) for 2 mo after the first planting date at a depth of 7.5 cm in 1984 and at 5, 15, and 30 cm in 1986. Soil temperatures were not recorded in 1985, but spring and summer ambient temperatures were slightly cooler than those in 1984, although April was warmer. Seedling emergence counts were made 2 wk after planting in 3.9 m of row in each of the center two rows of the subplots. During May, all subplots were thinned to the standard plant density of approximately 2 plants/30 cm of row, after which the total number of plants for the beginning of the season was recorded for each yield row.

***F. o. vasinfectum* isolation from plant tissue.** At 2 and 6 wk after planting, plant colonization by *F. o. vasinfectum* was determined. In 1984, 2 wk after planting, 5% (between 25 and 40 plants) of the plants in the outer two rows were collected for each cotton genotype and planting date, and *F. o. vasinfectum* was isolated. The plants were washed thoroughly under running water and surface-disinfested in 0.5% NaOCl for 1 min. Serial sections of the plants (radicle, hypocotyl, epicotyl, and cotyledons) were plated on P-PCNB medium to isolate *F. o. vasinfectum*. Six weeks after planting, 10 plants were collected from the outer rows of each subplot of the first and second planting-date treatments, and five plants of the third planting date, which was sampled after the field had been thinned, were collected. The plants were surface-disinfested, and serial sections of the root, stem, and petioles were plated on P-PCNB medium to isolate *F. o. vasinfectum*. In 1985, 10 plants for use in *F. o. vasinfectum* isolation were collected from the outer rows in each subplot 2 and 6 wk after planting.

The time of maximum boll stress (boll-growth demand) on cotton plants occurs near the end of July in this growing region, and in 1984, subplots were resampled at this time to determine the extent of *F. o. vasinfectum* colonization of cotton plants.

TABLE 2. Preplant soil populations of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* and effects of planting date and cotton genotype on end-of-season disease and nematode ratings and yield for 1985

Main effects and interactions	*F. o. vasinfectum* (p/g soil)[t]	*M. incognita* (J2/250 cm^3 soil)[t]	Vascular discoloration (%)[u,v]	Root-system discoloration (%)[u,w]	Weighted nematode rating (%)[u,x]	Yield (kg/ha)
Planting date						
1	680	5.4	36.6	50.0	57.1	864
2	955	4.4	35.8	44.6	57.1	1,062
3	848	7.7	38.7	37.9	50.9	1,046
Linear[y]	NS	NS	NS	*	NS	*
Nonlinear	NS	NS	NS	NS	NS	NS
Genotype	817 a[z]	6.7 a	96.6 a	86.4 a	93.3 a	625 c
Acala SJ-2	847 a	4.6 a	60.7 b	48.8 b	92.6 a	939 b
Acala SJC-1	910 a	6.0 a	28.2 c	24.3 c	19.5 b	1,184 a
N6072	737 a	6.0 a	15.1 c	17.1 c	14.8 b	1,215 a
N8577						
Genotype × Planting date						
Linear	NS	NS	NS	NS	NS	*
Nonlinear	NS	NS	NS	NS	NS	NS
Acala SJ-2 × 1	770	5.2	95.0	94.3	98.6	362
Acala SJ-2 × 2	880	4.2	100.0	89.3	96.4	717
Acala SJ-2 × 3	800	10.5	94.8	75.7	85.0	796
Linear	NS	NS	NS	*	*	***
Nonlinear	NS	NS	NS	NS	NS	NS
Acala SJC-1 × 1	620	4.5	65.1	57.1	96.4	812
Acala SJC-1 × 2	1,025	3.0	55.3	49.3	92.9	1,036
Acala SJC-1 × 3	870	6.4	61.6	40.0	88.6	969
Linear	NS	NS	NS	*	NS	NS
Nonlinear	NS	NS	NS	NS	NS	NS
N6072 × 1	700	8.0	29.5	30.0	21.4	1,176
N6072 × 2	1,010	3.9	34.8	21.4	20.7	1,198
N6072 × 3	1,020	6.1	20.4	21.4	16.4	1,179
Linear	NS	NS	NS	NS	NS	NS
Nonlinear	NS	NS	NS	NS	NS	NS
N8577 × 1	630	4.0	5.3	18.6	12.1	1,107
N8577 × 2	880	6.4	16.9	18.6	18.6	1,297
N8577 × 3	700	7.8	23.2	14.3	13.6	1,241
Linear	NS	NS	NS	NS	NS	NS
Nonlinear	NS	NS	NS	NS	NS	NS

[t] Preplant.
[u] Postharvest.
[v] Percentage of plants with vascular discoloration.
[w] Percent root discoloration (100% based on all plants with maximum score on index of 0–4).
[x] Percent weighted nematode rating (100% based on all plants with maximum root-gall score on index of 0–4).
[y] Probability levels for main effects and interactions are $P \leq 0.05$(*), 0.01 (**), and 0.001(***); NS = not significant.
[z] Means with no letters in common are significantly different ($P \leq 0.05$) on Fisher's protected LSD test.

Two plants per subplot were collected from the outer rows of three of the four subplots within each main plot. The small sample was taken because of the large number of tissue sections from each plant to be plated for *F. o. vasinfectum* isolations. The plants were surface-disinfested. Serial sections were taken every 15 cm up the main stem, beginning at the root crown, and a 1-cm section of each branch or petiole directly adjacent to the main stem also was collected. All sections were plated on P-PCNB medium. All putative isolates of *F. o. vasinfectum* obtained from plant tissue were confirmed with greenhouse pathogenicity tests. A percentage of the total plant height colonized by *F. o. vasinfectum* was determined. The same sampling procedure was used in 1985 and 1986 during the boll-stress period.

Nematode infection of young cotton plants. In 1986, 10 cotton plants were dug, to a depth of 20 cm, from the outer rows of the Acala SJ-2 and N8577 subplots at weekly intervals for 6 wk after planting. The plant and the soil ball surrounding the roots were placed in an elutriator, and the plant material was collected on a 40-mesh sieve (0.5-mm aperture). Roots from the four subplots of the same treatment were bulked and fixed in 10% formaldehyde solution. To identify and count *M. incognita* developmental stages (5), the root tissue was washed extensively in water, and three 1-g subsamples were cleared in 1.5% NaOCl for 3.5 min, rinsed in water, and stained in an acetic acid/acid fuchsin solution.

Foliar wilt symptoms. Approximately biweekly throughout each growing season, the numbers of dead plants and of those with Fusarium wilt symptoms were recorded. The final foliar wilt ratings and the total number of plants in the yield rows were determined during early September.

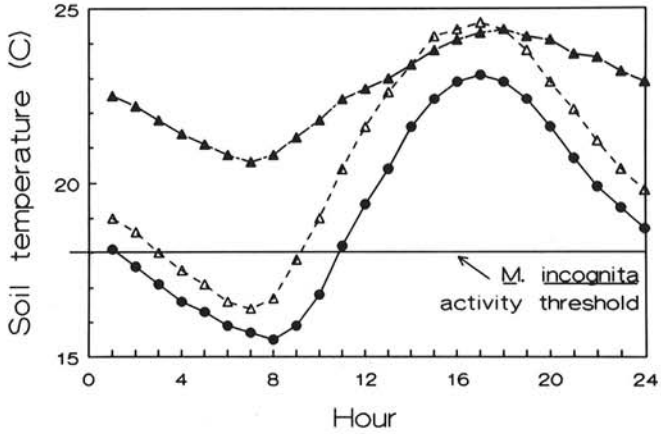

Fig. 1. Hourly average soil temperatures at a 15-cm depth for 2 wk after each of three planting dates, 24 March (●) and 8 (△) and 21 (▲) April 1986.

TABLE 3. Preplant soil populations of *Fusarium oxysporum* f. sp. *vasinfectum* and *Meloidogyne incognita* and effects of planting date and cotton genotype on end-of-season disease and nematode ratings and yield for 1986

Main effects and interactions	*F. o. vasinfectum* (p/g soil)[t]	*M. incognita* (J2/250 cm^3 soil)[t]	Vascular discoloration (%)[u,v]	Root-system discoloration (%)[u,w]	Weighted nematode rating (%)[u,x]	Yield (kg/ha)
Planting date						
1	634	22.3	90.0	33.9	58.8	538
2	600	21.5	78.3	33.4	55.6	569
3	630	23.4	82.0	34.3	54.2	627
Linear[y]	NS	NS	NS	NS	*	*
Nonlinear	NS	NS	NS	NS	NS	NS
Genotype						
Acala SJ-2	747 a[z]	23.0 a	97.8 a	66.5 a	92.5 a	252 c
Acala SJC-1	608 ab	16.9 a	88.3 ab	32.1 b	88.2 a	523 b
N6072	650 a	24.8 a	85.6 b	22.7 c	29.5 b	751 a
N8577	480 b	24.8 a	62.2 c	14.2 d	14.6 c	785 a
Genotype × Planting date						
Linear	NS	NS	NS	**	NS	***
Nonlinear	NS	NS	NS	NS	NS	NS
Acala SJ-2 × 1	760	18.8	100.0	62.4	94.8	102
Acala SJ-2 × 2	830	24.4	93.3	68.6	92.8	245
Acala SJ-2 × 3	650	25.8	100.0	68.6	90.0	408
Linear	NS	NS	NS	NS	NS	***
Nonlinear	NS	NS	NS	NS	NS	NS
Acala SJC-1 × 1	560	6.8	93.3	43.3	91.9	509
Acala SJC-1 × 2	620	20.1	80.0	25.2	86.4	515
Acala SJC-1 × 3	645	23.9	91.6	27.6	86.2	545
Linear	NS	NS	NS	*	NS	NS
Nonlinear	NS	NS	NS	*	NS	NS
N6072 × 1	735	22.4	90.0	15.7	33.8	759
N6072 × 2	530	29.0	81.7	25.7	29.8	719
N6072 × 3	685	23.1	85.0	26.7	25.0	775
Linear	NS	NS	NS	NS	*	NS
Nonlinear	NS	NS	NS	NS	NS	NS
N8577 × 1	480	41.1	76.6	14.3	14.8	780
N8577 × 2	420	12.6	58.3	14.0	13.3	795
N8577 × 3	540	20.8	51.7	14.3	15.7	780
Linear	NS	NS	*	NS	NS	NS
Nonlinear	NS	NS	NS	NS	NS	NS

[t] Preplant.
[u] Postharvest.
[v] Percentage of plants with vascular discoloration.
[w] Percent root discoloration (100% based on all plants with maximum score on index of 0–4).
[x] Percent weighted nematode rating (100% based on all plants with maximum root-gall score on index of 0–4).
[y] Probability levels for main effects and interactions are $P \leq 0.05$(*), 0.01 (**), and 0.001(***); NS = not significant.
[z] Means with no letters in common are significantly different ($P \leq 0.05$) on Fisher's protected LSD test.

Yield. The center two rows of each subplot were machine harvested once to obtain yield data. Lint yields were estimated for 1 ha of cotton, based on the harvest data for 36 m of row and a 33% gin turnout.

Postharvest disease ratings. The plants in a 3.9-m section of each (1984), in one (1985) of the two center rows, or 15 randomly collected plants per subplot (1986) were sectioned below the cotyledonary node to determine the percentage of plants with vascular discoloration. The center two rows were undercut at 20 cm to facilitate removal of 10 (1985), 15 (1986), or 20 (1984) plants per subplot to assay weighted nematode root-gall and external root-discoloration ratings. Root discoloration was rated on a scale of 0–4 (0 = healthy with no discoloration, 1 = discoloration only on the tertiary roots, 2 = discoloration of one or more secondary roots, 3 = discoloration of a portion of the taproot and secondary roots, and 4 = severe discoloration of the whole root system). Root galling was rated on a scale of 0–4 (0 = no root galling, 1 = galls on only a few roots, 2 = galls on several tertiary and secondary roots, 3 = galls on much of the root system, with clusters of galls on some roots, and 4 = roots severely galled, with many clusters of galls) to evaluate *M. incognita* root infection. The root-gall ratings were weighted for the number of occurrences at each level, and the sums of these values were expressed as a percentage of the highest possible rating (23). In 1984, root-discoloration ratings were not weighted, but a weighted rating (as for root galling) was determined for 1985 and 1986.

TABLE 4. Accumulated degree days above the temperature thresholds of 10, 12, and 18 C for 14 days after each planting date at 5-, 15-, and 30-cm soil depths in 1986

Soil depth (cm)	Planting date	Accumulated degree days (DD)[z]		
		DD10	DD12	DD18
5	March 24	178	150	68
	April 08	185	157	74
	April 21	199	171	87
15	March 24	131	103	29
	April 08	149	121	42
	April 21	179	151	67
30	March 24	149	121	37
	April 08	163	135	51
	April 21	180	152	68

[z] Determined by the single sine wave method.

RESULTS

Preplant soil inoculum. In 1984, *M. incognita* was detected in only three of the 48 subplots, and initial *F. o. vasinfectum*-population densities ranged from 60 to 640 propagules/g (p/g) of soil. In 1985, the number of *M. incognita* recovered ranged from 0.5 to 24.5 J2/250 cm^3 of soil, and *F. o. vasinfectum* propagules ranged from 400 to 1,440 p/g of soil. In 1986, an increased initial *M. incognita*-population density, 1.0–102 J2/250 cm^3 of soil, was present, with *F. o. vasinfectum* densities between 200 and 1,000 p/g of soil. Within years, initial densities of both organisms did not differ significantly between genotype or planting-date treatments (Tables 1–3).

Postplant soil temperature. For cotton, a developmental threshold of 12 C has been reported (16); for *M. incognita*, a developmental threshold of 10 C and an activity threshold of 18 C have been reported (14,34). In 1984, at a 7.5-cm soil depth, temperatures for 14 days after planting varied between 12 and 28, 15 and 32, and 24 and 42 C after the first, second, and third planting dates, respectively. In 1986, temperatures were monitored at 5-, 15-, and 30-cm soil depths. A mean soil temperature at a 15-cm soil depth was determined for each hour of the day in the 14-day period after each planting (29 March and 8 and 21 April) (Fig. 1). Soil temperatures after the first and second plantings were similar but differed from those after the third planting date, which had higher minimum values. Degree days above the threshold temperatures of 10, 12, and 18 C were calculated by the single sine wave method for minimum-maximum temperatures (14) (Table 4). The first planting-date treatment had the fewest accumulated degree days at each threshold temperature, and the second planting-date treatment had fewer than the third, but the soil temperatures did not limit cotton germination or *M. incognita* activity.

TABLE 5. Colonization by *Fusarium oxysporum* f. sp. *vasinfectum* of four cotton genotypes 2 and 6 wk after planting, presented as combined data for planting-date treatments in each year

Year and weeks	Genotype	Plant segment—proportion of samples colonized (%)							Total plants
		Radicle[u]	Hypocotyl	Epicotyl	Cotyledons	1st node	2nd node	Other nodes	
1984									
2 wk[v]	Acala SJ-2	39.3 a[w]	8.9 a	1.8 a	0.0 a	...[x]	...	...	112
	Acala SJC-1	40.4 a	10.1 a	0.9 a	0.0 a	...	...	...	109
	N6072	40.0 a	7.8 a	0.0 a	0.0 a	...	...	...	115
	N8577	35.8 a	2.1 a	0.0 a	0.0 a	...	...	...	95
6 wk[y]	Acala SJ-2	41.0 ab	1.0 a	1.0 a	1.0 a	0.0 a	1.0 a	1.0 a	100
	Acala SJC-1	53.0 a	3.0 a	1.0 a	1.0 a	1.0 a	1.0 a	0.0 a	100
	N6072	52.0 a	4.0 a	3.0 a	3.0 a	1.0 a	2.0 a	1.0 a	100
	N8577	30.0 b	1.0 a	0.0 a	1.0 a	2.0 a	1.0 a	0.0 a	100
1985									
2 wk[z]	Acala SJ-2	25.7 a	10.0 a	0.0 a	0.0 a	...	...	...	120
	Acala SJC-1	16.7 b	4.2 a	0.0 a	0.0 a	...	...	...	120
	N6072	20.0 ab	5.0 a	0.0 a	0.0 a	...	...	...	120
	N8577	19.2 ab	4.2 a	0.0 a	0.0 a	...	...	...	120
6 wk[z]	Acala SJ-2	66.7 a	5.8 a	2.5 a	3.3 a	0.8 a	1.7 a	0.8 a	120
	Acala SJC-1	73.3 a	0.8 a	0.8 a	0.0 a	0.0 a	0.0 a	0.8 a	120
	N6072	70.8 a	6.7 a	2.5 a	1.7 a	0.0 a	1.7 a	0.0 a	120
	N8577	64.2 a	8.3 a	2.5 a	0.8 a	0.8 a	0.8 a	0.0 a	120

[u] At 6 wks, the pathogen was isolated from the root-stem transition zone.

[v] A 25–40 plant sample was collected from each of the two outer rows in every subplot for *F. o. vasinfectum* isolation.

[w] Analysis of variance was performed on the arcsine-transformed percentage values. The three planting dates in each year were combined, and the nontransformed means are listed. Within each sampling time, values followed by the same letter in the same column do not differ significantly at $P = 0.05$ on the LSD t test.

[x] Plants at this developmental stage lack expanded tissue for these plant parts.

[y] Ten plants were collected from the outer rows for every subplot in the first and second planting, and five plants were collected from the outer rows in the third planting, which was sampled after thinning to two plants per 30 cm.

[z] Ten plants were collected from the outer rows of every subplot for *F. o. vasinfectum* isolation.

Plant-emergence and seedling disease rating. No significant within-year or between-year differences were observed in the emergence rate of the four cotton genotypes. Moreover, no differences were seen in the extent of colonization by *F. o. vasinfectum* within each cotton genotype for the three planting dates; therefore, the data presented are the combination of all three planting dates for each cotton genotype (Table 5). The extent of colonization of cotton seedlings by *F. o. vasinfectum* 2 wk after planting did not differ significantly among genotypes in 1984 or 1985 (Table 5). Six weeks after planting in 1984, N8577 had a significantly lower ($P = 0.05$) percent colonization of the radicle than had Acala SJC-1 and N6072. In 1985, at 6 wk, no significant differences occurred among the four cotton genotypes. More of the root-stem transition zone for all cotton genotypes was colonized after 6 wk in 1985 than was colonized in 1984.

Root population of *M. incognita* (1986). In the first planting-date treatment, Acala SJ-2 had higher root populations of *M. incognita* adults at 3 and 6 wk and of juveniles (all stages) at 4 wk when compared with the other planting dates (Fig. 2A and B), and total numbers of juveniles and adults were higher in the first than in the third planting-date treatment at 4–6 wk (Fig. 2C). *M. incognita* root populations did not differ significantly between planting dates 6 wk after planting in N8577. However, roots from the first planting date had significantly higher ($P =$

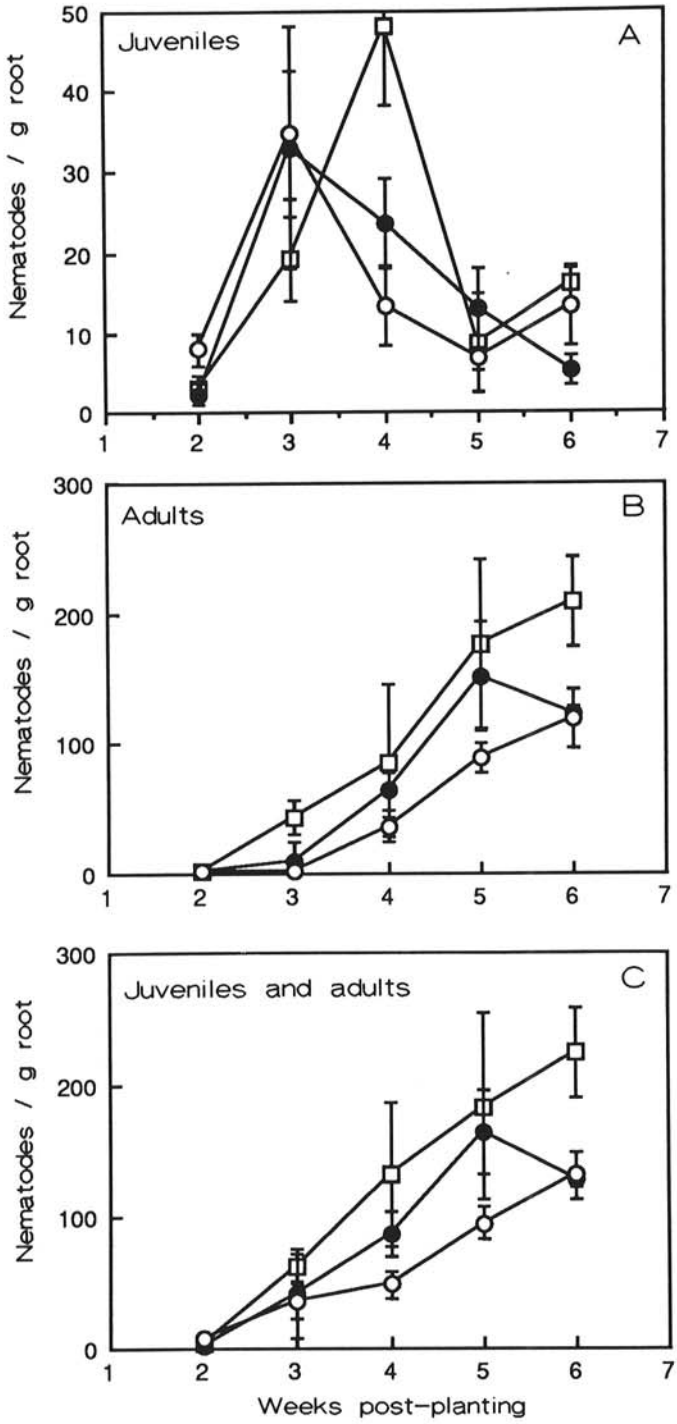

Fig. 2. *Meloidogyne incognita* **A,** juvenile (stages J2–J4), **B,** adult female, and **C,** juvenile and adult infection of Acala SJ-2 root tissue during 6 wk after each planting date, 24 March (□) and 8 (●) and 21 (○) April 1986. Mean (with standard error bars) of three 1-g root subsamples from 40 plants.

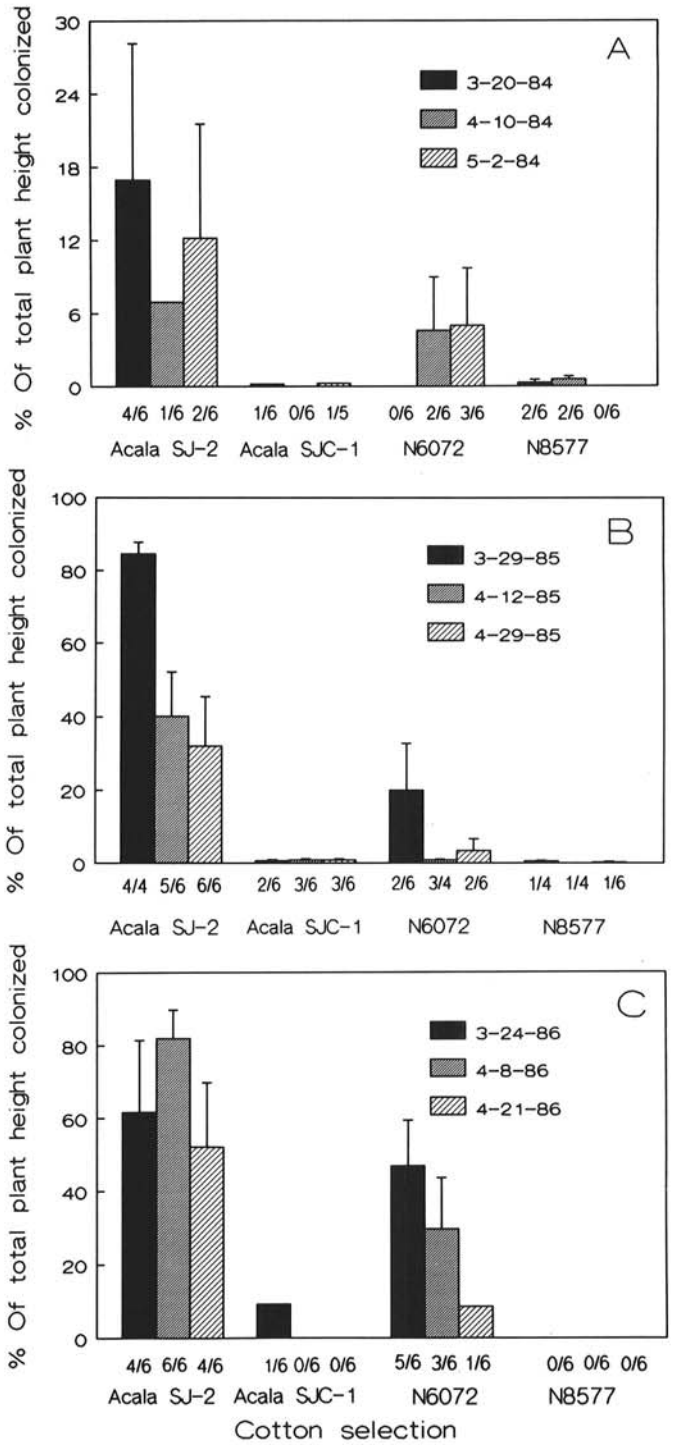

Fig. 3. Effect of cotton genotype and planting date on percentage of total plant height colonized by *Fusarium oxysporum* f. sp. *vasinfectum* at time of boll stress in **A,** 1984, **B,** 1985, and **C,** 1986. Values below the x axis indicate number of plants colonized per number of plants sampled. Bars indicate standard errors.

0.01) *M. incognita* populations 6 wk after planting in Acala SJ-2 than in N8577, with 223 *M. incognita*/g of root compared to 54 *M. incognita*/g of root, respectively.

Fusarium wilt development. Foliar symptoms of Fusarium wilt and plant death were not observed during the 1984 study but were present in all cotton genotypes in 1985 and 1986. Foliar symptoms became evident in all genotypes 3–5 wk after planting and were most prevalent in Acala SJ-2 by the end of May (9 wk). In all 3 yr, Acala SJ-2 was colonized most extensively by *F. o. vasinfectum*, based on isolations made during July, followed by N6072; Acala SJC-1 and N8577 were sparsely colonized by *F. o. vasinfectum* above the root-stem transition zone (Fig. 3). In 1984, except for N8577, all genotypes were colonized less extensively than in 1985 and 1986. No consistent trends in height of colonization by *F. o. vasinfectum* were associated with planting-date treatments (Fig. 3).

Acala SJ-2 had the highest level of foliar wilt symptoms and plant death for both 1985 and 1986 compared to other genotypes. N6072 and Acala SJC-1 were similar; N6072 had slightly more plant death and fewer foliar symptoms in 1986 than had Acala SJC-1, and Acala SJC-1 had slightly more plant death and foliar symptoms in 1985 than had N6072 (Figs. 4 and 5). In 1985, plant death of Acala SJ-2 in the first planting was higher than in the second and third plantings beginning during June (before 1,100 DD12) (Fig. 4A). In 1986, plant death of Acala SJ-2 in the first planting was higher than in the two later plantings by the second week of June (before 600 DD12), and all planting-dates differed by July (before 1,100 DD12) (Fig. 4B).

Although Acala SJC-1, N6072, and N8577 had less wilt disease than had Acala SJ-2, a similar planting-date trend of higher plant death in the first planting also was seen for these genotypes and became significant ($P = 0.05$) later in the season (Fig. 4), based on accumulated plant death and DD12. In a final sampling during early September 1985 and 1986, higher ($P = 0.05$) plant death and total (plant death plus foliar symptoms) wilt symptoms were present in the first planting compared to later plantings of Acala SJ-2 (Fig. 5A and B); the percentage of living plants with foliar symptoms did not differ (1985) or were higher in later plantings (1986) because fewer infected plants in later plantings died. On N6072, foliar and total wilt symptoms were higher ($P = 0.05$) in the first than in the second planting, but plant death alone did not differ among planting dates in 1985 (Fig. 5E). In 1986, N6072 plant death and foliar symptoms in the first planting were higher than in the third planting but not in the second, whereas total symptoms differed significantly ($P = 0.05$) for all three planting dates (Fig. 5F). No planting-date differences were observed in foliar wilt symptoms or plant death for Acala SJC-1 in 1985 (Fig 5C). In 1986, plant death and total wilt symptoms of Acala SJC-1 in the first planting were significantly higher than

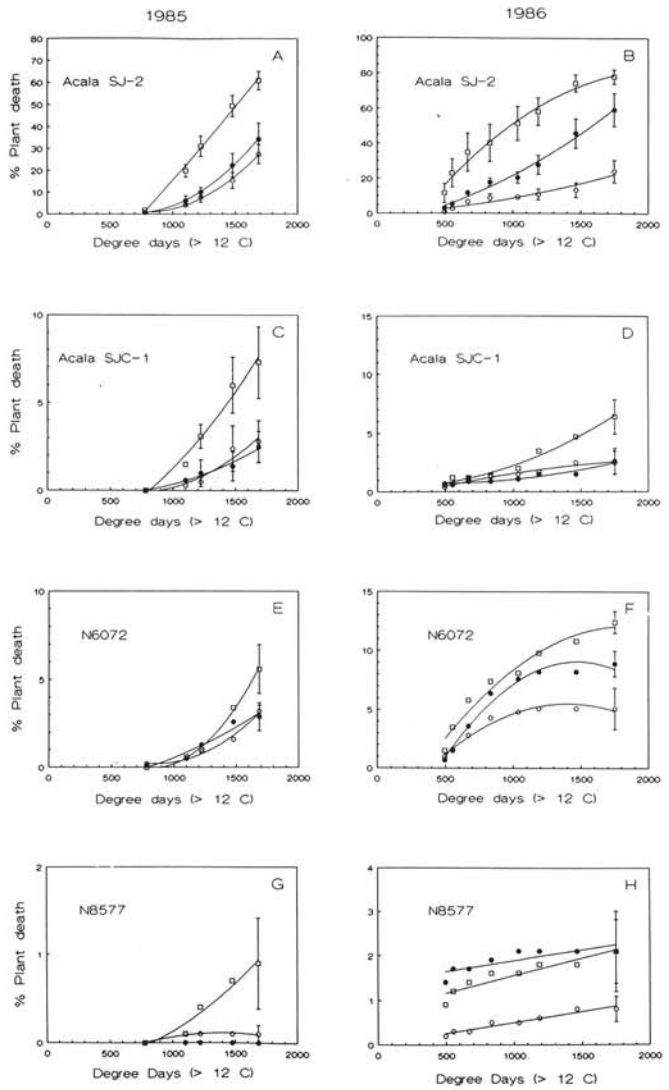

Fig. 4. Effects of cotton genotype and planting date on Fusarium wilt-induced percent plant death over physiological time. Planting dates for 1985 (**A, C, E, and G**) and 1986 (**B, D, F, and H**), respectively, were 24 and 29 March (□), 8 and 12 (●), and 21 and 29 April (○). Standard error bars are presented when there are differences between planting dates. Values of r^2 for the second order polynomial regression curves ranged from 0.911 to 0.999 (except for the nonsignificant regression of the second planting of N8577 in 1985).

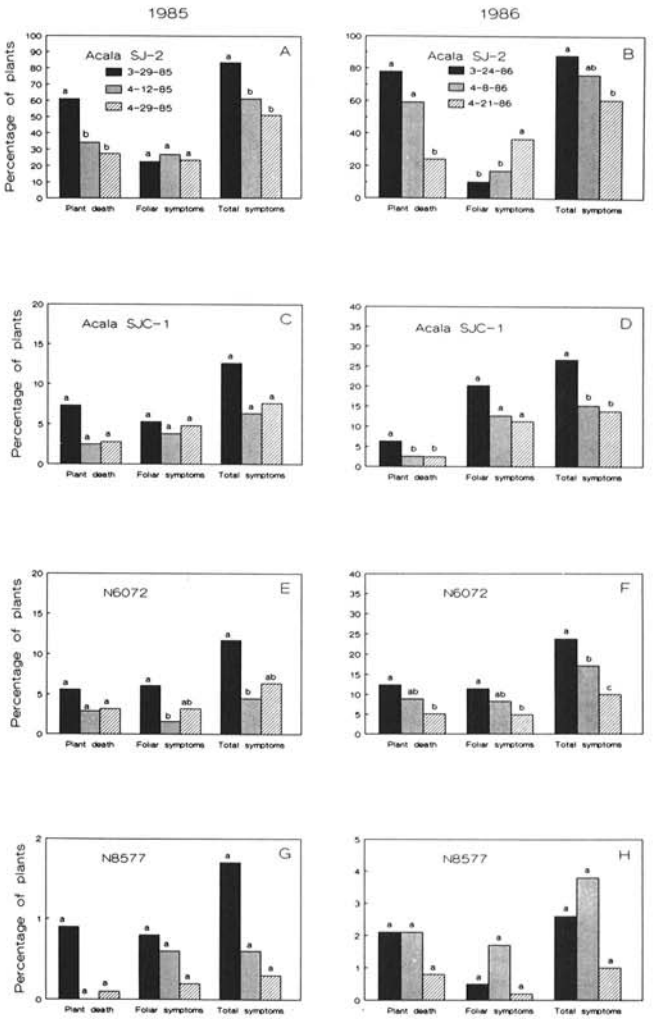

Fig. 5. Effects of cotton genotype and planting date on the percent plant death, foliar symptoms, and combined total Fusarium wilt symptoms present on 4 September 1985 (**A, C, E, and G**), and 6 September 1986 (**B, D, F, and H**). Planting dates within each category, plant death, foliar symptoms, and total symptoms, that have the same letter do not differ significantly at $P = 0.05$ according to the LSD t test.

in the second and third plantings (Fig. 5D). No differences occurred in wilt symptoms or plant death of N8577, which were very low in both years (Fig. 5G and H).

Postharvest disease ratings. Planting-date main effects on root galling had a significant linear trend of higher weighted nematode ratings (WNR) with earlier planting in 1984 and 1986 (Tables 1 and 3). Comparisons by genotype showed the trend was associated with *M. incognita*-susceptible Acala SJ-2 and Acala SJC-1 in 1984 (low nematode-population density) and with *M. incognita*-resistant N6072 in 1986 (high nematode-population density). Genotype main effects had significantly higher WNR values on *M. incognita*-susceptible Acala SJ-2 and Acala SJC-1 than on *M. incognita*-resistant N6072 and N8577 in all 3 yr (Tables 1–3). In 1986, under high-nematode initial densities, N8577 had significantly lower WNR values than had N6072 (Table 3).

A significant linear trend of higher root-system discoloration with earlier planting occurred in 1984 and 1985 (Tables 1 and 2), due to significant trends on the *Fusarium*-susceptible Acala SJ-2 and N6072 genotypes. In 1986, this trend was significant on Acala SJC-1 only, and a highly significant genotype × planting-date interaction (linear) occurred (Table 3). Genotype main effects revealed significantly higher root-discoloration ratings on Acala SJ-2 and Acala SJC-1 than on N6072 and N8577 in all 3 yr, and in 1985 and 1986, significant rankings of genotypes for root discoloration were Acala SJ-2 > Acala SJC-1 > N6072 > N8577 (Tables 1–3).

The percentage of plants with vascular discoloration was not influenced by planting date, except for a significant linear trend of more vascular discoloration with earlier planting on N8577 in 1986 (Table 3). Genotype main-effect comparisons revealed that Acala SJ-2 had the highest and N8577 had the lowest percentage of plants with vascular discoloration over the 3 yr. N6072 had significantly less vascular discoloration than Acala SJC-1 had in 1984 and 1985, significantly less than Acala SJ-2 had in all 3 yr, and significantly more than N8577 had in all 3 yr (Tables 1–3).

Yield. No planting-date effect on yield occurred in 1984 when *M. incognita* and *F. o. vasinfectum* initial densities in soil were low (Table 1). A small genotype effect (Acala SJC-1 and N6072 yielded more than Acala SJ-2 and N8577) occurred in 1984 (Table 1). A significant linear trend of lower yield with earlier planting date occurred in both 1985 and 1986, when *M. incognita* and *F. o. vasinfectum* initial densities in soil were high (Tables 2 and 3). A significant genotype × planting-date interaction (linear) on yield was found in both of these years; planting-date effect on yield by genotype was highly significant on *M. incognita*- and *F. o. vasinfectum*-susceptible Acala SJ-2 in both years, but not on yield of the other genotypes. Genotype main effects on yield in both 1985 and 1986 showed that N6072 and N8577 yielded significantly more than Acala SJC-1 and Acala SJ-2, and Acala SJC-1 yielded significantly more than did Acala SJ-2 (Tables 2 and 3). All cotton genotypes were stunted in 1986, due partly to limited irrigation.

DISCUSSION

Four cotton genotypes that express different resistances to *M. incognita* and/or *F. o. vasinfectum* were used to investigate which organism or organisms in the root-knot nematode-Fusarium wilt disease complex are most influenced by the effects of different planting dates. Results in 1985 and 1986 clearly showed that earlier planting within the normal spring-planting period promoted Fusarium wilt severity on all genotypes and suppressed cotton lint yield of Acala SJ-2, the genotype susceptible to both organisms. The environmental factors involved in this planting-date effect may have acted on the host plant, nematode, or wilt fungus separately or on any of the interactions that occur in the infection and disease-development process. Results of nematode-infection levels indicate effects on the nematode component were a major determinant of planting-date impact on wilt disease.

Soil temperatures were above the *M. incognita* developmental threshold of 10 C during the experimental period from the first planting date and were above the *M. incognita* activity threshold of 18 C for a time period every day at the soil depths measured in 1986. Thus, temperatures were not low enough after any of the planting dates to restrict root penetration and subsequent development of *M. incognita*. Trends of more nematodes in roots from earlier plantings were apparent, particularly adult females, at equivalent times up to 6 wk after planting. On the same calendar date (5 May 1986; 6 wk after the first planting in Acala SJ-2), 208, 63, and 0 *M. incognita* adults/g of root tissue were recovered from planting-date treatments one, two, and three, respectively. By this date, 438 DD10 had accumulated at a 15-cm soil depth since the time of the first planting. *M. arenaria*, with temperature requirements similar to those of *M. incognita*, lays eggs by 440 DD10 after inoculation of French Colombard grape (12), and a similar rate of development could be expected for *M. incognita* in cotton.

Temperature, time, and associated degree-days accumulated affected the metabolic reserves of *Meloidogyne* J2 and their ability to penetrate the root. For example, motility and infectivity of *M. javanica* J2 at 15 C were maintained for 16 days, but at temperatures between 25 and 35 C, stored lipids, motility, and infectivity declined. These reductions were more rapid as temperatures increased or fluctuated (42). In *M. incognita* J2 cohorts maintained in soil at 29 C, 90% were nonmotile by 500 DD10, with an average rate of decline in activity in moist soil of 0.2% of the original population per DD10 (14). Both eggs and J2 are important in the overwintering of *M. incognita* in California cotton fields, and egg hatch is promoted by increasing soil temperatures (21). *M. incognita* J2 can establish a feeding site after migrating 25–50 cm through soil, with roots serving as an attractant for migration (31). In the absence of host root tissue and with temperatures favorable for hatch and motility, *M. incognita* soil populations could decline significantly before a delayed planting, as suggested by lower root-infection levels in the later plantings. Based on the demonstrated positive correlation of *M. incognita* inoculum level to expression of Fusarium wilt (13), the lower *M. incognita* infection of cotton roots in later compared to earlier plantings could have played a key role in reducing Fusarium wilt severity in later planting-date treatments.

Lower *M. incognita* initial population densities were less damaging to cotton than were higher population densities (11,33,40), and lower *M. incognita* initial populations resulting from delayed planting could have lessened any direct nematode-injury effects to cotton growth and yield. On Acala SJ-2, a direct impact of nematode infection would have been most likely to occur in 1986 when initial *M. incognita*-population densities were well above the reported (11) tolerance or damage threshold (approximately 3–5 J2/250 cm^3 of soil) for this system, but any effects were masked by the severe-wilt impact. Acala SJC-1 has a *M. incognita* damage function similar to that of Acala SJ-2 (P. A. Roberts, *unpublished data*), but it is tolerant of Fusarium wilt. The relatively lower yields of Acala SJC-1 compared to *M. incognita*-resistant N6072 in 1985 and 1986, suggest that initial *M. incognita*-population densities in all planting-date treatments were high enough to limit yield of *M. incognita*-susceptible Acala SJC-1 directly but were not damaging in 1984. A greater sensitivity of cotton yield to changes in *M. incognita* initial densities occurs in the presence than occurs in the absence of *F. o. vasinfectum* (19,33,40). The planting-date effects on yield of *M. incognita*-susceptible genotypes differing in tolerance to Fusarium wilt support these reported relationships.

Planting-date effects on plant death in Acala SJ-2 became significant in 1986 at the time when development of second-generation *M. incognita* in roots was occurring in the first planting. With more *M. incognita* present in Acala SJ-2 roots in the first than in later planting-date treatments early in the season, these differences in nematode populations could be expected to increase from the first *M. incognita* root generation to later generations, until root injury limited population increase. High- compared to low-inoculum levels of *M. incognita* hasten Fusarium wilt development (13,35). Postharvest WNR represent the overall differences that occur throughout the season but do not express the

time schedule in which the differences were reached. An inverse relationship between high *M. incognita* root populations and root growth and health due to infections by *F. o. vasinfectum* and *M. incognita* could affect the suitability of the root tissue for further infection by *M. incognita* J2. Differences in WNR between planting-date treatments, higher on earlier plantings, were more apparent in 1984 on *M. incognita*-susceptible Acala SJ-2 and Acala SJC-1, when nematode initial-population densities were low. These differences were not apparent in 1985 and 1986 because high levels of *M. incognita* infection occurred in all planting dates by late season, even though important differences in nematode-infection levels occurred earlier in the season.

The effects of *M. incognita* soil-population densities on Fusarium wilt development have been studied in greenhouse and microplot experiments (13,40). Under 17–19 C (night) and 23–25 C (day) greenhouse temperatures and with population densities of 5,100 *F. o. vasinfectum* p/g of soil and 360 *M. incognita* per plant, Fusarium wilt symptoms developed in 44 days. With 50 *M. incognita* per plant and the same *F. o. vasinfectum* propagule level, wilt symptoms were not observed until 53 days (13). In a microplot study with either 2,300 or 4,300 *F. o. vasinfectum* cfu/g of soil and 0.1–50 *M. incognita*/100 cm^3 of soil, severity of Fusarium wilt development late in the season was increased by high *M. incognita* populations (40). These reports generally agree with our observed trends in differences in wilt expression between high or low *M. incognita* years, *M. incognita*-susceptible or -resistant genotypes, and planting dates. The data presented on *F. o. vasinfectum*-propagule densities in soil generally agree with a report that moderate levels of Fusarium wilt foliar symptoms occurred in cotton at 400 *F. o. vasinfectum* p/g of soil and high levels at 800 *F. o. vasinfectum* p/g of soil in the presence of *M. incognita* (39).

Temperatures below 15 C adversely affect cotton germination and seedling development (41). Root exudation, especially sugars, increases in cool soil (18). Carbohydrate content of root tissue is higher at 10–15 C than at 20 C or higher soil temperatures (15). Chilling injury at or below 10 C can cause the primary root tip to abort and cortical sloughing to occur in cotton seedlings (7). Soil temperature affected amino acids and carbohydrates quantitatively in cotton seed and root exudates, and these differences influenced host susceptibility to seedling disease caused by *Pythium ultimum* and *Rhizoctonia solani* (18). Although soil temperatures that severely impact (e.g., chilling injury) the physiological processes of germinating seed and cotton seedlings were not a factor in the present field studies, the possible impact of subtle changes in root physiology and chemistry with different planting date-associated temperature regimes on *F. o. vasinfectum* or *M. incognita* infection is not known.

Differences in Fusarium wilt susceptibility were not due solely to *M. incognita* susceptibility. Acala SJC-1 (*M. incognita* susceptible, *F. o. vasinfectum* tolerant), which for three years had higher WNR values than had N6072 (*M. incognita* resistant, *F. o. vasinfectum* susceptible), did not have greater *F. o. vasinfectum* colonization at boll stress, Fusarium wilt foliar symptoms, or plant death at the end of the season than had N6072, and in 1986, Acala SJC-1 had slower wilt development than had N6072. This reflects differences between the two cotton genotypes in Fusarium wilt tolerance. With higher *M. incognita* initial-population densities, N6072 was more susceptible to Fusarium wilt.

Early season root and stem colonization by *F. o. vasinfectum* did not differ between planting dates or genotypes in 1984, nor in 1985 when greater Fusarium wilt development and colonization of the root-stem transition zone occurred. Assessment of colonization apparently is a poor indicator of Fusarium wilt susceptibility under field conditions. Vascular colonization by *F. o. vasinfectum* was more extensive and intensive in *F. o. vasinfectum*-susceptible than in -resistant cotton in a study that used artificial inoculation of the root with *F. o. vasinfectum* (17). The percentage of plants with postharvest vascular discoloration below the cotyledonary node did not indicate planting-date effects, but it did provide overall separation of genotypes, with greater vascular discoloration on *M. incognita*-susceptible than on -resistant genotypes. Differences in vascular discoloration were smaller in 1986 under severe-disease potential, when all genotypes had 62% or more vascular discoloration. Foliar symptoms provided a better measure than did vascular discoloration of Fusarium wilt susceptibility in these genotypes under field conditions, contrary to other field studies in which foliar symptoms of Fusarium wilt could be confused with symptoms due to other causes (37). Root discoloration was useful for describing the health of the cotton root system, and it was associated more with *M. incognita* susceptibility than with *F. o. vasinfectum* susceptibility.

The four cotton genotypes responded differently to environmental conditions during the 3 yr of field studies, although their ranking for Fusarium wilt susceptibility did not change. Acala SJ-2, susceptible to *F. o. vasinfectum* and *M. incognita*, had the highest plant death, yield reduction, and planting-date differences when *M. incognita* initial-population densities were the greatest. N6072, resistant to *M. incognita* but susceptible to *F. o. vasinfectum*, had a smaller planting-date effect and was more sensitive to high-population densities of *M. incognita* than was Acala SJC-1, as indicated by plant-death progression. The postharvest root- and vascular discoloration ratings, however, were lower on N6072 than on Acala SJC-1, indicating that N6072 plants were healthier at maturity than were Acala SJC-1 plants. N8577 was highly resistant to *M. incognita* and tolerant of Fusarium wilt in all 3 yr. These genotype responses to the disease complex indicate the protective advantage of combined resistances to nematode and wilt in the same genotype, as in N8577. Resistance to one but not to both organisms provides partial protection from nematode and wilt infection effects, as in Acala SJC-1 and N6072. Nematode-resistant, Fusarium-susceptible genotype N6072 generally was able to develop and maintain a healthier root system and yield better than was nematode-susceptible, Fusarium-tolerant Acala SJC-1 in the presence of the disease complex, despite a susceptibility to wilt. This was particularly apparent at high-population densities of *M. incognita*.

The genotype comparisons indicate the significant direct-damage potential of the nematode on nematode-susceptible cottons, such as Acala SJC-1, together with the predisposing effect of the nematode for wilt expression, confirming other reports (19,33, 36,40). Thus, in N6072, nematode resistance protected plants from direct nematode injury and limited predisposition to wilt, whereas a lack of nematode resistance in Acala SJ-2 resulted in severe-wilt expression. Comparisons of Acala SJC-1 and N6072 indicate that in a choice between breeding for either nematode or wilt resistance (i.e., when combining the two traits may be difficult), nematode resistance would be of greater disease-management value than would Fusarium wilt resistance or tolerance, supporting other field and greenhouse studies (19,36). Factors that suppress *M. incognita*-infection levels in cotton (achieved traditionally by soil fumigation with nematicides [11,24]), whether genetic (nematode resistance) or environmental (planting-date effect), can provide significant protection from the root-knot nematode-Fusarium wilt disease complex. Our results suggest delayed planting of cotton may be an important Fusarium wilt disease-management tactic.

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