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Reducing plant abiotic and biotic stress: Drought and attacks of greenbugs, corn leaf aphids and virus disease in dryland sorghum

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Abstract

Multi-year spatial overlay patterns of plants, insects and soil water may yield insights for management for reducing biotic and abiotic stresses in dryland crops. A study of non-irrigated grain sorghum (*Sorghum bicolor* (L.) Moench) was conducted in a Pullman clay loam on the semi-arid High Plain of Texas during 2002–2005. The objectives of the 4-year study were to understand the mechanisms of plant spatial and temporal responses to stress from drought, infestations of greenbug, corn leaf aphid (CLA) and maize dwarf mosaic virus (MDMV) disease and soil water content (SWC) heterogeneity, and to reduce plant biotic and abiotic stress using their underlying relationships in space and time. Infrared IRT/c sensed-canopy temperature was measured at 18 or 54 sites along transects in a 6 m × 6 m grid across the years. Greenbugs, CLA, MDMV, SWC and hyperstrectral reflectance were determined at each IRT/c site. Natural infestations of greenbugs and CLA on sorghum occurred in early July and insect populations peaked in late July or early August. Insect attacks resulted in plant water stress and sorghum yield loss except a late replanting in early July in 2004. Sorghum grain yield was negatively correlated with canopy temperature, greenbug and CLA ($-0.38 < r < -0.75$, $P < 0.05$), and positively correlated with SWC and plant near infrared reflectance ($0.25 < r < 0.67$, $P < 0.05$). The IRT/c temperature decreased with SWC but increased with greenbugs and CLA ($0.26 < R^2 < 0.64$). Crosscorrelation analysis showed that these insect, crop, and soil variables were correlated in space within 48–54 m. Late planting in July or spray control in late July or early August would be options to reduce dryland sorghum water stress and yield loss from drought and insect attacks.

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1. Introduction

Most biotic and abiotic stresses (disease, insect, pathogen, temperature, drought, salinity, anaerobe, etc.) faced by plants were related to environmental conditions (Olson et al., 1990; Simpson and Daft, 1990; Kocsy et al., 2004; Luna et al., 2005; Li et al., 2004a, 2006; Garrett et al., 2006). In the semi-arid High Plains of Texas, water availability is one of major limitations to the productivity and sustainability of agricultural systems. With less and less water resource available, dryland (non-irrigation) practice has become common. Dryland sorghum (*Sorghum bicolor* (L.) Moench) had long-time drawn attentions mostly on plant abiotic stress from drought and precipitation

water use. Many studies found that soil water holding is the primary factor influencing cropping in the High Plain (Li et al., 2001, 2002; Payne, 2003; Nielsen et al., 2005). However, drought and high temperature would promote outbreaks of plant-eating (phytophagous) insects, which would result in more stresses from insect attacks and insect feeding-related diseases (White, 1984; Mattson and Haack, 1987; Olson et al., 1990; Srivastava, 2005; Garrett et al., 2006; Li et al., 2007a,b).

In Bushland on the Texas High Plain areas, growing season varies between 144 and 220 days per year, and annual precipitation is only 89–580 mm (mean 335 mm) (Baumhardt et al., 2005). The greenbug (*Schizaphis graminum*), corn leaf aphid (CLA) (*Rhopalosiphum maidis*), and maize dwarf mosaic virus disease (MDMV) are the most damaging pests and disease to many forage crops including grain sorghum on the High Plain (Drees and Jackman, 1999; Kindler et al., 2002). The greenbugs, light green aphids, usually migrate to the High Plain of Texas from southern regions during April and June each year. A single female can produce 1–8 offspring each day for 2–3 weeks

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and young insects reach maturity in 6–10 days and begin to reproduce without mating (Drees and Jackman, 1999). Usually from 12 to 20 generations can occur each season. Greenbugs are capable of causing sorghum plant mortality by feeding through removing juices from plant tissues and injecting a potent salivary toxin (Drees and Jackman, 1999; Kindler et al., 2002).

Corn leaf aphid populations can also increase quickly because the time required for growing adult females is short, only 7–14 days. There are 9–10 generations per season because mature females produce 2–3 young nymphs per day without mating over a 30-day period (Drees and Jackman, 1999). Leaf aphids feed on plants by sucking sap from the upper leaves and the infested leaves become covered with a sticky substance known as honeydew, causing plant to become sticky then may wilt and turn brown, which can reduce photosynthesis to affect yield. Under drought conditions severely aphid-infested plants can die (Bessin, 2004).

The MDMV disease is transmitted mechanically to plants by different aphids (Jardine, 1988). Many wild and cultivated grasses serve as MDMV overwintering hosts. The mosaic infestation would result in damages through stunting of plants and increasing susceptibility of secondary pathogens. The MDMV-infested plants may turn to a general yellowing and the youngest leaves have a light to dark green mottle or mosaic in narrow streaks along veins. Early infection is predisposed to root and stalk rots and plants may be barren and dead (Olson et al., 1990).

Up to these days, little information is available about the relationships between sorghum plant biotic and abiotic stress and sorghum yield loss from insect attacks, drought, and high temperatures on the High Plain. Studies in other areas reported that drought stress would increase pathogen and insect survival and growth through elevated plant nutrient levels, lowered plant defenses, and a more suitable physical environment such as limited water supply (White, 1984; Mattson and Haack, 1987; Garrett et al., 2006). When plants were attacked by root weevil adults or neonate larvae, plants were more water-stressed as indicated by the very low (near negative) leaf stomatal conductance (Li et al., 2004a, 2006). Gall-insects reduced plant inflorescence production (Fay et al., 1996), and water-stressed plants emitted little energy in the near infrared band (Carter and Knapp, 2001; Li et al., 2001). Also, it was established that spatial and temporal occurrence of citrus insect was positively associated with increasing air temperature, rainfall and soil water content (Li et al., 2007a,b,c). In some studies insect behavior was found to be affected by different crops (Risch, 1983), and the influence of insects on crop yield was greater than the influence of soil water holding on crop yield (Li et al., 2004b). However, other fungi such as mycorrhizal fungi associated with sorghum could increase the plant drought tolerance through increasing the plant osmotic adjustment (Simpson and Daft, 1990). The symbiosis of mycorrhizal fungal infection can enhance acclimation of asparagus plantlets by promoting initial growth in shoots and storage roots (Matsubara et al., 2001).

It is unknown the mechanisms by which drought would affect insect growth and population, and insect attacks would provoke more sorghum plant water stress and gain yield loss than

non-irrigation alone. No such spatial overlay patterns and complex relations between the abiotic and biotic factors have been established in the High Plain environment. Our intention was to understand if high temperatures and drought would become a more suitable physical environment to increase phytophagous insect survival and growth, and if insect attacks would contribute to increase plant water stress and cause yield loss.

We hypothesized that high air temperatures would influence the vigor of the sorghum plants on which the insects feed, and the spatial patterns of insect populations and disease incidence would be associated with environmental variations such as relative humidity, air temperature, and soil characteristics. Our objectives were to (i) assess overlay patterns of greenbug and leaf aphid populations, MDMV disease incidence, soil water content, sorghum canopy infrared temperature, plant and soil reflectance, and sorghum grain yield, (ii) determine the relationships between plant, insect, disease, soil, and the High Plain environment, and (iii) to develop management strategy for reducing crop abiotic and biotic stress through using overlay patterns of soil, water, crop and insect variables under the Texas High Plain pedoclimatic conditions.

2. Materials and methods

2.1. Study site

The study was conducted on Bushland Research Farm of Texas Agricultural Experiment Station on the High Plain of Texas during 2002–2005. The study site was a 20-ha, non-irrigated field. The soil was a Pullman (Pu) silty clay loam, classified as Fine, Mixed, Thermic Torrertic Paleustolls. Across the field, the Pullman clay loam contained two soil types, PuA and PuB, in which the PuA soil had a lower water holding capacity than the PuB soil (USDA-NRCS, 2003). The PuA type soil covered 95% of the field and the PuB soil was only within 10 m from the field edge in the east. The topsoil (0–0.3 m) contained $336 \pm 36 \text{ g kg}^{-1}$ clay, $406 \pm 13 \text{ g kg}^{-1}$ silt, and $258 \pm 32 \text{ g kg}^{-1}$ sand ($n = 54$). The site elevation was high (1131.9–1132.6 m) and the drought on the High Plain was associated with the high elevation (USDA-NRCS, 2003).

2.2. Field experiments

The experimental design in 2002 and 2003 was a single transect of 108 m running from west to east across the field. Along the transect, there were high clay content ($356 \pm 38 \text{ g kg}^{-1}$) in the west (24 m) and east (66 m), and low clay content ($252 \pm 32 \text{ g kg}^{-1}$) in the center-western areas (18 m). The transect was formed using 18 neutron access tubes, placed 6 m apart, within the PuA soil type zone. To capture more variability of soils, insects and sorghum plants in the field, in 2004 and 2005 two more transects were added parallelly, one in the north and the other in the south 6 m apart from the previous transect, also using 18 neutron access tubes, placed 6 m apart along each transect. As a result, the measurement points (or access tubes) were structured in a $6 \text{ m} \times 6 \text{ m}$ grid in the area of $108 \text{ m} \times 18 \text{ m}$. Within the grid, site elevation varied between $1132 \pm 0.3 \text{ m}$.

During the 4-year study, sorghum planting time was within the last week of May and the 2nd week of June each year, depending on rain patterns. The sorghum seed variety was Warner W560-T and sown at the rate of 2.3 kg ha^{-1} (or $32,000 \text{ seeds ha}^{-1}$). In 2004, because of the prolonged drought in the spring (for example, 5.41 mm rain for the month of May 2004), in early June, water (318 mm) was applied to the soil for the need of moisture for seeding. However, 3 weeks later, the emerged sorghum plants were destroyed by heavy hails. The field was rolling again for re-planting in early July. During the 4-year experiment, only 1 year (2004) sorghum planting and emergence were affected by the severe drought and hails in the spring. No fertilizers or waters or insecticides were applied to the sorghum plants during the four growing seasons. The only treatment was the weed control by applications of herbicides using Bicep II Magnum at the rate of 168 kg ha^{-1} and Larduroster BW at the rate of $1.523 \text{ m}^3 \text{ ha}^{-1}$ following the seeding each year.

Air temperature, relative humidity, rainfall and soil temperature (at 0.6 m depth) at the study site were obtained from Texas High Plains EvapoTranspiration (ET) Network, Texas A&M University. The daily mean air temperature (at 0.6 m) during the growing season (June–October) varied between $21.1 \pm 6.1 \text{ }^\circ\text{C}$ in 2002, $21.6 \pm 4.8 \text{ }^\circ\text{C}$ in 2003, $20.5 \pm 3.8 \text{ }^\circ\text{C}$ in 2004, and $21.7 \pm 4.3 \text{ }^\circ\text{C}$ in 2005. The annual precipitation totaled 349, 256, 502, and 315 mm in 2002, 2003, 2004 and 2005, respectively. The 4-year rainfall was highly variable ($356 \pm 105 \text{ mm}$) and the rain patterns were different from year to year (Fig. 1). The in-season monthly rainfall (June–October) varied between 55 ± 24 , 39 ± 31 , 59 ± 24 , and $35 \pm 30 \text{ mm}$ with decline of the in-season rainfall (79, 77, 59 and 55% of total yearly rainfall) from 2002 to 2005, respectively. The warmest growing season (2005) was also the driest season with only 173.1 mm rainfall concentrated in June (67 mm) and August (66 mm).

2.3. Insect, plant and soil measurements

Natural infestation of adult insect populations of greenbugs and corn leaf aphids were monitored weekly from early vegetative stage (late June) to the population disappearance each year. The adult insects were detected by carefully inspecting the sorghum leaf blades for the presence of greenbug and leaf aphid colonies. In 2002 and 2003, each week ten sorghum plants were randomly used for visually counting for total numbers of greenbugs and leaf aphids at each neutron assess tube site. In 2004 and

2005, because of the increase of monitoring sites, insect numbers were visually counted from three random plants at each site to calculate insect density per plant. Overall, weekly density of insects per plant was obtained from a total of 180 plants along the transect during 2002 and 2003, and from 162 plants in the $6 \text{ m} \times 6 \text{ m}$ grid during 2004 and 2005. Leaf tissue was randomly sampled at each site for determining MDMV disease infestation using enzyme-linked immunosorbent assay (ELISA) using the method shown in Olson et al. (1990).

Infrared thermocouple sensors IRT/c (Exergen, Watertown, MA) were used to continuously detect real-time canopy temperature 24 h per day at all neutron access tubes during the growing season. The mast-mounted IRT/c sensors were positioned along transects, with each IRT/c sensor per neutron tube site, to detect spatial and temporal variations of canopy temperature along the transect and in the $6 \text{ m} \times 6 \text{ m}$ grid. The IRT/c sensors were wired on multiplexers then connected to a CR23X datalogger (Campbell Science Inc., Logan, UT), which was programmed to record the sensors canopy temperature data in an interval of 10 min. The dataloggers were powered using solar panels (Campbell Scientific Inc.).

Relative humidity and air temperatures in the field were detected using HMP45C sensors (Campbell Scientific). The HMP45C sensor outputs were simultaneously recorded together with the IRT/c sensors data by the dataloggers in an interval of 10 min, 24 h per day during the growing seasons. Each week, the stored data were downloaded from the dataloggers in the field.

Monthly hyperspectral plant reflectance in the visible, near-infrared (NIR) and mid-infrared (MIR) band was measured using spectroradiometer (HR2000, Ocean Optics, Dunedin, FL). The hyperspectral reflectance was detected at an interval of 10 nm within 380–1000 nm wavelength at each IRT/c sensor site monthly during the growing season in 2005.

Soil was sampled at each IRT/c site in the depth of 0–1.2 m in an increment of 0.3 m a week before planting. Two cores of soils were sampled at each site. One core of soil was air dried for analysis of soil texture using the laser diffraction method (Zobeck, 2004), and the other core of soil was oven-dried at $110 \text{ }^\circ\text{C}$ for 24 h to determine soil gravimetric water content. Soil volumetric water content in the depth of 0–2.2 m was determined in the increment of 0.3 m using neutron probe, calibrated with soil gravimetric water content as described in Li et al. (2002).

Sorghum was hand harvested in an area of $2 \text{ m} \times 2 \text{ m}$ at each IRT/c sensor site (or neutron access tube site) along the

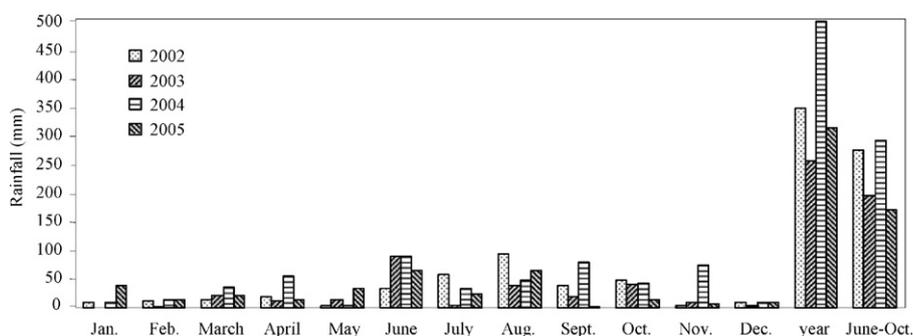


Fig. 1. Distributions of monthly, yearly, and in-season (June–October) rainfall at the study site across the 4-year experiment (2002–2005).

transects to determine the grain yield. Whole field sorghum was harvested using a combine monitor equipped by a differential Global Positioning System (DGPS) for yield mapping each year. In 2003 sorghum yield data were missed unexpectedly. In 2005, sorghum grain quality was determined for crude protein (CP) and acid detergent fiber (ADF) by Plant and Soil Analysis Laboratory at Texas A&M University (College Station, Texas). The CP was analyzed using the Kjeldahl method with the formula $CP = N\% \times 6.25$ (conversion factor) and the ADF, a parameter referring to the cell wall portions made up of cellulose and lignin, was determined using the sulfuric acid digestion-extraction method (Horwitz, 2000).

2.4. Data statistics

Descriptive statistics, correlation and regression analysis to insect, plant and soil data were done using PROC UNIVARIATE, PROC CORR and PROC GLM (SAS Institute, 1990). Homogeneity of variance of datasets was verified using the Bartlett test, and normality and residual distribution of data sets were confirmed using PROC UNIVARIATE (SAS Institute, 1990). For semivariogram analysis we used PROC VARIOGRAM (SAS Institute, 1996). Crosscorrelation, a statistical measure timing the movement and proximity of alignment between two different information sets, was done for all soil, water, plant and insect variables using SAS PROC ARIMA procedure (SAS Institute, 1993).

3. Results

3.1. Spatial and temporal patterns of greenbugs and leaf aphids

The dates of natural infestations of greenbugs and corn leaf aphids to the sorghum plants varied from year to year. In 2002, insects did not appear until August. In 2003, the initial date of insect infestation was in the 1st week of July and the infestation lasted 7 weeks. No insect infestation was found in the sorghum field in 2004, which would be because of the later replanting in early July (first planting was damaged by hails). In 2005, insects were naturally infested the sorghum plants from the 1st week of July until the end of August.

Insect density in the sorghum field also varied from year to year. In 2002, greenbug population changed between 5 and 345 adults plant^{-1} (plant $n=10$) at each site in the 1st week of August and decreased to 0–16 adults plant^{-1} in the following week. For the leaf aphids, the numbers were between 0 and 85 adults plant^{-1} in the 1st week of infestation (plant $n=10$) at each site (data not shown). The greenbug infestations were severer in the east areas than in the west and center along transects (Fig. 2A). The leaf aphid infestation appeared more in the western areas (Fig. 2B). The percentage of plant leaves infested by MDMV disease was higher in the east areas than in the other areas (Fig. 2C). Only the greenbug population distribution was skewed towards the east (kurtosis 11 and skewness 3.3).

In 2003, the insect infestation lasted 7 weeks in the sorghum field during the growing season (Fig. 3). The leaf

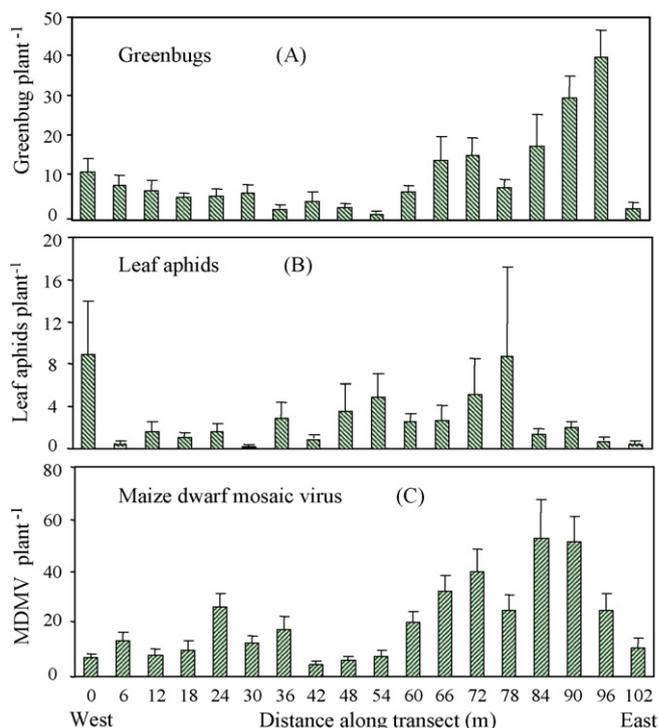


Fig. 2. Spatial patterns of greenbugs (A), leaf aphids (B), and maize dwarf mosaic virus disease incidence (C) along transect in 2002. Each bar was the mean and standard error of monitoring data $n=20$ plants.

aphid infestation debuted in early July (5 ± 2 aphids plant^{-1} , mean \pm standard error). The population reached the peak in 4 weeks (132 ± 26 adults plant^{-1}) then the density declined rapidly and finally disappeared from the field in mid August (Fig. 3). The temporal variation of the aphid population was marked by the most variable numbers in the week of peak (24 July, Fig. 3) during the infestation time. The aphid population in the week of peak had the highest sample variance (7927), which counted for 63% of the total sample variance (12,546). The standard deviations for the aphid population were variable (8, 63, 89, 112, 59, 10 and 2 aphids plant^{-1} , respectively, for the 7 weeks), and the deviation increased with the total number. The aphid population distributions were not skewed (kurtosis and skewness values <3 , the skewness threshold value). Along the transect, the leaf aphid density tended to increase in the center and the peak appeared at the 66-m site in 2003 (Fig. 4A).

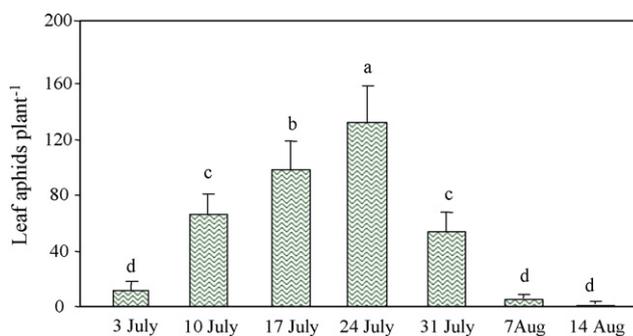


Fig. 3. Temporal development of corn leaf aphid population in 2003. Each bar is the mean and standard error of monitoring data $n=180$ plants.

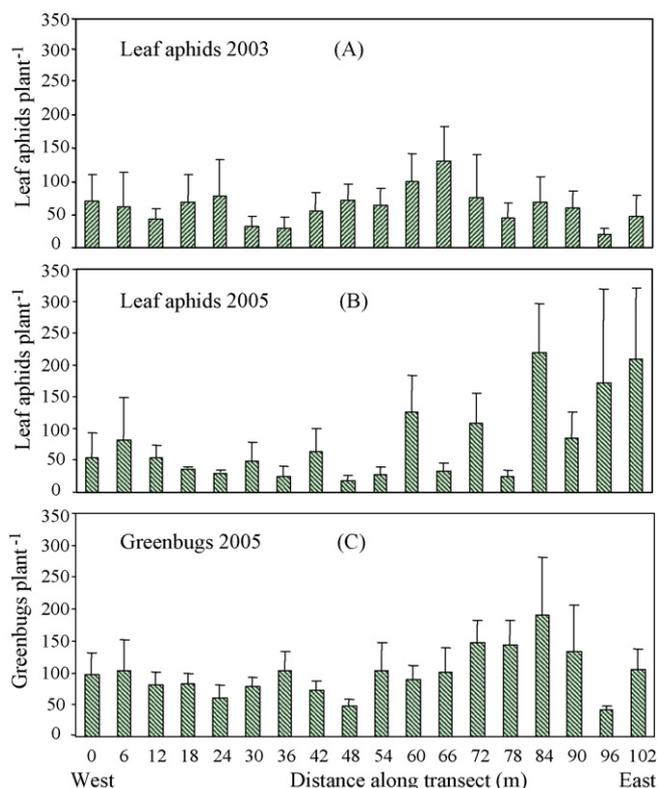


Fig. 4. Spatial distributions of corn leaf aphids in 2003 (each bar $n = 10$ plants, (A) and in 2005 (each bar $n = 3 \times 3$, plant \times transect, (B), and greenbugs in 2005 (each bar $n = 3 \times 3$, plant \times transect, (C) from the west to the east along transects.

No significant infestation of greenbugs or MDMV disease was found in the field in 2003.

In 2005, the leaf aphids infested the sorghum field starting in the 2nd week of July. The greenbug population peaked in the 2nd week of August, 4 weeks later (Table 1). The leaf aphids disappeared from the field after a rainfall in the end of August. The greenbug density varied between 0.1 and 930 adults plant⁻¹ during the infestation period and the highest

density was 5500 adults plant⁻¹ at the time of population peak. The leaf aphids peaked (481 adults plant⁻¹) a week earlier than the peak of greenbugs, and aphid numbers were 2–100 times higher than the greenbug numbers before the greenbug reaching the peak (Table 1). The standard deviations for the insect populations were greater than the mean values when the populations became dense, and the population distributions were mostly skewed throughout the infestation period (kurtosis 5.7–51.8 for greenbugs; kurtosis 2.4–50.6 for leaf aphids; Table 1).

By combining the insect numbers monitored on the three transects (2005), leaf aphid population also tended to be higher in the east areas (Fig. 4B). The greenbug populations were high (highest mean 371 adults plant⁻¹, plant $n = 3 \times 3$ each bar) towards the east areas (Fig. 4C). From the start of the infestations to the population peak in the summer, the developments of the greenbug and leaf aphid populations were exponential. The infestation rate (or growth number plant⁻¹) of corn leaf aphids and greenbugs (GB) with time (t) would be described by the exponential equations as follows:

$$t = \text{week} : \text{CLA} = 0.4743 e^{1.2947t} \quad (R^2 = 0.93, P < 0.001) \quad (1)$$

$$\text{GB} = 0.0142 e^{2.3616t} \quad (R^2 = 0.97, P < 0.001) \quad (2)$$

$$t = \text{day} : \text{CLA} = 1.5742 e^{0.1890t} \quad (R^2 = 0.92, P < 0.001) \quad (3)$$

$$\text{GB} = 0.125 e^{0.3456t} \quad (R^2 = 0.97, P < 0.001) \quad (4)$$

3.2. Correlations of insects, canopy temperature, plant reflectance and soil water content

Insect populations were correlated each other on different dates (Table 2). In 2002, the greenbug populations monitored within 2 subsequent weeks were negatively correlated ($r = -0.92, p < 0.001$, Table 2). The correlation was positive for

Table 1

Descriptive statistics of weekly greenbug and corn leaf aphid populations at different dates during the infection periods in the sorghum field from July to August in 2005

Date	13 July	20 July	26 July	4 August	10 August	17 August	24 August	31 August
Greenbugs								
Mean ^a	0.1	1.5	39	275	930	390	1.7	0.2
S.D. ^a	0.4	5.2	71	320	949	365	6.0	1.4
Minimum ^a	0	0	0	24	131	18	0	0
Maximum ^a	2	31	374	1840	5500	1857	41	10
Kurtosis	18.9	20.9	10.5	10.8	9.7	5.7	36.4	51.8
Skewness	4.4	4.4	3.1	2.9	2.7	2.2	5.7	7.1
Corn leaf aphids								
Mean ^a	25	104	415	481	280	161	1	0.2
S.D. ^a	39	116	538	1060	1176	705	3.4	1.1
Minimum ^a	0	0	6	0	0	0	0	0
Maximum ^a	210	462	2472	5370	8000	4800	20	8
Kurtosis	9.5	2.4	5.6	11.7	37.2	37.4	18.0	50.6
Skewness	2.9	1.8	2.3	3.4	5.9	5.9	3.9	7.0

^a Data were in adults plant⁻¹, taken at 54 canopy infrared temperature sensor IRt/c sites along three transects in the sorghum field. There were 18 IRt/c sensors per transect, and three random plants were taken for counting greenbugs and leaf aphids at each IRt/c site.

Table 2

Pearson correlation coefficients of greenbugs (GB), corn leaf aphids (CLA), and maize dwarf mosaic virus (MDMV) disease, determined on different days of year in 2002 (* and **: significant at probability $p < 0.05$ and at $p < 0.01$, $n = 18$)

	GB224 ^a	CLA224 ^a	GB231 ^a	CLA231 ^a	MDMV231 ^a
GB224 ^a	1				
CLA224 ^a	0.37	1			
GB231 ^a	-0.92**	-0.07	1		
CLA231 ^a	0.03	0.47*	-0.13	1	
MDMV231 ^a	0.35	0.90**	-0.20	0.80**	1

^a The numbers with GB, CLZ and MDMV are the days of the year.

the leaf aphid populations within 2 subsequent weeks ($r = 0.47$, $P < 0.05$, Table 2). The MDMV disease developed simultaneously with leaf aphids in 2002 ($0.80 < r < 0.90$, $P < 0.01$, Table 2) but it had no relationship with the greenbugs. In the drier and warmer year in 2005, there was a linear correlation between greenbug (GB plant⁻¹) and leaf aphid (CLA plant⁻¹), described by the regression equation as follows: $GB = 0.2223CLA + 65.4$ ($R^2 = 0.26$, $P < 0.05$).

During the insect infection periods, the IRT/c-sensed sorghum canopy temperature varied between $23.8 \pm 9.3^\circ\text{C}$ on a 24-h basis. In the day-time hours (7:00–20:00), canopy temperature was within $26.7 \pm 8.7^\circ\text{C}$. In the highest temperature hours (12:00–16:00), canopy temperature increased up to $30.8 \pm 4.9^\circ\text{C}$. As plotted against the mean canopy temperature within 12:00–16:00, leaf aphid populations showed a consistent trend to increase significantly with increasing canopy temperature in 2002 ($R^2 = 0.62$, $P < 0.01$, $n = 18$, Fig. 5A), in 2003 ($R^2 = 0.51$, $P < 0.01$, $n = 18$, Fig. 5B) and in 2005 ($R^2 = 0.32$, $P < 0.05$, $n = 54$, Fig. 5C). Greenbug population had no regression trend related to canopy temperature in 2002 and 2003 but their regression relation was linearly significant in 2005 ($R^2 = 0.27$, $P < 0.05$, $n = 54$, Fig. 5D).

Sorghum hyperspectral reflectance in the near-infrared band (wavelength range 760–840 nm) varied between 13.2 and 51.7% in the interval of 10 nm during the insect infestation period (2005). Within the near-infrared band, the reflectance was the highest ($40.6 \pm 6.2\%$, $n = 54$) at the 780 nm, and the lowest ($37.3 \pm 5.7\%$) at the 840 nm. As plotted against the sorghum plant reflectance at the different wavelength in the NIR band, leaf aphid population was consistently showing a trend to increase with increasing of sorghum plant reflectance. The relationships between leaf aphid (CLA) population and sorghum plant reflectance (NIR) could be described as:

$$780 \text{ nm} : \text{CLA} = 7.230\text{NIR} - 168.4$$

$$R^2 = 0.18, P < 0.05, n = 54 \quad (5)$$

$$800 \text{ nm} : \text{CLA} = 6.826\text{NIR} - 162.5$$

$$R^2 = 0.17, P < 0.05, n = 54 \quad (6)$$

$$820 \text{ nm} : \text{CLA} = 6.576\text{NIR} - 143.9$$

$$R^2 = 0.17, P < 0.05, n = 54 \quad (7)$$

Soil hyperspectral reflectance (TM red and red edge band, 610–690 nm) varied between 1.7 and 8.6% and the mean reflectance was the lowest ($3.1 \pm 1.2\%$, $n = 54$) at the 670 nm during the insect infestation period (2005). The hyperspectral reflectance was higher in the green band ($14.2 \pm 3.2\%$, 540–580 nm) than in the blue band ($6.3 \pm 4.5\%$, <480 nm). However, leaf aphid population had no correlation with reflectance in the blue, green or red band. Greenbug population had no significant correlation with hyperspectral reflectance in any band.

Weekly soil water content in the depth of 0–2.0 m was variable (range 0.11 – $0.21 \text{ m}^3 \text{ m}^{-3}$, and standard deviation 0.07 – $0.16 \text{ m}^3 \text{ m}^{-3}$) from planting to harvest. Soil water content was correlated within two neighboring measurement dates

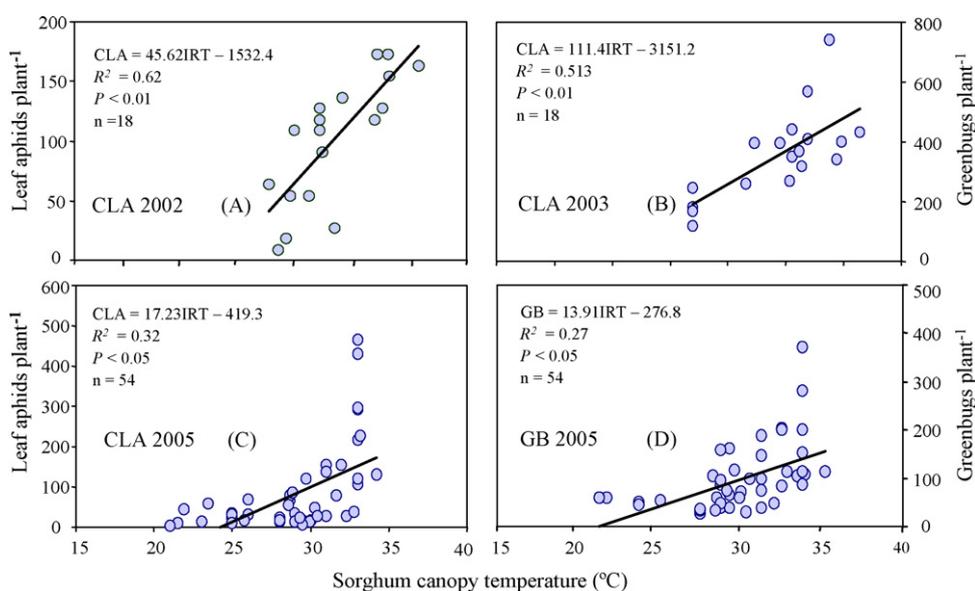


Fig. 5. Regression relationships of corn leaf aphids (CLA) and canopy infrared IRT/c temperature in 2002 (A), in 2003 (B) and in 2005 (C), and greenbugs (GB) and canopy infrared IRT/c temperature in 2005 (D) in sorghum plants.

Table 3

Pearson correlation coefficients of soil water content (SWC) on different days of year in 2002 (* and **: significant at probability $p < 0.05$ and $p < 0.01$, $n = 18$)

	SWC179 ^a	SWC207 ^a	SWC228 ^a	SWC248 ^a	SWC268 ^a	SWC311 ^a
SWC179 ^a	1					
SWC207 ^a	0.87**	1				
SWC228 ^a	0.70*	0.88**	1			
SWC248 ^a	0.25	0.52*	0.67*	1		
SWC268 ^a	0.11	0.26	0.34	0.64*	1	
SWC311 ^a	0.15	0.15	0.25	0.38	0.82**	1

^a The numbers with SWC are the days of the year.

(within 2 or 3 weeks) only ($0.64 < r < 0.87$, $P < 0.05$, Table 3). Soil water content was associated with insect development. In 2002, greenbug density (GB plant⁻¹) increased significantly with SWC ($\text{m}^3 \text{m}^{-3}$) as $\text{GB} = 746.4\text{SWC} - 116.4$ ($R^2 = 0.33$, $P < 0.05$, $n = 18$). In 2005, leaf aphid density (CLA plant⁻¹) increased more with increasing SWC ($\text{m}^3 \text{m}^{-3}$) than greenbug density (GB plant⁻¹) as: $\text{CLA} = 1210\text{SWC} - 259.22$ ($R^2 = 0.25$, $P < 0.05$, $n = 54$), and $\text{GB} = 746.82\text{SWC} - 111.3$ ($R^2 = 0.12$, $P < 0.06$, $n = 54$). The regression analysis showed that sorghum canopy temperature decreased with increasing SWC (Fig. 6AB). Sorghum grain yields were significantly higher with increasing water in the soil across years (Fig. 6C and D).

3.3. Sorghum yield and grain quality versus insects, and plant and soil variables

Sorghum grain yield showed a trend to decrease across the years. The hand-harvested grain yield at the IRT/c sites varied between $6.84 \pm 0.97 \text{ Mg ha}^{-1}$ ($n = 18$) in 2002, $4.49 \pm 0.86 \text{ Mg ha}^{-1}$ ($n = 54$) in 2004, and $3.92 \pm 0.76 \text{ Mg ha}^{-1}$ ($n = 54$) in 2005. Compared to the 1st year yield (2002), the decrease in grain yield was 34.3% in 2004 and 42.7% in 2005. Across the years, the yields showed no consistent

change in the west-east direction across the field. However, there was a consistent trend of increase in grain yields in the direction from the north to the south across the field (2005). By transect, the sorghum grain yield was significantly higher ($4.04 \pm 0.71 \text{ Mg ha}^{-1}$, $n = 18$) on the southern transect than on the northern transect ($3.73 \pm 0.57 \text{ Mg ha}^{-1}$, $n = 18$) ($P < 0.05$, Fig. 7A). The percentage of acid detergent fiber (ADF), or the amount of acid soluble fiber material and lignin in sorghum grains, increased also significantly ($P < 0.05$) from the north (8.8%) to the center (10.2%) to the south (11.4%) in the measurement grid (Fig. 7B).

The increase trend in sorghum grain yields from north to south in the field was opposite to the patterns of insect populations (2005). As shown in Fig. 7C, the leaf aphid density decreased consistently from the north (121 ± 93 adults plant⁻¹, $n = 18$) to the south (79 ± 34 adults plant⁻¹, $n = 18$). The greenbug population also significantly higher in the north (97 ± 32 adults plant⁻¹, $n = 18$) than in the south (60 ± 17 adults plant⁻¹, $n = 18$) (Fig. 7D). Crude protein content in the sorghum grains was slightly higher in the north ($11.9 \pm 0.9\%$) than in the south ($11.6 \pm 0.7\%$), but the difference was not significant.

The linear decreases of sorghum grain yield with increasing of insect population and canopy temperatures were consistent

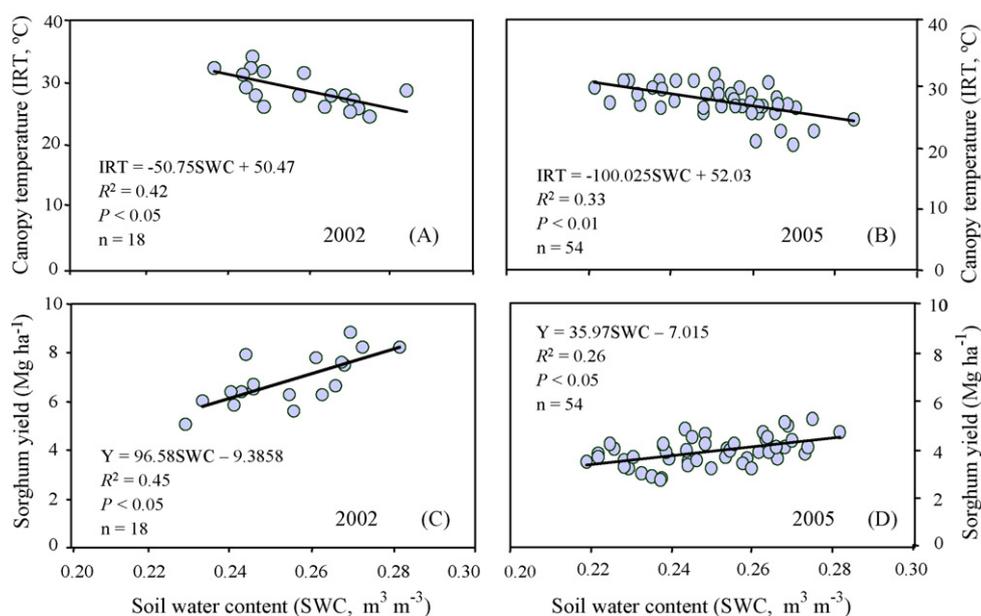


Fig. 6. Trends of canopy infrared temperature (IRT) vs. soil water content (SWC) in 2002 (A) and in 2005 (B), and sorghum grain yield (Y) vs. SWC in 2002 (C) and in 2005 (D). Soil water content was measured in the depth of 0–1.2 m.

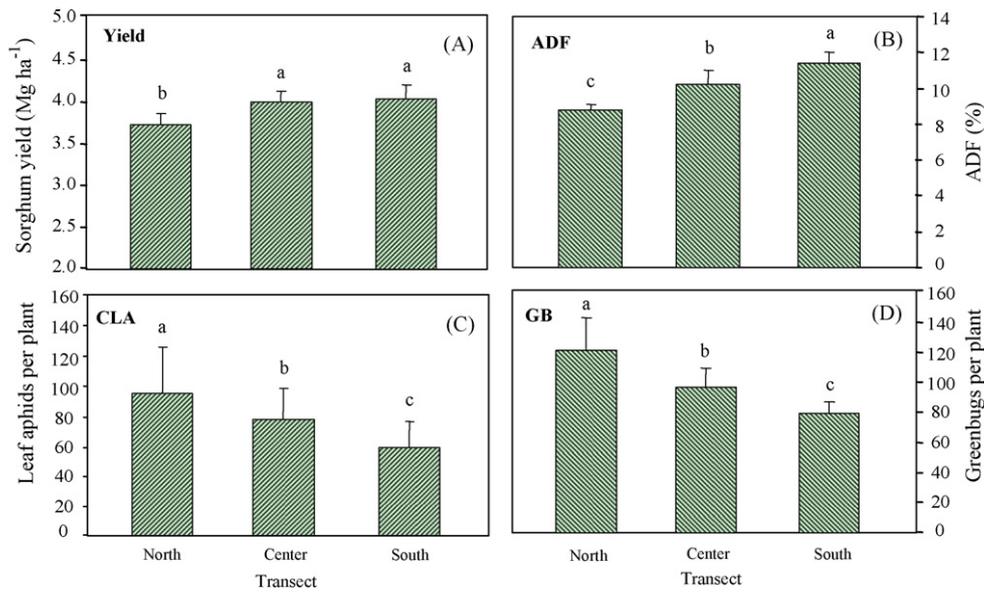


Fig. 7. Distribution of sorghum grain yield (A), sorghum grain acid detergent fiber content (ADF, B), corn leaf aphids (CLA, C), and greenbugs (GB, D) on the north, center and south transects in 2005. Each bar was the mean and standard error of 18 measurements for sorghum yield and ADF, and 6 × 18 monitoring data for CLA and GB.

across the years (Fig. 8). As plotted against canopy IRT/c temperature and insect populations, higher sorghum grain yields were related with lower IRT/c temperatures <35 °C, and the yield decreased with increasing IRT/c temperatures at a coefficient of 0.803 (Fig. 8A). The decreases of sorghum yield were also linearly with increasing CLA density in 2002 (Fig. 8B) and in 2005 (Fig. 8C). The linear decreases of sorghum yield were also related to increasing of greenbug density (Fig. 8D). In the drier and higher temperature year as in 2005, grain yield loss of

greenbug and aphid-susceptible sorghum crops was associated with an insect density >150 aphids plant⁻¹ (Fig. 8C) and also >150 greenbugs plant⁻¹ (Fig. 8D).

3.4. Crosscorrelation of sorghum yield, insects and soil water content

Crosscorrelation functions, $\gamma_{xy}(h)$, varied between -0.82 and 0.54, showing a cyclic, negative feedback relationship between

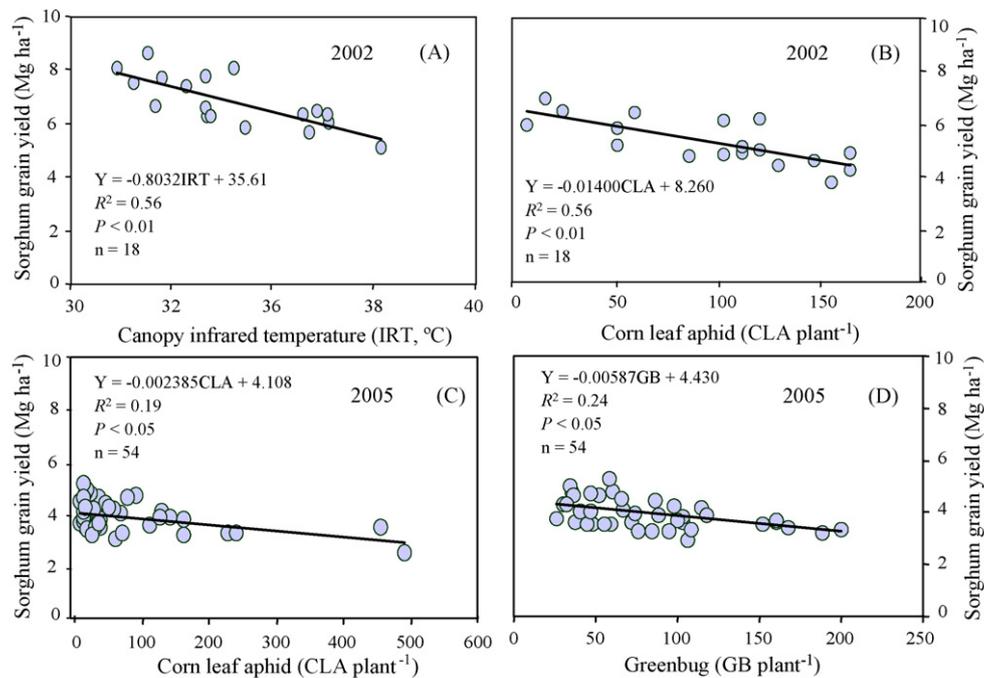


Fig. 8. Relationships of sorghum grain yield, canopy infrared temperature (IRT), corn leaf aphid (CLA), and greenbugs (GB) in 2002 (A and B) and in 2005 (C and D).

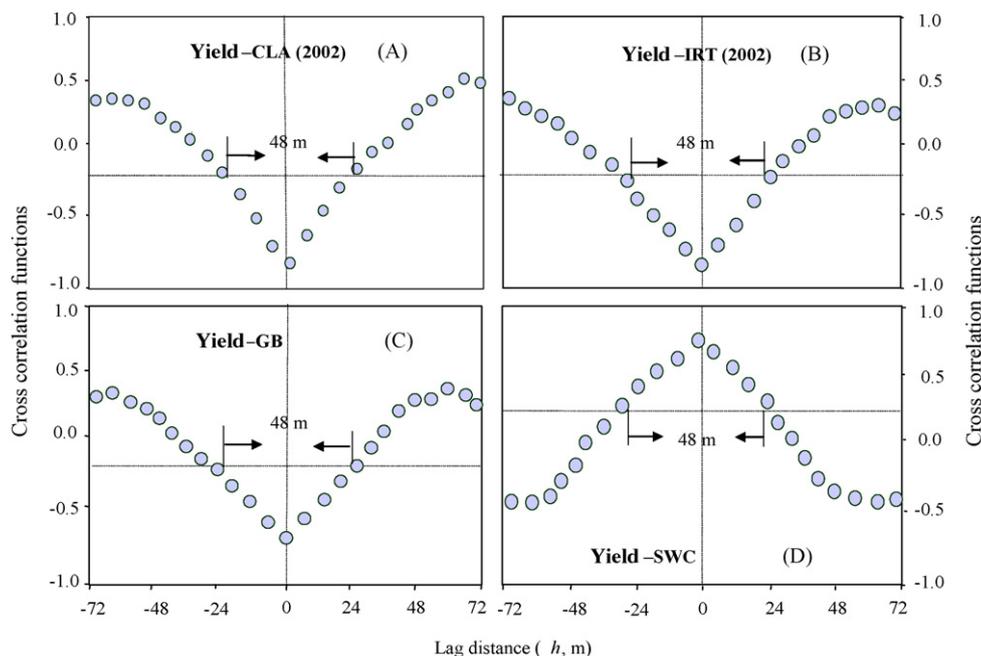


Fig. 9. Crosscorrelation patterns of sorghum yield vs. corn leaf aphids (A), yield vs. canopy infrared temperatures (IRT, B), yield vs. greenbug (GB, C), and yield vs. soil water content (SWC, D).

sorghum grain yield (y), leaf aphid (x), greenbug (x) and canopy IRT/c temperature (x), and a cyclic, positive feedback relationship between yield (y) and soil water content (x) (Fig. 9A and B). By accounting 95% of confidence threshold as described in Li et al. (2002), the yield, insect, plant and soil variables were spatially crossed a lag distance of 48–54 m (± 24 or ± 27 m) along the transect (Fig. 9). As the lag distance became greater than the crosscorrelation range, the crosscorrelation functions became more positive or negative (Fig. 9). Semivariogram ranges for these variables were also within 48–54 m (graph not shown).

4. Discussion

4.1. Insect development, drought and temperatures

The abundance of greenbugs and leaf aphid populations during late July (Fig. 3) and mid August (Table 1), positive correlations between greenbugs, leaf aphids and sorghum canopy IRT/c temperatures (Fig. 6), and positive regression relationships of insects versus sorghum plant NIR hyperspectral reflectance (Eqs. (1)–(4)) suggested that the insect development was associated with high temperatures and heat-stressed plants. It was reported that insects such as leaf feeders were typically preceded by unusually warm weather (Mattson and Haack, 1987; Li et al., 2007b). The higher densities of greenbug and leaf aphid populations in higher temperature and drier year, for example, 2005 (Fig. 4) versus 2002 (Fig. 2), suggested that high temperature would promote outbreaks of greenbugs and leaf aphids. Arguments for high temperatures promoting greenbug and leaf aphid development would be revealed from the reports of White (1984) and Mattson and Haack (1987).

These studies reported that dry conditions would add stress to plants and also prevent the development of fungal pathogens that could infect and kill plant-eating insects. Drought would become debilitating to the plants and phytophagous insects because during dry periods, concentrations of nutrients such as amino acids (proline), nitrate, betaine, and sugars would accumulate to higher than normal levels in the tissues of drought-stressed plants (Mattson and Haack, 1987). It would be useful to further verify if these nutritional levels would be higher in drought-stressed sorghum plant tissues to explain insect change patterns.

Outbreaks of greenbugs and leaf aphids could last for 3–4 weeks, and thereafter decline (Fig. 3 and Table 1). Growth rates of the whole insect typically increased in a sigmoidal fashion in relation to temperature (White, 1984; Li et al., 2007b,c). Because the insect reproduction first increased to an optimum in the suitability of conditions (Mattson and Haack, 1987; Li et al., 2007a), a much drier condition during the insect infestation period (July–August, 154.2 mm rain in 2002 and 90.1 mm rain in 2005) would evoke large responses by the insects in 2005 (highest 930 greenbugs plant⁻¹ and 481 aphids plant⁻¹). The more abundant insects in drier conditions would be because higher air and host plant temperatures were associated with drought, which would enable plant-eating insects to grow and reproduce in a more nearly optimal temperature regime (Mattson and Haack, 1987). With the higher insect density occurring in the drier year (2005, maximum yearly mean 210 aphids site⁻¹ and 180 greenbugs site⁻¹ (9 plants), Fig. 4) and the much lower density in the relatively rainy year (2002, maximum yearly mean 10 aphids site⁻¹ and 38 greenbugs site⁻¹ (10 plants), Fig. 2), it was also suggested that drought stressed plants would be more attractive or acceptable for insects.

Mattson and Haack (1987) summarized six mechanisms by which drought might affect aspects of insect growth and outbreaks. Our results supported their ideas that drought would provide a more favorable thermal environment for growth of phytophagous insects. In the same study, Mattson and Haack (1987) also indicated that plants responded to diverse environmental signals in order to survive from stresses such as drought, and some insects would have heat and infrared receptors because leaf yellowing and higher temperatures of drought-stressed plants might make them more attractive to insects. In our study, leaf aphid population was more correlated to plant NIR hyperspectral reflectance than the greenbugs (Eqs. (1)–(4)). However, it was not clear if leaf aphids have heat and infrared receptors to be more attractive to plants than greenbugs.

4.2. Yield loss from sorghum biotic and abiotic stress by insect attacks and drought

Abiotic stress of sorghum plants was the combination of drought and temperature stress from non-irrigation and lacks of rain, and biotic stress of sorghum plants was because of attacks of greenbugs and leaf aphids. The decreases of sorghum grain yield (Fig. 8) meant the reduced plant growth and net returns from plant biotic and abiotic stress by insect attacks, drought and high temperature. The causes of plant biotic and abiotic stress and yield loss from attacks of insects would be complex. As indicated in several studies, biotic stress would act upon plant development by modifying the plant protective roles (Kocsy et al., 2004), decreasing leaf catalase activities (Luna et al., 2005), and leaf stomatal conductance (Li et al., 2004a, 2006). Damage of pathogen attacks on plants would be through reducing photosynthetic activity, and modifying secondary metabolism in their hosts (Garrett et al., 2006).

The susceptible sorghum exhibited similar yield loss in relation to the intensity of greenbug or aphid infestations, as indicated by a common slope parameter in the regression models (Fig. 8). Winter wheat yield loss for greenbug-susceptible cultivars was 0.51 kg ha^{-1} per greenbug-day in years with near normal precipitation, and a loss of 1.17 kg ha^{-1} under severe drought conditions (Kindler et al., 2002). The decreases of sorghum grain yields cross the years would be the results of complex of no fertilizer input and no insecticide applications over the period of 4 years. The linear correlation between water-stressed plant reflectance, soil water and crop yield was in agreement with the results reported in the other field studies conducted on the High Plain of Texas (Li et al., 2001, 2002).

There was also uncertainty in the relationships between sorghum yield and MDMV disease. The strongly positive correlation between the MDMV disease and leaf aphid population ($0.80 < r < 0.90$, Table 2) agreed that the MDMV disease could be transmitted mechanically to the sorghum plants by leaf aphids (Jardine, 1988; Olson et al., 1990), although there were only 1 year data. Variation in the intensity of insects or pathogens would be explained by quantitative and qualitative differences in suitability between potential host plants (Kindler et al., 2002; Garrett

et al., 2006). Drought, high temperature or heat shock was known to upset natural patterns of plant and pathogen growth (Mattson and Haack, 1987; Olson et al., 1990). Because our datasets were about sorghum plant responses to drought, non-irrigation, and un-controlled, natural infestations, it would be useful to further conducting a greenhouse study for determining plant–insect–soil water relations under controlled environmental conditions (Li et al., 2006).

4.3. Options for reducing dryland plant biotic and abiotic stress

The correlations between the sorghum yield, insect population, canopy IRt/c temperature, plant NIR reflectance and SWC across the years (Figs. 6–8) suggested that the relationships between insect, soil and sorghum plant variables were relatively constant from year to year and their correlations were not due to chance. The exponential growth of insect population from the initial infestation to the peak in late July (Fig. 3) or mid August (Table 1) was in agreement with other field observations (Li et al., 2007c). The insect density threshold of causing significant yield loss (150 greenbugs or leaf aphids per plant) in the drier and warmer year (Fig. 8), and the exponential insect growth equations suggested that the best timing of spray control should be close to the period of late July-early August, before insects became denser and more damaging.

The lower sorghum grain yield and soil water content and higher canopy temperature and insect density in the east (Figs. 2 and 4) and in the south (Fig. 7) than in other areas in the field suggested that insecticide spray control should be done using variable rates rather than uniform rates for the entire field. The variable-rate application zones would be based on the crosscorrelation distance for the yield-insect or canopy IRt/c temperature-insect, which would be 48 or 54 m (Fig. 9). Cross-correlation has generally been used when measuring information between two different time series. The range of the crosscorrelation functions is -1 to 1 such that the closer the cross-correlation value is to 1 (or -1), the more closely the information sets are (Li et al., 2001, 2002, 2007b). The similar crosscorrelations between sorghum yield and insects (Fig. 9A and C) and between yield and soil water (Fig. 9D) showed that insect control and soil water management would be equally important for the dryland sorghum.

Late planting would be an option for reducing plant biotic stress from insect attacks. Because greenbugs and leaf aphids migrate to the High Plain from southern regions during April and June, no insect infestation occurred in the sorghum field in 2004 as a result of late replanting in early July. Typical planting recommendations for dryland sorghum in the southern High Plains were to delay until soil moisture became adequate, depending on precipitation patterns for crop establishment (Baumhardt et al., 2005). Weather (temperature, rain or hail) in the spring would be highly variable on the High Plains. Weather-dependent natural infestation patterns of insect pests were useful for management planning (Li et al., 2007a).

Other phases of greenbug and leaf aphid cycle and their damage have not understood from our data. We would suggest a

future study of intercropping of sorghum with other crops as a cultural control for reducing sorghum plant abiotic and biotic stress. Intercropping was an efficient way of reducing insect population because insect behavior could be affected by intercropping not only with different crops but also with different cultivars of the same crop (Windle and Franz, 1979; Risch, 1983). Plant responses to abiotic and biotic stress were quantitatively and qualitatively different (Simpson and Daft, 1990; Li et al., 2006). Mechanisms by which drought promote insect growth were also that drought-stressed plants would be physiologically more suitable for insects, and drought would induce genetic changes in insects (Mattson and Haack, 1987), and pathogens have evolved to survive on highly biotic interaction with drought-stressed plants (Olson et al., 1990). Future field studies of relationships between temperature and water-stressed sorghum plants, greenbugs, leaf aphids and MDMV would be the mechanisms such as nutrient levels that can be high in stressed plants by which temperature and draught would affect plant physiological aspects linked to insect and pathogen breakout.

5. Conclusions

Drought (non-irrigation and lacks of rain) and natural infestation of greenbugs and corn leaf aphids were the abiotic and biotic stress factors causing water stress and reduced plant growth in dryland sorghum. The associations of abiotic and biotic stresses in dryland sorghum were shown by the correlations between insect population dynamics, host plant canopy infrared temperature, plant hyperspectral reflectance, soil water and grain yield loss. The natural infestations of greenbugs and leaf aphids to dryland sorghum plants occurred from early July to the end of August. The insect populations peaked late in mid August in prolonged dry summer. Dry weather would favor the development of greenbugs and leaf aphids. The consistence in the correlations between greenbugs, leaf aphids, sorghum grain yield, sensed host-plant infrared temperatures, hyperspectral reflectance have given insights into reducing biotic and abiotic stress of dryland sorghum crops. Late planting and spray control at variable rates in late July and early August would be options for reducing water and insect stress from drought and attacks of insects for the dryland sorghum. From the outcome of host plant–insect–soil interactions of this study, it is suggested the needs for further examination of the overlay patterns of insects, diseases, canopy temperature, plant reflectance, soil water and texture across multi-years.

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